



Reviving the Arabian leopard: Harnessing historical data to map habitat and pave the way for reintroduction

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ABSTRACT

The Arabian leopard (*Panthera pardus nimr*) has experienced dramatic range and population contractions over the last century. Conservation efforts for this felid focused on captive breeding and identification of suitable conditions for reintroductions. With this study, we unravelled historical collaring and direct observations data to understand the spatial use of the last leopards recorded in the region of Israel and the West Bank (IWB). Through datasets of leopard occurrence, we characterised suitable habitats, assessed niche overlap with the Arabian leopard's main prey, the Nubian ibex (*Capra nubiana*), and evaluated their distributions with respect to currently protected habitats. We estimated home-ranges employing area-corrected density kernel methods and investigated suitable conditions through multiple scales habitat modelling. Average home ranges for the population were $73.24 \pm 47.91 \text{ km}^2$ and $77.46 \pm 54.94 \text{ km}^2$, depending on the time lag adopted. Ecological response to predictors highlighted reliance by both predator and prey on the same habitat characteristics, suggesting they occupied essentially identical niches. These characteristics were intermediately rugged topographic conditions and high indices of vegetation in sparsely populated desert environments, mostly encompassed within protected areas. The distribution of leopard and ibex overlapped substantially according to several metrics. Notably, more than half of potential habitat for both species is encompassed by protected areas and military zones. Given the coincidence in their ecological requirements, and highly congruent distributions, an important step towards future reintroduction of Arabian leopards will include gaining a better understanding of ibex populations, alongside attention to the practicality of enforcing habitat protection.

1. Introduction

The Arabian leopard (*Panthera pardus nimr*) is an iconic large felid native to the arid and desert environments of the Arabian Peninsula. This leopard subspecies has experienced a severe decline, with its range reduced by approximately 98 % since 1750 (Jacobson et al., 2016). Historically, the Arabian leopard roamed diverse regions from the Sinai Peninsula in Egypt, through Israel, the West Bank, and Jordan, all the way to the mountainous areas of Saudi Arabia, Yemen, Oman, and the UAE (Jacobson et al., 2016; Spalton, and al Hikmani, 2006). However, since the 19th century, its range has been more than decimated, primarily due to habitat loss and fragmentation caused by human encroachment, declining prey populations, as well as direct hunting,

retaliatory killings provoked by livestock losses, and poisoning (Jacobson et al., 2016; Islam et al., 2015, 2018; Breitenmoser et al., 2006).

Presently, the Arabian leopard survives in small, fragmented populations primarily confined to Yemen (Al Jumaily et al., 2006) and Oman, with the latter being its last prominent stronghold (Spalton and Al Hikmani, 2014; Spalton et al., 2006; Farhadinia et al., 2021). While areas of uncertainty, and even probable presence, are still depicted on IUCN range maps (Stein et al., 2020), the Arabian leopard has vanished from Israel, the West Bank, Jordan (Qarqaz and Baker, 2006), and Saudi Arabia (Andrew Spalton, personal communication, 2022; Islam et al., 2018, 2020, 2021; Dunford et al., 2023), and much uncertainty surrounds the status of the extant Yemeni population. With so few individuals remaining in the wild, accurately identifying the location of

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existing populations and estimating the number of leopards present in each is a daunting task (Dunford et al., 2023). Current informed opinion is that as few as 120 individuals may persist within the region spanning from Oman to Yemen (Andrew Spalton, personal communication, 2022).

Leopard populations in Israel and the West Bank (hereafter IWB) declined with increasing human population size and herding activities over thousands of years (Lazagabaster et al., 2021). Available information in the area indicates an exacerbation of this downward population trend throughout the 20th century. Formal conservation initiatives identified hunting, low breeding success, human-leopard conflicts and ineffective conservation management as key drivers of decline (Qum-siyeh, 1996; Timna, 2000). By the late 1980s, the IWB region had no >25 Arabian leopards (Ilany, 1988, 1990). Since then, an increase in human-leopard conflicts and road accidents further impacted the population. Skewed sex ratios and inbreeding worsened their situation, compromising fitness (Ilany, 1990; Khalaf, 2005; Perez et al., 2006). Genetic analyses in 2000–2001 confirmed ten leopards in the Judean Desert and Negev highlands, marking the last published evidence of their survival in IWB (Perez et al., 2006). Chance deaths and prey fluctuations continued to reduce their numbers until breeding females disappeared. The last anecdotal sightings of a leopard in the area were in 2009/2010, a date marking the species' probable extirpation from IWB.

Efforts to conserve the severely endangered Arabian leopard populations in the wild have shifted towards captive breeding initiatives (Budd and Leus, 2011; Edmonds et al., 2006), with potential reintroduction as a long-term goal (Dunford et al., 2022; Islam et al., 2020). Ex-situ conservation is considered a crucial strategy for the persistence of endangered species (Farhadinia et al., 2020; see also Thomas et al., 2023), and ongoing research aims to identify suitable conditions for the successful reestablishment of breeding populations through conservation translocations of Arabian leopards (Dunford et al., 2022; Islam et al., 2021). In fact, feasibility assessments for reintroductions often begin by exploring suitable habitat conditions (Stadtman and Seddon, 2020) that can support carnivores and their potential prey species (Hebblewhite et al., 2011; Gwynn and Symeonakis, 2022; Halsey et al., 2015; Qin et al., 2015; MacPherson et al., 2019; Schadt et al., 2002; Thatcher et al., 2006).

A fundamental pre-requisite for successful large carnivore reintroductions is the presence of stable and sufficient prey populations (Wolf and Ripple, 2016; Stier et al., 2016; Miller et al., 1999). The primary natural prey of the Arabian leopard throughout IWB include the mountain gazelle (*Gazella gazella*), Dorcas gazelle (*Gazella dorcas*), Nubian ibex (*Capra nubiana*), Cape hare (*Lepus capensis*), rock hyrax (*Procapra capensis*), Indian crested porcupine (*Hystrix indica*), Ethiopian hedgehog (*Paraechinus aethiopicus*), various bird species, small rodents, and even insects (Ilany, 1990; Timna, 2000; Judas et al., 2006; Qarqaz and Baker, 2006; Al Jumaily et al., 2006; Al-Johany, 2007). In IWB, the Arabian leopard relied heavily on Nubian ibex and hyrax, which together constituted approximately 90 % of its diet (Ilany, 1990). Timna (2000) analysed 266 leopard scats from IWB and found that ibex accounted for 39 % of undigested prey by volume, followed by domestic cat (20 %), hyrax (18 %), and porcupine (8 %). Based on 169 recorded leopard kills and remains, the frequency of ibex was 27 %, hyrax 33 %, porcupine 4 %, and domestic cat 31 % (Timna, 2000).

The Nubian ibex population in IWB is recognized as one of the largest worldwide and is primarily concentrated in two clusters: the Judean Desert and the Negev Desert Highlands, with a smaller population in the Elat mountains south of the Negev (Ross et al., 2020). In 2000, it was estimated that there were approximately 1000 Nubian ibexes inhabiting 750 km² in the Judean Desert, around 500 individuals spread over 1000 km² in the Negev, and approximately 150 individuals occupying 850 km² in Elat (Shkedy and Saltz, 2000). A recent study by Tichon (2020) employed Mark-Resight and Robust-Approach Mark-Resight analyses, estimating around 598 and 489 Nubian ibex individuals, respectively, in the northern Judean Desert. These figures represent a significant portion

of the estimated 800 individuals comprising the entire population of the Judean Desert (Tichon, 2020).

Spanning roughly 3000 km², the territories historically inhabited by leopards prominently overlap with those of the Nubian Ibex in the Negev and Judean deserts (Perez et al., 2006; Tichon, 2020; Shkedy and Saltz, 2000). In these regions, Arabian leopards were found in remote and rugged mountainous desert areas that provided them with security from human activities and vantage points for ambushing prey. These habitats remain relatively untouched and are thought to be highly suitable for leopards due to the rugged landscape and presence of wadis and rocky cliffs (Ilany, 1990; Timna, 2000; Spalton et al., 2006; Al-Johany, 2007). Significantly, about 85 % of these areas are encompassed within protected areas (PAs) (Perez et al., 2006). Additionally, these regions intersect with military training grounds, which, having restricted access, may sometimes de facto preserve the habitat available for these species.

In this study, we utilized two datasets containing verified sightings, presence signs, and VHF-collar verified locations, together representing the most recent information on Arabian leopards in IWB. Additionally, we incorporated a comprehensive dataset of verified Nubian ibex sightings collected over a period of five decades. Our objectives were twofold: first, to estimate the landscape that had been used by Arabian leopards in IWB, also providing insights into their home-range; second, we employed multiple-scale species distribution models (McGarigal et al., 2016) to identify ecological factors strongly associated with a higher probability of occurrence for leopards and ibexes. Furthermore, we compared the ecological niches of both species, quantifying suitable areas and potential spatial overlap. Assessing the extent of congruence in the use of habitats by leopards and ibex, and their reliance on similar ecological factors is fundamental to the assessment of suitable landscapes for current wild populations and potential reintroductions across its former range.

2. Methods

2.1. Study area

All the data in this manuscript were obtained in the jurisdictions of Israel and the West Bank (IWB) (Fig. 1). The area encompassed by our datasets (see next section) is characterised by elevations ranging from approximately 1000 m in the Negev highlands to −400 m along the Dead Sea coast. The area consists of a desert environment, with precipitation of <100 mm per year. These precipitation trends have been stable for the last seven decades (Yosef et al., 2009, 2019; Climate Change Knowledge Portal, 2023a, 2023b). Human population densities in these territories are also very low (1–5 persons per Km²). Agricultural activities are concentrated around a few sporadic small towns and settlements. Permanent and seasonal waterholes, flowing springs and creeks, ensure water availability for wildlife species. Despite the extreme aridity of Arabian leopard habitat, many sites support trees and perennial vegetation. The most notable trees and bushes in areas of leopard sightings in IWB are *Acacia tortilis*, *Acacia negevensis*, *Ziziphus spina-christi*, *Moringa peregrina*, *Salvadora persica*, *Pistacia atlantica*, and bushes such as *Capparis zoharyi*, *Ochradenus baccatus*, and *Retama raetam*. In addition, there are many other perennial and annual plants (Timna, 2000; Al-Johany, 2007). This vegetation supports important prey for leopards, such as Nubian ibexes (*Capra nubiana*), rock hyraxes (*Procapra capensis*), and Indian porcupines (*Hystrix indica*) (Timna, 2000; Shkedy and Saltz, 2000). Most of the observations in our datasets were collected inside protected areas and military training grounds (Fig. 1) (see next section). Several military grounds overlap with protected areas. Fences are only found at the border with Egypt. Protected areas and military grounds are fully enforced. Some recreational use by visitors from the general public is possible within designated times and days.

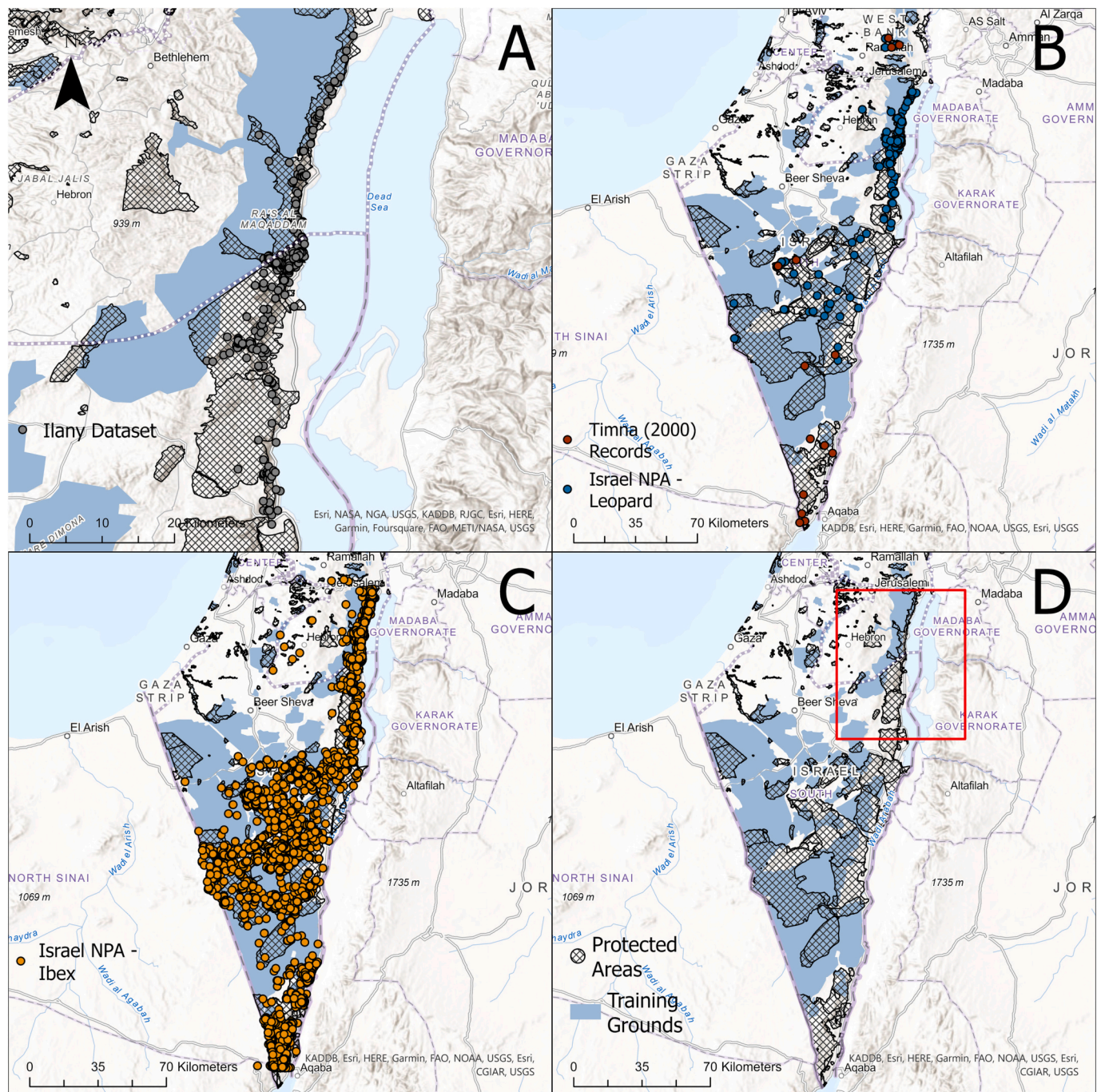


Fig. 1. Overview of the study area and datasets used. **A:** Locations of the ‘Ilany’ dataset, a collection of 1159 Arabian leopard presence signs, direct observations, and VHF tracking data. **B:** Locations of 419 Arabian leopard presence records compiled by Israel Nature and Park Authority (NPA) and 14 records catalogued by [Timna \(2000\)](#). **C:** Locations of 12,022 Nubian ibex presence points compiled by NPA. **D:** Position of Protected Areas and military training grounds in the areas surveyed for Arabian leopard and Nubian ibex. The red square in D indicates the extent of the Ilany dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Datasets

Our analyses were based on two different datasets of Arabian leopard occurrences, and one dataset of Nubian Ibex presence records (Fig. 1).

The first dataset used in this study comprises a collection of 1159 observations of Arabian leopard presence compiled by the late Giora Ilany from 20/08/1970 to 26/09/1989 (henceforth named ‘Ilany’). Along with recorded signs of presence and observations of prey remains (178 records), this dataset contains 981 verified leopard locations from 10 individual leopards’ radio-tracked at various periods between 29/

11/1978 to 26/09/1989 (Supplementary Tables 1 and 2; Supplementary Fig. 1). These records are based on direct observations of the collared animals after their location was determined by VHF. Individuals were fitted with Telsonics VHF collars (~60 bpm), designed to work continuously for 2.5–3.5 years. Individuals were tracked based on encounter frequency, leading to a different tracking effort among the leopards. Considering individuals with >10 total observations per year, the average collaring period consisted of 230.26 days per year (range 20–365) or 32.89 weeks per year (range 2.86–52.14), producing an average number of observations equal to 41.17 ± 22.36 (range 11–87)

(Supplementary Table 2).

The second dataset is a collection of 419 Arabian leopard presence locations compiled by Israel's Nature and Parks Authority (NPA) from 22/12/1974 to 15/12/2009 (Supplementary Fig. 2). These records were collected by NPA rangers and other reliable naturalists, based on direct observations, scat pits, and pawprints of leopards. This dataset was supplemented with 14 more historical records of Arabian leopard occurrence from the work of [Timna \(2000\)](#). We will refer collectively to these 433 observations as the 'NPA Leopard' dataset.

The third dataset consists of 12,022 presence records of Nubian Ibex, collected by Israel NPA from 24/09/1975 to 27/03/2023 (henceforth named the 'NPA Ibex' dataset). These opportunistic records were derived from direct observations of ibex reported by NPA rangers traveling by car on dirt roads and on foot (Supplementary Fig. 3).

2.3. Home range estimations

Before calculating home ranges, we first removed duplicate coordinates coming from multiple daily observations, and we excluded two animals (Bavta, Enigma) from the 'Ilany' dataset due to the extremely low numbers of sightings. After this screening, the dataset consisted of 976 observations, of which only 6 were collected on the same day but in different locations (two on two different days for Amrafel, two in a single day for Hordus). Due to the irregular observations and long periods without sightings, for each animal we subset the observations into survey sessions separated by at least 30 days of no sightings. We kept all the animals and survey sessions that spanned at least 12 weeks for home ranges calculation (Supplementary Table 3). We also subset the observations per animal and year, regardless of the time lag between any two observations for any given individual ([Dunford et al., 2022](#)) and inspected all the years with at least 10 observations. To account for biases induced by small sample size, missing observations, and irregular data, we used the *ctmm* package ([Calabrese et al., 2016](#); [Fleming and Calabrese, 2022](#)) to calculate Kernel Density Estimators (KDE). We plotted empirical variograms to estimate semi-variance as a function of the time lag between observations, providing insights into space use ([Calabrese et al., 2016](#)). An asymptote in the semi-variogram indicates a resident individual, while its absence suggests shifting home ranges or inadequate tracking duration ([Calabrese et al., 2016](#)). We discussed the limitations and uncertainties of including the individuals in a population average in all cases where the expected indication of stable home range was not met. Models were fitted through the function *ctmm.select* feeding an object created through the function *ctmm.guess*. We used the function *akde* to fit area-corrected KDE models (KDEC) or area-corrected autocorrelated KDE (aKDEC) ([Fleming and Calabrese, 2017](#)), depending on the most supported movement model, to avoid

overestimating home ranges. We fitted all models applying the perturbative hybrid REML-based estimator (pHREML) ([Fleming et al., 2019](#)). Additionally, we implemented a polygon mask of the Dead Sea to prevent overestimation in areas patently unsuitable for leopard presence.

2.4. Distribution models

We used the 'NPA Leopard' and 'NPA Ibex' datasets to fit species distribution models applying three algorithms: General Linear Model for binomial data with logit link function (GLM; [Cox, 1958](#)), Maximum Entropy (MaxEnt; [Phillips et al., 2006](#)) and Random Forest (RF; [Breiman, 2001](#)). Pseudo-absences were generated randomly at a 1:5 ratio across the whole IWB due to the lack of recorded absences. Since we were mainly interested in assessing which conditions may currently allow persistence of both species, we selected the entirety of IWB as extent for pseudo-absence points to investigate second orders of selection (*sensu* [Johnson, 1980](#)).

Our selection of predictors was influenced by the recent work by [Dunford et al. \(2022\)](#), who estimated resource selection functions for the Arabian leopard in Saudi Arabia. We evaluated 10 variables ([Table 1](#)): four pertaining to topography (terrain ruggedness index - TRI, topographic position index - TPI, focal mean of elevation - FME, focal mean of slope - SLOPE), two associated with human footprint (density of built-up areas - BUILT, human population focal mean - HUM-POP), two concerning vegetation cover (enhanced vegetation index focal mean - EVI, normalized difference vegetation index focal mean - NDVI), and two related to protected areas (percentage of landscape composed of protected areas - PLAND PAs, percentage of landscape of protected areas and military training grounds - PLAND PAs_tr). These two latter predictors consist of continuous landscape composition metrics derived from categorical binary rasters (presence and non-presence of PAs or PAs_tr in this case) and were computed using Fragstats ([McGarigal et al., 2012](#)). [Table 1](#) provides abbreviations, datasets, and methods used to derive each variable. Satellite-derived predictors (EVI, NDVI) were averaged in Google Earth Engine ([Gorelick et al., 2017](#)) from the earliest available time series (18/02/2000, [Didan, 2021](#)) until the conclusion of the leopard (15/12/2009) and ibex (27/03/2023) sampling periods.

All variables were computed at multiple focal scales, obtained by calculating the variables at radii of 100, 250, 500, 1000, 2000, 4000, and 8000 m ([Table 1](#)). We resampled all variables to have a pixel size of 100 m and a UTM36N projection. Incorporating relevant ecological scales that account for animals' perception of landscape characteristics has consistently resulted in more accurate and realistic distribution models ([McGarigal et al., 2016](#); [Atzeni et al., 2020](#); [Ding et al., 2023](#); [Chen et al., 2022](#); [Vergara et al., 2015](#); [Timm et al., 2016](#)).

To determine the optimal focal scale for each predictor in different

Table 1
List of habitat predictors included in this study.

Predictor	Abbreviation	Dataset	Dataset data type	Reference	Computation
Terrain Ruggedness Index	TRI	NASA SRTM Digital Elevation (30 m)	Raster	Farr et al. (2007)	Evans et al., 2014
Topographic Position Index	TPI				Evans et al., 2014
Focal Mean of Slope	SLOPE				Focal Statistics
Focal Mean of Elevation	FME				Focal Statistics
Density of built-up areas (year 2020)	BUILT	GHSL - Global Human Settlement Layer - GHS-BUILT-S - R2023A (100 m)	Raster	Pesaresi and Politis (2023)	Kernel Density Tool
Human Population Focal Mean (year 2021)	HUM-POP	LandScan Global 2021 (~ 1 km)	Raster	Sims et al. (2022)	Focal Statistics
Enhanced Vegetation Index	EVI	MOD13Q1.061 (250 m)	Raster	Didan (2021)	Focal Statistics
Normalized Difference Vegetation Index	NDVI				Focal Statistics
Percentage of Landscape: Protected Areas	PLAND PAs	Nature and Parks Authority	Shapefile	Nature and Parks Authority	Fragstats (McGarigal et al., 2012)
Percentage of Landscape: Protected Areas and Military Training Grounds	PLAND PAs_tr				

algorithms, we ran single-scale univariate models and evaluated them based on different criteria, depending on the method used. For GLM, we conducted logistic regressions using the function *glm* from the R base package (R Core Team, 2022) and selected the scale with the lowest AIC. MaxEnt scale selection was based on the highest Area Under the Curve (AUC) value through 10-fold cross-validations. Maxent models were implemented in the *dismo* package (Hijmans et al., 2022), using default settings. In the case of RF, the *randomForest* package (Liaw and Wiener, 2002) was used with 999 trees, and the scale with the lowest out-of-bag fraction (OOB) was chosen. The selected scales were assessed for pairwise collinearity, considering a threshold of Pearson's $r = 0.7$. In correlated pairs, variables with higher AIC, higher OOB, or lower AUC were excluded.

We then used the final set of variables to fit the models. For GLM, after fitting logistic regression with the retained variables at their best scale, model selection was conducted in *MuMIn* (Bartoń, 2023) using the *dredge* function. The model with the lowest AIC was selected as best, and odds ratio changes calculated through the package *effectsize* (Ben-Shachar et al., 2020). In MaxEnt, all the retained predictors after collinearity check were modelled with default settings (Valavi et al., 2023), as MaxEnt predictions are minimally affected by variables with low importance. Model selection for RF, was conducted using package *rfUtilities* (Evans and Murphy, 2018) and the function *rf.modelSel*, with 999 trees and selection based on OOB. Effect size for RF was based on the *rf.effectSize* function, using the partial dependency method of Cafri and Bailey (2016). Variables were standardised prior to multiscale model selection in GLM and RF.

For the Arabian leopard, the final models were validated against the entire 'Ilany' dataset, considered as an independent dataset, validated using 10 iterations of an 80 % to 20 % subsampling approach for training and testing (GLM and RF) or 10-fold cross-validation (MaxEnt). For the Nubian ibex, model selection was conducted using 10 iterations of an 80 % partition of occurrences as training data. The best models were validated against for the same number of iterations using a 20 % partition of occurrences as test data % (GLM and RF). For Maxent, models were selected and validated using a 10-fold cross-validation (MaxEnt). Model diagnostics not directly provided by the package outputs were obtained through *dismo* (Hijmans et al., 2022), *pROC* (Robin et al., 2011), *caret* (Kuhn, 2008) and *ROCR* (Sing et al., 2005). To evaluate the models, we calculated AUC, True Skill Statistics (TSS), Kappa statistics (K), PCC (Percentage of Correct Classification), Sensitivity, and Specificity. Final predictions for the three modelling methods were generated through the function *predict*, using *dismo* (Hijmans et al., 2022) and *terra* (Hijmans, 2023) for MaxEnt and RF, respectively. Final predictions for GLM models were generated through the formula:

$$P = (\exp(z)) / (1 + (\exp(z)))$$

where P is the predicted probability of habitat suitability and z is the linear combination of independent variables (log-odds). All outputs for each species were normalized in the range 0–1 and used to build ensemble surfaces (further normalized 0–1).

2.5. Niche overlap and ecological responses

We assessed pairwise correlations between final models (all algorithms and species ensemble) using Pearson's and Spearman's coefficients. Niche overlap was quantified using Hellinger's I and Schoener's D indices (Warren et al., 2009) via the *nicheOverlap* function in *dismo* (Hijmans et al., 2022). We compared models within the same method (e.g., GLM) and ensembles. The ecological effects of the variables included in final models (GLM and RF) or those with >1 % contribution (MaxEnt), were displayed fitting lowess smoothers using *stat.plsmo* (Harrell Jr, 2023) in *ggplot2* (Wickham, 2016) to allow comparability across methods.

2.6. Suitable habitats and protection status

To determine suitable habitat, fixed thresholds were applied to transform the ensemble habitat suitability distribution into binary outputs. Values above the lowest 5 % and 10 % suitability values were considered potential habitat. The total habitat area for the species, including shared space, was then determined. The amount of habitat in protected areas and encompassed by both protected areas and military training grounds was also calculated. We further calculated the proportion of suitable habitat in each protected area.

3. Results

3.1. Home range estimates

Splitting the data by animals and by year generated 36 subsets of which 23, containing at least 10 observations, were inspected using semi-variogram functions (Supplementary Table 2 and Supplementary Fig. 4). The 95 % home range estimates varied from 4.64 km² to 217.69 km² across the whole set of 23 breaks (Table 2). We retained 11 yearly sets (Table 2; Supplementary Fig. 4) that were selected as indicative of stable home ranges following inspection of variograms. These sets were chosen to compute a population average (95 % KDEc = 73.24 ± 47.91 km²; 50 % KDEc = 15.95 ± 10.88 km²). The subset of data in continuous survey sessions separated by a lag of >30 days produced 76 sets (Supplementary Table 3), of which 16 were at least 12 weeks long. The 95 % home range estimates varied from 26.27 km² to 176.74 km² across the whole set of 16 breaks (Table 3). In this case, nine survey sessions (Table 3; Supplementary Fig. 5) were selected as indicative of stable home ranges and were chosen to compute a population average (95 % KDEc = 77.46 ± 54.94 km², 50 % KDEc = 17.87 ± 13.28 km²). Estimates of 95 % KDEc for males and females (not reported in Tables 2 and 3) amounted 121.89 and 62.42 km² for the yearly subsets, and 118.98 and 65.59 km² for the continuous subsets.

3.2. Scale selection

Overall, scale selection was consistent for many variables across modelling methods and species (Table 4). BUILT, HUM-POP, EVI and NDVI were always selected at 8000 m. Among topographical variables, SLOPE was selected for both species at 1000 m by GLM and MaxEnt, and at adjacent radii by RF (500 m for the leopard, 2000 for the ibex). TPI was always selected at 2000 m, except for 8000 m for ibex in GLM. TRI was generally selected at 2000 m (leopard) or 1000 and 2000 m (ibex) apart from 8000 m selected by MaxEnt for the leopard. FME was selected at fine scales for ibex and leopard by GLM (100 m), MaxEnt and RF for the leopard (500 and 100 m, respectively), and at coarse scales by MaxEnt and RF for ibex (8000 m). Scales of selection for PLAND PAS were more heterogeneous, ranging from 100 m for leopard in GLM to 8000 m for ibex in RF. PLAND PAS_{tr} was selected by MaxEnt and RF at 8000 m for both species, and at finer scales by GLM (100 and 1000 m for leopard and ibex, respectively). Full details on scale selection are reported in Supplementary Table 4.

3.3. Final models and variables contribution

Overall, the variables retained across all modelling methods after testing for pairwise correlations were FME, NDVI, PLAND_PAS, TRI, TPI, BUILT (Supplementary Table 5). Exceptions were represented by the exclusion of BUILT in RF for both species, PLAND_PAS in RF for ibex, and NDVI in MaxEnt for ibex.

Final models in GLM and RF differed in their complexity between the two species (Supplementary Table 6). The best GLM model for leopard was composed only by NDVI, TPI and TRI. According to the model coefficients, leopards selected areas characterised by low values of NDVI (indicative of arid environments), positively selected rugged areas along

Table 2

Yearly estimates of home range using the perturbative-hybrid REML corrected kernel density estimator (pHREML KDEc), reported for the 50, 75 and 95 % of KDEc area. *Low* = lower confidence interval; *est* = estimated values; *high* = higher confidence interval. *En* represents the effective sample size. Breaks highlighted in bold have been chosen for estimates population averages.

Breaks	Model	En	KDEc 95 %			KDEc 75 %			KDEc 50 %		
			low	est	high	low	est	high	low	est	high
Amrafel_1989	IID anisotropic	42.00	109.24	151.58	200.73	41.31	57.32	75.91	16.34	22.67	30.02
Hordus_1985	IID anisotropic	38.00	20.54	29.03	38.96	7.60	10.74	14.41	4.04	5.71	7.66
Hordus_1984	Ouf anisotropic	5.47	21.59	62.44	124.61	11.74	33.96	67.78	6.12	17.69	35.31
Hordus_1989	Ouf anisotropic	2.82	51.61	92.21	144.40	23.24	44.02	71.32	9.58	18.14	29.40
Humbaba_1981	Ouf anisotropic	8.52	67.79	152.15	270.05	34.80	78.12	138.66	18.75	42.08	74.68
Humbaba_1982	IID anisotropic	40.00	20.96	29.34	39.10	11.97	16.76	22.34	6.74	9.43	12.57
Humbaba_1983	IID anisotropic	40.00	38.59	54.01	71.99	21.26	29.76	39.66	11.14	15.59	20.78
Humbaba_1984	IID anisotropic	59.00	57.24	75.19	95.56	31.23	41.03	52.14	15.66	20.57	26.14
Humbaba_1985	IID anisotropic	70.00	65.11	83.53	104.20	24.19	31.03	38.71	12.44	15.96	19.91
Humbaba_1986	IID anisotropic	33.00	100.62	146.18	200.10	30.13	43.77	59.92	10.07	14.63	20.03
Humbaba_1987	IID anisotropic	14.00	36.83	67.37	106.98	18.50	33.83	53.72	8.44	15.43	24.51
Humbaba_1989	IID anisotropic	42.00	36.06	50.03	66.26	14.78	20.51	27.16	4.87	6.75	8.95
Ktushion_1983	IID anisotropic	10.00	89.74	187.14	319.72	43.15	89.98	153.74	20.93	43.65	74.58
Rishat Ninlil_1986	IID anisotropic	19.00	54.96	91.29	136.68	30.28	50.29	75.30	15.89	26.40	39.52
Shlomtsion_1982	IID anisotropic	30.00	134.99	200.08	277.77	60.01	88.94	123.48	29.98	44.44	61.69
Shlomtsion_1983	IID anisotropic	20.00	76.46	125.17	185.69	48.28	79.05	117.27	28.16	46.10	68.39
Shlomtsion_1984	IID anisotropic	56.00	164.44	217.69	278.29	95.42	126.32	161.49	51.89	68.69	87.81
Shlomtsion_1985	IID anisotropic	57.00	126.62	167.18	213.29	65.06	85.89	109.58	32.98	43.55	55.56
Shlomtsion_1987	IID anisotropic	36.00	28.87	41.22	55.74	13.57	19.37	26.19	5.70	8.14	11.00
Shlomtsion_1989	IID anisotropic	83.00	20.93	26.28	32.22	7.48	9.39	11.51	3.66	4.60	5.64
Tihamat_1984	IID anisotropic	28.00	3.64	5.48	7.69	2.39	3.59	5.04	1.15	1.73	2.43
Tihamat_1985	OU anisotropic	2.44	17.15	35.02	59.17	9.53	19.46	32.89	4.93	10.07	17.01
Tsruyah_1984	IID anisotropic	57.00	3.52	4.64	5.93	1.25	1.65	2.10	0.04	0.05	0.06
Average			52.03	73.24	98.42	23.96	34.05	46.13	11.28	15.95	21.54
SD			36.27	47.91	62.30	16.93	22.19	28.95	8.43	10.88	13.92

Table 3

Continuous estimates of home range spanning at least 12 weeks, with no >30 days lag between any two observations. The estimates have been fitted using the perturbative-hybrid REML corrected kernel density estimator (pHREML KDEc), reported for the 50, 75 and 95 % of KDEc area. *Low* = lower confidence interval; *est* = estimated values; *high* = higher confidence interval. *En* represents the effective sample size. Breaks highlighted in bold have been chosen for estimates population averages.

Breaks	Model	En	KDEc 95 %			KDEc 75 %			KDEc 50 %		
			low	est	high	low	est	high	low	est	high
Amrafel_1988-12-11_1989-05-25	IID anisotropic	43.00	107.99	149.22	197.01	40.23	55.59	73.40	16.13	22.28	29.42
Hordus_1984-11-27_1985-02-23	IID anisotropic	46.00	44.39	60.63	79.37	13.20	18.03	23.60	5.90	8.05	10.54
Hordus_1988-12-21_1989-03-27	IID anisotropic	16.00	50.72	88.74	137.22	23.15	40.50	62.63	9.33	16.32	25.24
Humbaba_1981-06-04_1981-12-17	Ouf anisotropic	7.53	70.70	168.99	309.38	36.16	86.42	158.22	19.79	47.31	86.61
Humbaba_1982-04-03_1982-09-20	IID anisotropic	33.00	19.24	27.96	38.27	10.57	15.36	21.02	5.62	8.16	11.18
Humbaba_1983-01-03_1983-08-23	IID anisotropic	31.00	24.33	35.81	49.48	11.25	16.56	22.88	5.95	8.76	12.10
Humbaba_1983-12-24_1984-04-15	Ouf anisotropic	15.06	36.12	64.45	100.84	18.90	33.72	52.76	9.47	16.89	26.43
Humbaba_1984-05-16_1984-08-10	Ouf anisotropic	5.60	28.29	80.57	159.73	13.93	39.68	78.65	7.11	20.25	40.14
Humbaba_1984-09-12_1985-07-31	IID anisotropic	94.00	57.42	71.06	86.12	21.26	26.31	31.88	10.89	13.47	16.33
Humbaba_1986-05-11_1986-09-23	IID anisotropic	31.00	99.58	146.56	202.48	26.45	38.92	53.77	9.25	13.61	18.80
Humbaba_1989-01-03_1989-04-14	IID anisotropic	42.00	36.06	50.03	66.26	14.78	20.51	27.16	4.87	6.75	8.95
Rishat Ninlil_1986-06-24_1986-09-22	IID anisotropic	18.00	55.06	92.90	140.48	29.58	49.91	75.47	15.25	25.73	38.91
Shlomtsion_1983-12-26_1984-04-02	OU anisotropic	8.20	42.03	96.16	172.31	24.53	56.11	100.55	13.07	29.90	53.58
Shlomtsion_1984-10-25_1985-07-11	IID anisotropic	90.00	142.12	176.74	215.08	76.16	94.72	115.26	38.65	48.07	58.50
Shlomtsion_1988-12-12_1989-06-07	IID anisotropic	81.00	20.86	26.27	32.29	7.38	9.29	11.42	3.64	4.58	5.63
Tihamat_1985-01-15_1985-06-17	OU anisotropic	2.44	17.15	35.02	59.17	9.53	19.46	32.89	4.93	10.07	17.01
Average			52.62	77.46	107.76	25.20	37.24	51.97	12.11	17.87	24.93
SD			44.07	54.94	68.69	21.96	26.99	33.44	10.89	13.28	16.33

terrain depressions (as explained by the positive and negative relationships with TRI and TPI respectively). The effect sizes for this model highlighted the importance of TRI in the odds ratio changes. The best GLM for ibex included six variables, with ecological relationships concordant with the equivalent model for the leopard, but with a stronger preference for desert environments (NDVI) and terrain depressions (TPI). The effect sizes revealed the major importance of TRI followed by FME, BUILT and PLAND-PAs, all with similar values. MaxEnt models for the two species also found the most important variables to be NDVI (leopard), EVI (ibex), TRI (both species) and PLAND

PAs (ibex). The least contributing variables in Maxent were FME (both species) and BUILT (ibex). RF confirmed the observations of the other modelling methods (Supplementary Table 6). According to the mean decrease in accuracy (MDA) and mean decrease in Gini index (MDG), the most important variable was NDVI for both species, followed by TPI and TRI. Effect sizes were negative for all variables except TRI for both species. Noteworthy are the large negative relationships with NDVI and HUM-POP, remarking results from GLM models for both species (Supplementary Table 6). Habitat suitability maps are illustrated in Fig. 2.

Table 4

Scale selection for each variable across modelling methods and species. In *italic*, variables discarded after pairwise collinearity check; in **bold**, variables retained in the final models. Note that for Maxent models, variables in bold are those above 1 % contribution.

Predictor	GLM		MaxEnt		RF	
	Leopard	Ibex	Leopard	Ibex	Leopard	Ibex
BUILT	8000	8000	8000	8000	<i>8000</i>	<i>8000</i>
EVI	<i>8000</i>	<i>8000</i>	<i>8000</i>	8000	<i>8000</i>	<i>8000</i>
FME	100	100	500	8000	100	8000
HUM-POP	<i>8000</i>	<i>8000</i>	<i>8000</i>	<i>8000</i>	8000	8000
NDVI	8000	8000	8000	<i>8000</i>	8000	8000
PLAND PAs	100	1000	1000	4000	4000	<i>8000</i>
PLAND PAs_tr	<i>100</i>	<i>1000</i>	<i>8000</i>	<i>8000</i>	<i>8000</i>	<i>8000</i>
SLOPE	<i>1000</i>	<i>1000</i>	<i>1000</i>	<i>1000</i>	500	<i>2000</i>
TPI	2000	8000	2000	2000	2000	2000
TRI	2000	1000	8000	1000	2000	2000

3.4. Models' performance

The leopard models demonstrated strong performance on average (Supplementary Table 7). They achieved high discrimination capacity, with AUC values reaching an average of 0.958 for the test fractions. The models showed excellent accuracy, with an average test PCC of 98.278. Additionally, they exhibited high values of specificity and sensitivity, averaging 0.909 and 0.976 for the test sets, respectively. The TSS values varied across methods but were on average 0.895 for the test fractions. Similarly, the values of K were consistent between the GLM and RF models and peaked for the test fraction of MaxEnt (0.819 on average for the test sets).

The ibex models also showed strong performance (Supplementary Table 7). On average, the ibex models achieved a discrimination ability with AUC values of 0.949 for the test fractions. The models demonstrated robust performance on the test partitions, maintaining high accuracy with an average PCC of 93.605, average TSS values of 0.777, and average K values of 0.766. The specificity values for the test sets averaged at 0.917, and the sensitivity values were slightly lower averaging at 0.845.

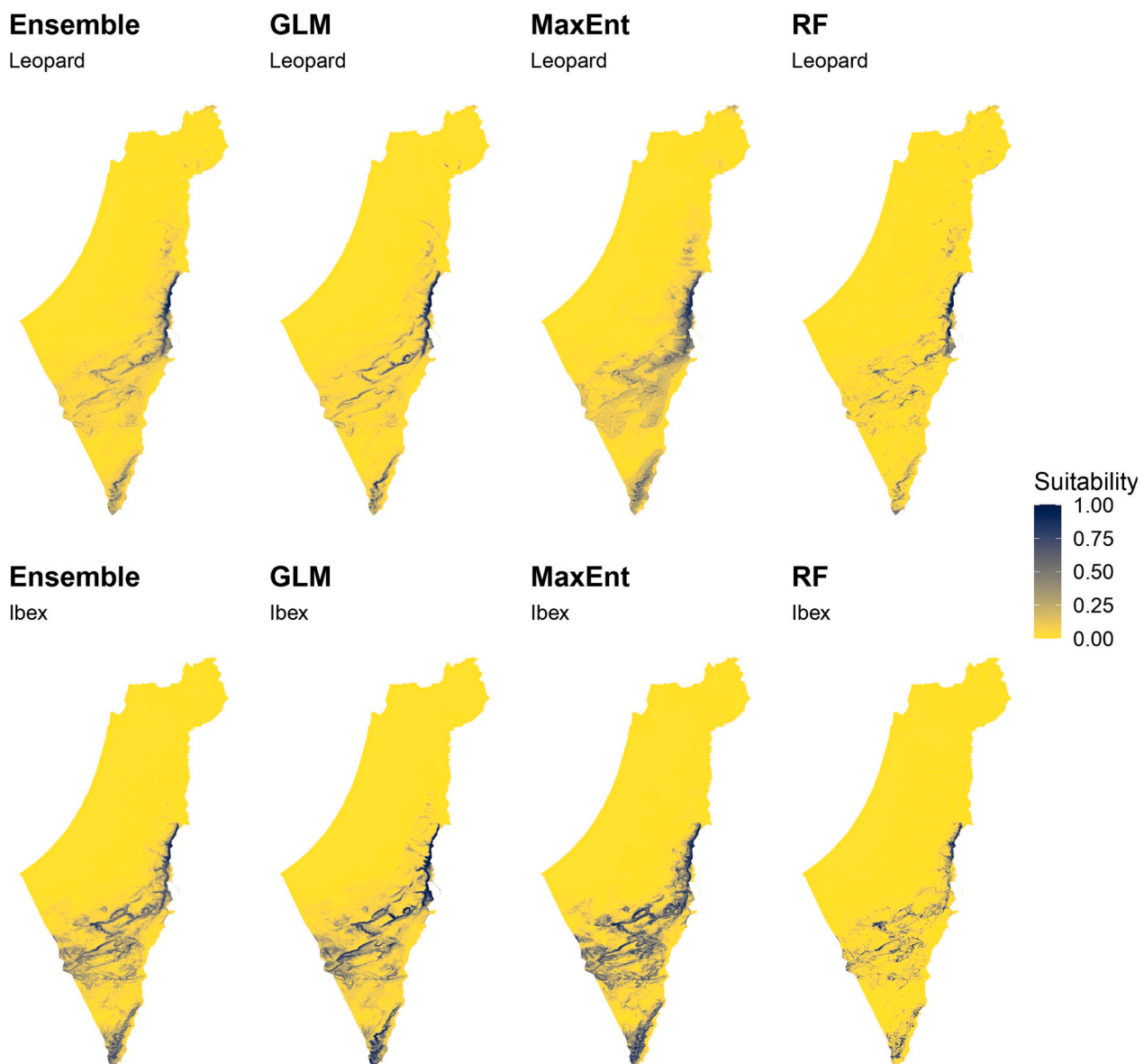


Fig. 2. Habitat suitability patterns for Arabian leopard and Nubian ibex obtained through logistic regression (GLM), MaxEnt modelling, Random Forest (RF) and ensemble modelling.

3.5. Overlap metrics and lowess curves

All pairwise correlation values are provided in Supplementary Table 8. Here we report only values for the ensemble models for the leopard and ibex, which overlapped 0.93 and 0.83 according to Spearman's and Pearson's correlations. Metrics of Hellinger's I index of niche overlap between the species were high for the ensembles (0.93), GLM (0.93) and MaxEnt (0.91) models, while RF models had lower correlation between predicted ibex and leopard habitat (0.75). Values of Schoener's D index of overlap were lower, reaching 0.73 for the ensembles, 0.72 for GLM, 0.68 for MaxEnt, and 0.50 for RF (Supplementary Table 9).

Lowess curves were highly congruent for the two species (Supplementary Figs. 6 and 7). In summary, presence of leopard and ibex increases at high values of medium-scale ruggedness and is lowest when the relative topographic position at medium-scales is flat. Presence is also higher in low populated large-scale areas (both low human presence and sporadic settlements) and in desert and semi-desert environments. Moreover, the presence of either species tends to increase as the medium-scale percentage of PAs reaches ~50 % and stabilises above that.

3.6. Estimates of habitat

Considering a fixed 5 % threshold, we estimated 6160.28, 7127.56 and 5275.58 km² for the leopard, ibex, and their shared habitat, respectively. Further, for the same sequence, protected areas encompassed 65 %, 64 % and 70 % of the habitat, while protected areas and military training grounds accounted for 82 %, 87 % and 86 % of the habitat (Table 4). At the 10 % fixed threshold we estimated 3120.08, 5106.41 and 2738.74 km² for the leopard, ibex, and shared habitat, respectively. At this threshold, protected areas included 72 %, 74 % and 76 % of the total, while protected areas and military training grounds encompassed 83 %, 88 % and 85 % following the same order (Table 4). We ranked the 25 most important protected areas for either species or their shared habitat, at both thresholds (details are presented in Supplementary Table 10). In summary, the most important protected areas recurrently include Midbar Yehuda, Mazuq Ha-Zinnim, Har Ha-Negev, Massiv Elat, Ashosh, Makhteshim En Yahav, Zuqe Shayyarot, Ramat Mazzar and Mazuq Ha-He'teqim.

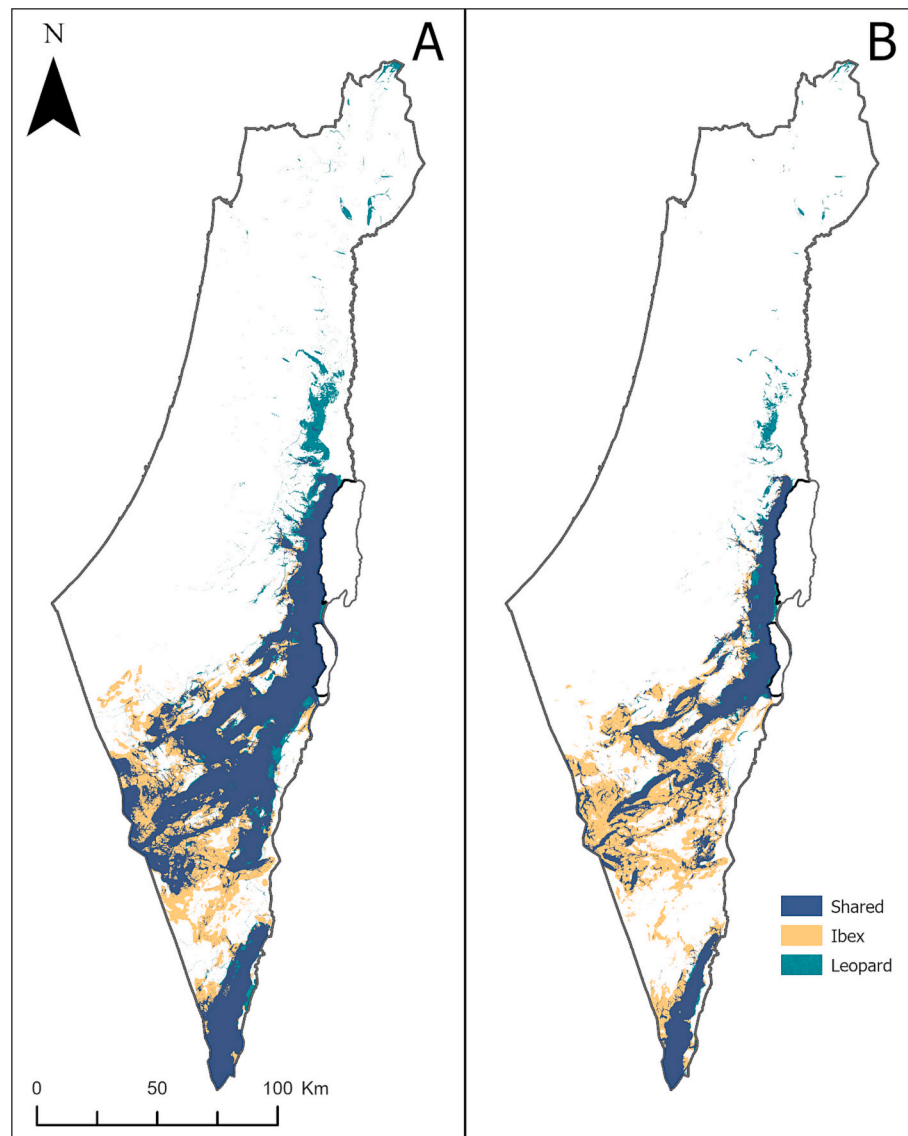


Fig. 3. Thresholded habitat predictions. A) illustrates suitable areas for Arabian leopard and Nubian ibex at a 5 % fixed threshold (removing thus the 5 % lowest habitat suitability values). B) shows suitable areas for Arabian leopard and Nubian ibex at a 10 % fixed threshold (removing thus the 10 % lowest habitat suitability values).

4. Discussion

With this work, we harnessed historical Arabian leopard and Nubian ibex data to uncover the ecological requirements of both species, providing baseline information to inform potential future restoration of the leopard population in the IWB region. We found that the distribution and ecological drivers of leopard occurrence are largely the same as those driving ibex occurrence, which was the main prey in the region (Ilany, 1990; Timna, 2000), and whose careful management now offers a promising foundation for reviving a lost top predator in IWB.

Our study demonstrates that both Arabian leopards and Nubian ibex habitat preferences are affected by environmental and human factors at different scales, highlighting the significance of considering ecological scales in studies of species distribution (McGarigal et al., 2016). Specifically, topography emerged as a prominent influence at finer scales, while diffuse human disturbance and landscape-level vegetation patterns exerted their influence at larger scales (Table 4). The distribution of large carnivores is often affected by broad-scale patterns of human presence (Atzeni et al., 2020; Macdonald et al., 2018, 2019), and fine-scale topographical complexity (Krishnamurthy et al., 2016; Atzeni et al., 2020; Hacker et al., 2022; Macdonald et al., 2018; Bouyer et al., 2015; Shahsavarzadeh et al., 2023), both to minimize human disturbance and maximize foraging opportunities at different life stages. Likewise, large ungulates often exhibit avoidance of anthropogenic environments at large scales (Jakes et al., 2020; Penjor et al., 2021; Sawyer et al., 2007; Stabach et al., 2017) and prefer complex terrain (Nezer et al., 2017; Stabach et al., 2017; Iribarren and Kotler, 2012; Tadesse and Kotler, 2010, 2011; Shkedy and Saltz, 2000).

Only minor scale differences between the two species were observed (Table 4), likely deriving from a spatial bias of leopard data towards the Judean desert, compared to the widespread distribution of ibex occurrences. However, since the two species overlapped highly in space (Fig. 3; Supplementary Tables 8 and 9) and in ecological responses to predictors (Supplementary Figs. 6 and 7), such differences would have been minimized if our data set had included more leopard records from the Negev and Massif Elat, where leopards were once widespread (Spalton and al Hikmani, 2006). Furthermore, we observed few differences in scale selection among the algorithms (Table 4), attributable to the limited extent of the IWB area. Different modelling methods can yield varying probability patterns (Chiaverini et al., 2023; Millar and Blouin-Demers, 2012; Bucklin et al., 2015), selected scales (Chiaverini et al., 2023; Pittman and Brown, 2011), or performance (Valavi et al., 2022, 2023). While some algorithms have consistently performed well in distribution modelling studies (Valavi et al., 2022, 2023), no single method is considered universally superior (Hysen et al., 2022; Chiaverini et al., 2023; Elith and Graham, 2009; Konowalik and Nosol, 2021), as supported by our findings (Supplementary Table 7). To account for algorithm variability, it is advisable to combine predictions from multiple modelling methods to prevent under- or overestimating species distribution, providing a more realistic estimation of suitable conditions (Meller et al., 2014; Farhadinia et al., 2015; Shahnaseri et al., 2019).

The final models for both species exhibited minimal variation in the importance of different variables across algorithms (Supplementary Table 6). Specifically, TRI had a major influence on GLM predictions, while NDVI and TRI were important for MaxEnt and RF models. The variables NDVI and TRI thus represent the key habitat characteristics that currently support the existence of ibex, and formerly supported the leopards too, indicating altogether that very rugged areas in desert and semi-desert landscapes provide optimal potential habitat for both species within the IWB region. (Supplementary Table 6; Supplementary Figs. 6 and 7). Previous distribution models of the Arabian leopard have reported habitat associations that differ from those we found. Studies by Dunford et al. (2022) and Islam et al. (2021) found positive correlations between the species' occurrence and variables like EVI and NDVI, suggesting that areas with higher primary productivity were more likely to

be associated with leopard presence. However, our study yielded negative correlations between leopard occurrence probability and vegetation patterns (Supplementary Table 6). The differences in the associations between leopard occurrence and vegetation patterns may suggest the influence of different limiting factors for the Arabian leopard in relation to habitat conditions throughout its range, as observed in other carnivores in different regions (Atzeni et al., 2020; Vergara et al., 2015; Short Bull et al., 2011), or may reflect that the grain of our analysis was not fine enough to resolve positive associations with vegetation patterns (Lehmann et al., 2020; Nezer et al., 2017) and water availability (Henley et al., 2007; Nezer et al., 2017; Tadesse and Kotler, 2010).

The congruence of lowess curves clearly demonstrated a strong association between leopard occurrence and the distribution of ibex (Supplementary Figs. 6 and 7), highlighting strong niche identity (Peterson, 2011), as observed in other predator-prey contexts (Holt et al., 2018; Aryal et al., 2016; Farhadinia et al., 2015; Shahsavarzadeh et al., 2023; Loveridge et al., 2009). Leopards are known to be adaptable predators capable of thriving in various vegetative, topographical, and temperature conditions (Stein et al., 2020). On the other hand, Nubian ibexes have evolved to inhabit rocky desert mountains across their historical range encompassing the Arabian Peninsula and north-eastern Africa (Ross et al., 2020). Therefore, while the habitat choices of ibexes appear to align with the selection of their fundamental niche, the habitat selection of leopards in the modern IWB region may reflect not only the spatial patterns of presence of this primary prey, but also the spatial pattern of anthropogenic factors variously inimical to both the leopards and their prey (e.g., Farhadinia et al., 2015; Shahsavarzadeh et al., 2023).

Leopards were historically known to inhabit a large portion of IWB, including the northern regions of Galilee and the Golan Heights (Timna, 2000), which exhibit varied vegetative and topographical conditions and support a diverse range of prey species (Yom-Tov et al., 2021; Timna, 2000; Ben-Moshe et al., 2023). Leopards in northern IWB may have represented individuals residing at the lower extent of the *P. p. tulliana* distribution (Nowell and Jackson, 1996; Pajmans et al., 2021; Riaño et al., 2022 [preprint]), for which our models successfully identified a few favourable habitat areas in the northern parts of modern IWB (Figs. 2 and 3). However, the prospects for leopard survival in these areas may initially appear daunting due to factors such as the seemingly inevitable expansion of human development and the risk of poaching. Promisingly, a significant portion of the current habitat shared with ibex, which can serve as a proxy for the potential habitat of the Arabian leopard in the region, is already under some form of protection. Specifically, more than half of the suitable conditions for both species identified in this study are encompassed by existing protected areas (Table 5). Furthermore, a significant proportion of the suitable habitat for both species are included areas designed for military training, which, in common with other areas of restricted access, might provide additional long-term protection against habitat alteration and development.

Our study has made accessible much of the information collected by Ilany (1981, 1988, 1990) on Arabian leopard home range size and landscape utilization in IWB. Using new analytical methodologies and a unique accumulation of data, our study extends prior work and provides more rigorous estimates of home range size. However, we acknowledge that our data, despite representing the oldest and largest compilation for this species in IWB, is characterised by severe sampling gaps, unequal effort, and infrequent sampling, common traits for VHF data (Hebblewhite and Haydon, 2010; Kie et al., 2010). For all these reasons, we adopted two different approaches to enhance the confidence in our estimates. First, we chose to subset the observations in annual sampling sessions across individuals to define a common sampling period. Second, we identified continuous sampling sessions spanning at least 12 weeks keeping the maximum lag between observations as <30 days. Both approaches presented the desirable advantage of being limited in time enough to avoid overestimating possible home range sizes, regardless of

Table 5

Estimates of habitat (in km²) for the two species distinctively and for their shared habitat, according to fixed 5 % and 10 % suitability thresholds. PAs refers to the amount of habitat contained within protected areas, while PAs_tr refers to the amount of habitat contained within protected areas and military training grounds. Percentage values in brackets.

	Threshold 0.05			Threshold 0.1		
	Habitat	PAs	PAs_tr	Habitat	PAs	PAs_tr
Leopard	6160.28	3991.34 (0.65)	5071.62 (0.82)	3120.08	2239.43 (0.72)	2598.37 (0.83)
Ibex	7127.56	4555.11 (0.64)	6183.55 (0.87)	5106.41	3772.89 (0.74)	4510.87 (0.88)
Shared	5275.58	3712.18 (0.70)	4518.8 (0.86)	2738.74	2080.45 (0.76)	2327.65 (0.85)

the sample size within each break (Fleming et al., 2019; Silva et al., 2022).

We also recognize that insufficient and infrequent sampling may have caused many semi-variogram functions not to be deemed idoneous for a home-range size analysis, and as such, to the best of our judgement, we have excluded breaks not meeting the recommended criteria (Calabrese et al., 2016). On the other hand, we have included breaks which met the desired criteria of stationarity for the largest part of the semi-variogram functions. Fluctuations observed in the semi-variograms may be indicative of exploratory short-term excursions within home ranges. Indeed, up to 15 animals were thought to inhabit a 1200 km² stretch along the Dead Sea (Ilany, 1990). Given the limited extent of habitat, movements of up to 30 km were frequently observed in several animals (Timna, 2000). These cautions should be kept in mind when interpreting the variograms.

It is very difficult to secure reliable baseline information on the rare and elusive Arabian leopard, a difficulty that has hindered understanding of the species (Spalton and Al Hikmani, 2014). Our home-range estimates (Tables 2 and 3) add usefully to those of Arabian leopards in Oman. Spalton and Al Hikmani (2014) reported a female leopard with a home range of 64 km² and a male with a range of 168 km² in the Dhofar mountains of Oman. They further estimated the female's winter and summer home ranges as 50 km² and 36 km², respectively. Ilany (1990) reported female and male home range sizes of 84 and 137 km², respectively. Our findings closely align with previous estimates (Tables 2 and 3). Female home range sizes from both our approaches are consistent with Spalton and Al Hikmani (2014) and slightly lower than Ilany (1990). Conversely, our estimates of male home range size are lower than what was previously reported for the species (Spalton and Al Hikmani, 2014; Ilany, 1990), a fact attributable to the infrequent sampling of the two males from which these estimates were taken (Tables 2 and 3, Supplementary Fig. 1).

We recognize the high standard deviation in the estimated home ranges of our studied leopards (Tables 2 and 3). Although this may be indicative of home range shifting and behavioural characteristics related to life stages, we do not exclude that unequal sample sizes and inconstant effort may have affected results. It is likely therefore that average home range estimates for the population may be underestimated (Ilany, 1990). While we have generated estimates for Arabian leopards located in the Judean desert, we lack comparable evidence from the Negev region. However, it is reasonable to deduce an increase in home range sizes in regions where the number of primary prey species declines (Loveridge et al., 2009; Simcharoen et al., 2014; Nilsen et al., 2005; Ross et al., 2020; Shkedy and Saltz, 2000).

5. Conclusions

Our findings exemplify how the ecological requirements of ibex and leopards are intertwined, with both species exhibiting similar responses to habitat characteristics. This similarity in habitat preference could be indicative of the leopards' tendency to track ibex populations or perhaps a mutual inclination for terrain that provides refuge from human activities. Consequently, data on ibex locations serve as a significant proxy for identifying potential habitats suitable for the reintroduction of leopards.

Expanding on this ecological relationship, our analysis suggests that the conservative estimate of shared habitat with ibex at the 10 % threshold (2738.74 km²; Table 5), would sustain an approximate number of ~35 leopard individuals, considering the average 95 % KDEc estimates across all individuals (73.24 ± 47.91 km²; 77.46 ± 54.94 km²; Tables 2 and 3). However, these projections, while informative, must be interpreted with caution, as they derive from a VHF telemetry dataset presenting inherent sampling limitations potentially leading to an underestimation of actual home ranges. Moreover, the size of a potential Arabian leopard population would not depend exclusively on available territory but also on ecological factors. These include the delicate equilibrium of the ecosystems involved, the consistent availability of prey biomass, and the competitive dynamics with other carnivore species (Ilany, 1990; Timna, 2000), as well as spatial patterns of mortality risk (Ash et al., 2022).

Recognizing that predator populations are inherently tied to prey availability, a comprehensive understanding of the prey base is essential. This relationship underscores the importance of assessing how many leopards the current ibex population and other key prey species could sustain, considering competition from other predators and the leopards' dietary diversity (Timna, 2000). In this context, Tichon (2020) has significantly advanced understanding of ibex population estimates in the Judean Desert, and protection measures have so far been successful in bolstering their populations. Nonetheless, research is required in other areas hosting Nubian ibex populations (Tadesse and Kotler, 2010, 2011, 2012; Iribarren and Kotler, 2012). Despite knowledge gaps, information regarding other significant prey species for the Arabian leopard is extensive (Ben-Moshe et al., 2023; Shalmon et al., 2020; Nezer et al., 2017; Breslau et al., 2020; Giotto et al., 2015).

Most critically, aligning with the IUCN's guidelines on reintroductions (IUCN/SSC, 2013), it is imperative to address the causes that initially led to the local extinction of the Arabian leopard. This necessitates a synergic conservation strategy that considers both biological and anthropogenic factors. Beyond ecological considerations, fostering social acceptance of leopards and developing strategies to mitigate potential human-leopard conflicts remain paramount (Bonsen et al., 2022; Hadad, 2017; Hadad et al., 2023; Wachs and Tal, 2009). Successful conservation is deeply rooted in adaptive management practices that respect contemporary local circumstances and livelihoods. In this context, valuable insights can be gleaned from previous translocation initiatives (Weise et al., 2015; Briers-Louw et al., 2019; Thomas et al., 2023). Lastly, regional collaboration is essential to range-wide connectivity and to avoid population isolation. Establishing a shared conservation vision with other Arabian leopard range countries presents an opportunity to unify and strengthen efforts across borders (Dunford et al., 2022, 2023; Royal Commission for AlUla, 2023), igniting hope for the resurgence of this majestic and iconic felid within the region.

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CRediT authorship contribution statement

Luciano Atzeni: Conceptualization, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing, Data curation, Formal analysis. **Amiyaal Ilany:** Conceptualization, Resources, Writing – original draft, Writing – review & editing, Data curation, Supervision. **Eli Geffen:** Conceptualization, Data curation, Resources, Writing – original draft, Writing – review & editing, Supervision. **Samuel A. Cushman:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Zaneta Kaszta:** Conceptualization, Methodology, Writing – review & editing. **David W. Macdonald:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110440>.

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