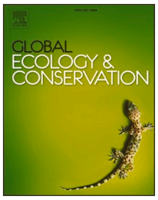
Global Ecology and Conservation 51 (2024) e02937

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Safeguarding the last stronghold: Ecology and conservation of Asiatic Cheetah's prey species in Turan Biosphere Reserve (Iran)

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ARTICLE INFO

Keywords:
Habitat selection
Capra aegagrus
Ovis vignei
Gazella subgutturosa
Gazella bennettii
Lepus capensis
Ecological niche modeling
MaxEnt

ABSTRACT

Identifying suitable habitats for wild felids is essential for effective area-based conservation efforts. However, modeling habitat suitability for extremely rare and endangered taxa such as the Asiatic Cheetah (*Acinonyx jubatus venaticus*) is challenging due to limited data availability. To address this, our study focused on analysing the distribution factors of the Asiatic Cheetah's main prey species, including the Wild Goat (*Capra aegagrus*), Urial (Ovis *vignei*), Goitered Gazelle (*Gazella subgutturosa*), Jebeer Gazelle (*Gazella bennettii*), and Cape Hare (*Lepus capensis*) in the Turan Biosphere Reserve (TBR), a critical Cheetah habitat in Iran. To determine habitat suitability for these prey species, we conducted a systematic field survey along 30 transects measuring 16 km each by collecting data in each 1 km interval, resulting in 1172 direct observations of their presence. These observations were then correlated with 44 variables grouped into four categories: bioclimatic, topography, vegetation, and distance to anthropogenic and natural features. Suitability maps were generated using a hierarchical modeling approach. Among the observed prey species, Urial had the highest frequency of sightings (675 visual observations over eight seasons), followed by Goitered Gazelle (564 observations), Cape Hare (278 observations), Jebeer Gazelle (232 observations), and Wild Goat (208 observations). The most influential predictors affecting prey species distribution were mean summer temperature (with optimal ranges at lower temperatures), terrain relief roughness (with optimal ranges at intermediate roughness), distance to wells (with optimal ranges at shorter distances), and distance to corrals (with variable optimal ranges across species). Our findings indicate that the western and eastern mountainous areas, along with their hilly surroundings, as well as the northwest and western plains of TBR, constitute the most suitable habitats for these five prey species. These models and suitability maps provide crucial evidence for implementing conservation measures in the vulnerable habitats of the Asiatic Cheetah and its primary prey species. Environmental conditions can be enhanced through the management of water sources, roads, corrals, and livestock grazing. In addition, the fragmentation of suitable areas within TBR highlights the importance of preserving corridors between these

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https://doi.org/10.1016/j.gecco.2024.e02937
Received 27 November 2023; Received in revised form 20 March 2024; Accepted 4 April 2024

fragmented habitats. We recommend re-evaluating and expanding the boundaries of Turan National Park, Turan Wildlife Refuge, and Turan Biosphere Reserve to ensure the long-term conservation of this threatened felid species and its associated ecosystems.

1. Introduction

The Asiatic Cheetah, *Acinonyx jubatus venaticus*, is one of the most threatened and rare felids globally (Durant et al., 2017). It historically had a distribution across Southwest and Central Asia to India (Nowell and Jackson, 1996; Mallon, 2007; IUCN, 2008), but has experienced a drastic range contraction over the last century (Nowell and Jackson, 1996). Currently, the Asiatic Cheetah only occurs in the arid and semi-arid deserts of Iran (Farhadinia and Hemami, 2010) at very low density (Farhadinia et al., 2013). Before World War II, the Iranian population of Cheetahs was estimated at almost 400 individuals (Harington, 1971). In recent decades, its population has been anecdotally estimated as less than 70 (Farhadinia et al., 2017) or less than 50 individuals (Durant et al., 2017). Recent research in Central Iran has shown that illegal human killing, mainly by herders and their dogs or poachers, is the main cause of mortality, followed by roadkill (Farhadinia et al., 2016). Given its small population size, continued decline and fragmented distribution, the survival of the species is highly uncertain (Moqanaki and Cushman, 2017; see also Caughley, 1994). Asiatic Cheetahs have been observed to move exceptionally long distances in Central Iran (Farhadinia et al., 2013) to find required resources and cope with harsh environments in dry lands (Farhadinia et al., 2016). They primarily prey on wild ungulates, with Wild Sheep species (Urial, *Ovis vignei* and mouflon *O. gmelini*) being the most frequent prey (Hunter et al., 2007; Farhadinia and Hemami, 2010; Zamani et al., 2017), followed by Wild Goat *Capra aegagrus*, Goitered Gazelle *Gazella subgutturosa*, and Jebeer Gazelle *G. bennettii* (Farhadinia and Hemami, 2010). While Iranian Cheetahs traditionally inhabited dry and desert-like plains, due to the decline in prey populations, such as gazelle species, they are meanwhile also reported from remote hills, foothills, and even mountainous habitats (Farhadinia, 2007; Hunter et al., 2007; Farhadinia and Hemami, 2010; Sarhangzadeh et al., 2015).

Turan Biosphere Reserve (TBR) in Northeastern Iran is the global stronghold for Asiatic Cheetah and together with five smaller adjacent areas, it is known as the main breeding area of the species (Farhadinia et al., 2016). The total number of observed Cheetahs in TBR in 2009 was almost twice the total number of sightings elsewhere (Farhadinia et al., 2017). Nevertheless, Cheetah observations are still scarce within TBR, precluding a sound quantitative analysis of the species' habitat requirements and population trends and thus efficient conservation management (Durant et al., 2017; Farhadinia et al., 2017). It is clear, however, that availability of food resources, and hence the distribution of its main prey species, must be a major factor determining the Cheetah's distribution (Ahmadi et al., 2017; see also Hayward et al., 2007 for evidence that prey characteristics strongly influence the abundance of African Cheetah and other predator species). In absence of sufficient data on habitat selection of the Cheetah, identifying factors determining the distribution of its main prey species should hence provide important information for area-based conservation management. As elsewhere, the four most important prey species for cheetah in TBR are Urial, Goitered Gazelle, Jebeer Gazelle, and Wild Goat. In addition, Cape Hare *Lepus capensis* and other small mammals as well as young camel *Camelus dromedarius*, domestic sheep *Ovis aries*, and domestic goat *Capra hircus* have been reported (Farhadinia et al., 2016). Among the wild prey species, Urial and Goitered Gazelle are themselves considered vulnerable by the IUCN (Michel and Ghoddousi, 2020; IUCN, 2017b), Wild Goat is classified as near threatened (Weinberg and Ambarli, 2020), while Jebeer Gazelle and Cape Hare are classified as least concern species (Johnston et al., 2019; IUCN, 2017a).

In this study, we use an extensive dataset of field observations of the main prey species to analyze their habitat requirements. Specifically, we assess a) the distribution of the five prey species of Asiatic Cheetah in its stronghold Turan Biosphere Reserve, b) the

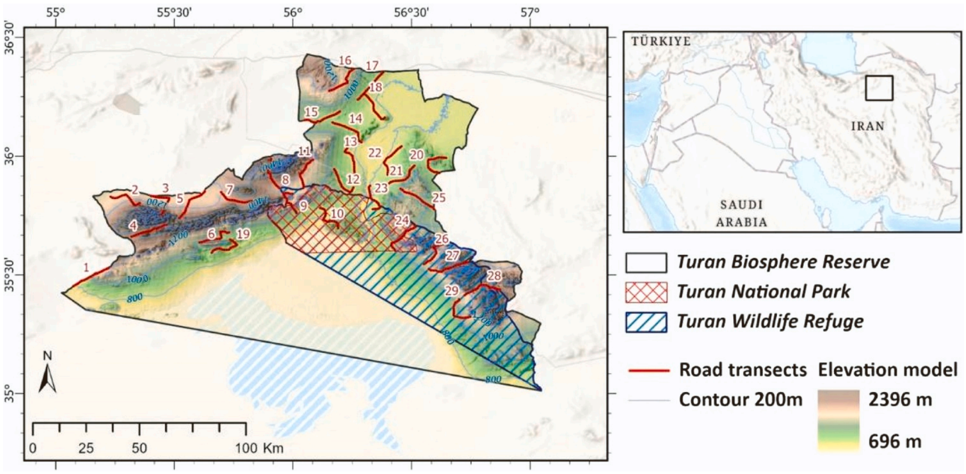


Fig. 1. Turan Biosphere Reserve (14,650 sqkm) and its zones, located in northeast Iran at altitudes of 700–2400 m a.s.l.

most important factors influencing these prey species distributions and c) the overall prey species habitat suitability as a proxy of Cheetah habitat suitability. We thereby aim at improving the empirical basis for designing efficient Cheetah conservation measures.

2. Methods

2.1. Study area

The study was conducted in Turan Biosphere Reserve, located in Semnan province in Northeastern Iran (34°56′–36°33′ N and 54°57′–57°04′ E). TBR covers an area of 14,650 square kilometers and is the largest biosphere reserve in Iran. It was designated as a protected area by the Department of Environment in Iran (DOE) in 1972. In 1976, the area was divided into two parts: a wildlife refuge and a protected area. These two complexes were subsequently registered as Turan Biosphere Reserves. In 2002, a national park was established in the parts of the wildlife refuge that hosted particularly relevant populations of threatened species (Fig. 1).

TBR experiences a dry continental climate, with average temperatures ranging from −15°C in January to 40°C in August. The mean annual precipitation is 141 mm. The region consists of vast expanses of flat plains and mountains, with altitudes ranging from 700–2400 m above sea level (Darvishsefat, 2006). The specific topographic conditions have created a suitable habitat for wildlife, with mountainous slopes, hills, sand dunes, and clay soils in the central and surrounding areas. The dominant land cover is desert with little to no vegetation (80.1%), followed by open areas with sparse vegetation, wild cereals, and grasses (18.2%), water land (1.6%), crops (0.1%), and built areas (0.01%) (Karra et al., 2021).

The flora of the region is classified as Irano-Turanian (Asadi, 1987) and consists of various perennial, shrub, and tree species, totaling 654 species (Nieamir and Zanjanpour, 2002). The mammal fauna in TBR is diverse and includes the Striped hyena (*Hyaena hyaena*) and Persian Leopard (*Panthera pardus saxicolor*) (Semnan DoE, 2017). In addition, TBR is known for hosting the largest populations of Asiatic Cheetah (Farhadinia, 2004); at least 15 cheetahs have been observed in this area in 2020 (Nezami et al., 2023). TBR also hosts important populations of the Cheetah's prey species, approximately 1000 individuals of Wild Goat, 1200 individuals of Urial, 500 individuals of Goitered Gazelle, and more than 100 individuals of Jebeer Gazelle have been estimated (A. Radman, pers. comm.).

2.2. Study approach

We conducted a comprehensive study to investigate the habitat requirements and distribution of five important prey species of the Asiatic Cheetah: Wild Goat, Urial, Goitered Gazelle, Jebeer Gazelle, and Cape Hare. A systematic field survey was carried out to collect data on these species. The collected data were then used to model the species distribution taking into account various environmental variables such as bioclimate, topography, vegetation, distance to anthropogenic features, and natural characteristics. To achieve this, we employed maximum entropy (MaxEnt) modeling (Elith et al., 2006; Phillips et al., 2006) and applied a hierarchical modeling approach (Phillips et al., 2006; Kati et al., 2009; Poirazidis et al., 2011, 2019). This approach involved identifying the fundamental bioclimatic requirements of each species in the first step, followed by refining the species' niche using the remaining environmental dimensions (Poirazidis et al., 2019). Subsequently, we used the developed models to create habitat suitability maps for the Cheetah's prey species across the study area, identified areas of conservation concern, and derived management recommendations.

Data collection for the species was performed systematically within the Turan Biosphere Reserve (TBR) by establishing 30 transects (Fig. 1). The location of these transects was selected based on maximizing the distance between them while ensuring accessibility through field roads and tracks, considering the limitations imposed by the study area. While the transects covered the entire accessible area of TBR, the mostly inaccessible southern region, consisting mainly of unsuitable salt pans, remained uncovered (Fig. 1). Each transect had a standardized length of 16 km and was surveyed eight times over two consecutive years, representing each season (spring, summer, autumn, winter), starting from summer 2012 until spring 2014. Transects were divided into 1 km intervals, with at least one stop made in each interval for careful observation of the target species. The collected observations were recorded and assigned to the respective transect intervals, providing information on herd size, distance of the animals to the transects, and their precise locations.

2.3. Bioclimatic and environmental dataset

We compiled information on 44 variables representing bioclimate, topography, vegetation, and distance to anthropogenic and natural features (ESM-Table 1). Nineteen bioclimatic variables were derived from the WorldClim dataset (Hijmans et al., 2005), with a spatial resolution of 30 seconds (approx. 1 km) (Graham and Hijmans, 2006). Elevation data (Digital Elevation Model; DEM) with a spatial resolution of 30 m were downloaded from NASA (2009). Aspect and slope were derived from the DEM, with aspect then converted to eastness and northness units ranging from −1 to +1. A value of 0 represents flat terrain, while +1 denotes east and northward aspects (Zar, 1999). For vegetation characterization, datasets for five vegetation indices at a spatial resolution of 30 m were acquired from Landsat 8 on August 29, 2014 (Normalized Difference Vegetation Index - NDVI, Enhanced Vegetation Index - EVI, Optimized Soil Adjusted Vegetation Index - OSAVI, Normalized Burn Ratio - NBR, Modified Triangular Vegetation Index - MTVI, and Transformed Difference Vegetation Index - TDVI). Additionally, we used a thematic vegetation map consisting of 55 different types of vegetation and datasets of anthropogenic and natural features such as roads, corrals, wells, and streams, which were digitally available in the management plan of TBR (Semnan DoE, 2017). We considered a movement pattern scale of 1000 m for Cheetah and its prey species and re-estimated all topographic and vegetation variables using Neighborhood statistics to calculate the mean value within a circle with a radius of 1000 m (while maintaining a grain size of 30 m). Furthermore, employing an inverse weighted distance approach, we downscaled the bioclimatic variables to a spatial resolution of 30 m, matching that of the topographic and vegetation variables. For the distance variables, Euclidean distances to the closest feature were calculated for all cells of the 30 m raster (cf. Table 1, ESM-Table 1).

2.4. Analysis of bioclimatic niches

To model the bioclimatic niches of the species, we first reduced the set of 19 bioclimatic variables. Three variables were excluded because of their low variance in the area, leaving us with 16 variables. We checked these remaining variables for multicollinearity using the "vifstep" function of the "usdm" package in R environment (Naimi, 2014). Based on a step-wise procedure, we finally selected a set of six bioclimatic variables (BIO 4, BIO 8, BIO 9, BIO 15, BIO18, and BIO 19, Table 1) with VIF<10 (Hair et al., 2009).

Using the "MaxentVariableSelection" package in the R environment (Jueterbock, 2015), we identified the best set of relevant variables. Initially, we defined the most parsimonious models based on two criteria: the variables had to contribute more than 2% to the variance explained by the model, and their Pearson's correlation coefficient with any other variable had to be less than 0.7. With the resulting set of variables, we evaluated different Maxent models by using four regularization numbers ranging from 0.5 to 2 with steps of 0.5 (Elith et al., 2011). The model with the highest performance was selected based on the Akaike Information Criterion (AICc) (Burnham and Anderson, 2002). We ran MaxEnt with the best set of predictor variables selected through this procedure and computed ten replicates to average the results using the cross-validation method (He et al., 2022). The study area was represented by 10,000 random points with random seeds, which were used as background to comprehensively sample and represent the region of interest (Valavi et al., 2022). 70% of the records were randomly selected for the training set, and the remaining 30% were used as the independent set for model evaluation using the subsampling method.

To evaluate the performance of the individual models, we used the Area Under the Curve (AUC) of the Receiver Operating Characteristics Curve (ROC) (Elith et al., 2006; Phillips et al., 2006; Hernández et al., 2006). AUC values range from 0 to 1 (Fielding and Bell, 1997), with values equal to or below 0.5 indicating models performing no better than random. Model performance is rated as invalid between 0.5 and 0.6, poor between 0.6 and 0.7, average between 0.7 and 0.8, good between 0.8 and 0.9, and excellent between 0.9 and 1.0 (Araújo et al., 2005). We employed a leaving-one-out jack-knife method to determine relative importance of each variable (on a 100% scale) and generate response curves illustrating the variable's impact on the habitat suitability of each species (Phillips et al., 2006; Elith et al., 2011; Warren and Seifert, 2011).

Maps extracted from both the bioclimatic and environmental final models provided probability of occurrence estimates for each species (Phillips et al., 2006; Elith et al., 2011; Warren and Seifert, 2011). The logistic output format, ranging from 0 (lowest suitability) to 1 (highest suitability), was employed as it is simpler and potentially more accurately interpretable than other approaches (Phillips and Dudik, 2008; Baldwin, 2009). To convert continuous suitability into a binary classification of suitable and unsuitable habitat, a threshold needs to be set (Baldwin, 2009). Several approaches exist for setting threshold values. In this study, we employed the Minimum Training Presence and the Fixed Cumulative Value 1 (FC1) thresholds, selecting the lower threshold for each species (Pearson et al., 2007; Guevara et al., 2018). This approach maintains areas with marginal bioclimatic suitability as parts of the

Table 1
Summary statistics (mean, standard deviation, maximum, minimum) of the selected bioclimatic (n=6), topographic (n=5), vegetation (n=3), and distance (n=4) variables. Refer to ESM-Table 1 for the complete set of 44 variables, which includes those excluded to reduce multicolinearity as described in the text.

Variable names	Units	Scale	Mean	SD	Max	Min
Bioclimatic variables (n = 6 selected from 19)						
BIO4 = Temperature Seasonality (standard deviation ×100)	*Degrees Celsius X 100*	Downscaled to 30 m	8588.2	139.9	9096.2	8296.4
BIO8 = Mean Temperature of Wettest Quarter	*Degrees Celsius X 10*	Downscaled to 30 m	123.7	13.3	166.9	83.2
BIO9 = Mean Temperature of Driest Quarter	*Degrees Celsius X 10*	Downscaled to 30 m	274.3	14.9	304	206.6
BIO15 = Precipitation Seasonality (Coefficient of Variation)	*Percent*	Downscaled to 30 m	72.5	3.5	84.5	60.6
BIO18 = Precipitation of Warmest Quarter	*Millimeters*	Downscaled to 30 m	5.5	1.6	10.5	0.9
BIO19 = Precipitation of Coldest Quarter	*Millimeters*	Downscaled to 30 m	56.4	5.4	71.2	40.8
Topographical variables (n = 5 selected from 9)						
Elevation	m	30 m	933.6	236.7	2434	633
Eastness	scale (-1 to +1)	30 m	-0.004	0.7	1	-1
Northness	scale (-1 to +1)	30 m	-0.04	0.7	1	-1
Roughness (degree of irregularity of the surface)		30 m	15	42.4	4351.6	0
IMI (integrated moisture index)		30 m	91.5	8.3	1492.6	30
Vegetation variables (n = 3 selected from 7)						
EVI - Enhanced Vegetation Index	scale (-1 to +1)	30 m	0.07	0.02	0.99	0
NBR- Normalized Burn Ratio	scale (-1 to +1)	30 m	0.02	0.09	0.79	-0.36
MTVI - Modified Triangular Vegetation Index	scale (-1 to +1)	30 m	-0.005	0.008	0.71	-0.26
Distance variables (n = 5 selected from 9)						
Distance to farmland	km	30 m	25,752	14.441	69.096	0
Distance to corrals	km	30 m	12.821	9.605	50.779	0
Distance to well	km	30 m	27.709	18.217	86.303	0
Distance to streams	km	30 m	3.367	4.072	22.878	0
Road density	km	30 m	3.368	4.073	22.878	0

fundamental niche and preserves these areas for subsequent analytical steps.

2.5. Analyses of environmental niches

After fitting the bioclimatic niches, we refined the models with additional environmental variables, thereby elucidating the specific habitats most suitable for the target species. For this purpose, we used the corresponding bioclimatic suitable area of each species as mask for fitting its respective environmental model. Then, we selected 13 out of 25 variables based on a multicollinearity assessment (see above; Table 1, ESM-Table 1). Using the MaxentVariableSelection package within the R environment, we then employed the same two selection criteria mentioned above to determine the best environmental predictors for each prey species based on the AICc. Subsequently, we executed MaxEnt models with 10 replicates, cross-validating for each prey species, and averaging the results. The resulting MaxEnt models were then reclassified into four classes (unsuitable, marginal, suitable, and optimal) for each species using three thresholds: Minimum Training Presence, Fixed Cumulative Value 5 (FC5), and Fixed Cumulative Value 10 (FC10). These threshold values assume a minimum omission rate, a maximum omission rate of 5%, and a maximum omission rate of 10% respectively (refer to ESM-Table 2).

2.6. Overall habitat suitability for Cheetah prey species

We created an additional overall suitability map for Cheetah prey species with six categories (0–5), depending on the presence of the five prey species within suitable habitat zones. For this purpose, each species map was reclassified into binary values: 0 representing unsuitable and marginal classes, and 1 representing suitable and optimal classes. Next, we generated an aggregated map representing combined habitat suitability, where categories are ranked from 0 (unsuitable/marginal for all species) to 5 (suitable/optimal for all species). In between, each category represents an area suitable for a progressively increasing number of the studied species.

3. Results

Results revealed that Urial and Goitered Gazelle were the most frequently observed species, with a total of 675 Urials and 564 Goitered Gazelles recorded over the course of eight seasons. The maximum numbers recorded across all transects in a single season were 117 sightings of Urial in autumn 2013 and 133 Goitered Gazelles in winter 2012/13 (see Table 2).

3.1. Bioclimatic models

Of the five bioclimatic models assessed, four displayed a high level of efficacy, ranging from 'good' to 'excellent' with AUC values between 0.84 and 0.91 for test data (Wild Goat: 0.87; Urial: 0.84; Goitered Gazelle: 0.90; Jebeer Gazelle: 0.91). The only exception was the Cape Hare, which exhibited an 'average' model with an AUC value of 0.74. The number of predictor variables in the best bioclimatic models varied: two for Wild Goat, three for Urial, Goitered Gazelle, and Cape Hare, and four for Jebeer Gazelle. While these models encompassed predictor variables related to temperature and precipitation, it was evident that the most influential variable determining the distribution of all species was the mean temperature of the driest quarter (summer in TBR). This single variable accounted for contributions of 72.9%, 73.5%, 44.7%, 39.8%, and 91.4% for Wild Goat, Urial, Goitered Gazelle, Jebeer Gazelle, and Cape Hare, respectively (see Table 3).

The significance of the primary bioclimatic variables in shaping the species' climate niche is further supported by the response curves (Fig. 2). Generally, areas with low to average mean summer temperatures and pronounced temperature seasonality were found to be most suitable for Wild Goat. Similarly, Urial favored regions with cool mean summer temperatures, along with low winter precipitation and average precipitation seasonality. Goitered Gazelle displayed preferences for areas with average mean summer temperatures, temperature seasonality, and summer precipitation. The sharp peaks in the response curves indicate the species' narrow bioclimatic tolerances. Jebeer Gazelle also exhibited sharp response curve peaks, indicating a preference for areas with average levels

Table 2
Number of individual prey detected by visual observations along the 30 transects of 16 km each in the eight consecutive studied seasons, and the overall maximum, sum and mean number of individuals detected across all eight seasons.

Species	Season								Overall maximum	Sum across 8 seasons	Mean per season
	Summer		Autumn		Winter		Spring				
	2012	2013	2012	2013	2012/13	2013/14	2013	2014			
Wild Goat	46	42	4	40	32	13	27	4	46	208	26,0
Urial	97	93	64	117	98	49	52	105	117	675	84,4
Goitered Gazelle	41	58	58	63	133	113	40	58	133	564	70,5
Jebeer Gazelle	39	29	37	35	23	21	20	28	39	232	29,0
Cape Hare	19	36	38	41	42	23	52	27	52	278	34,8

Table 3

The percent contribution and percent permutation importance of bioclimatic variables to the distribution models of the five studied species. The most important variable determining prey species distributions is bold.

Species	Variables	Full name of variables	Contribution (%)	Permutation importance (%)
Wild Goat	**BIO9**	Mean Temperature of Driest Quarter	**72.9**	**76.1**
	BIO4	Temperature Seasonality	27.1	23.9
Urial	**BIO9**	Mean Temperature of Driest Quarter	**73.5**	**71.1**
	BIO19	Precipitation of Coldest Quarter	18.2	16.7
	BIO15	Precipitation Seasonality	8.2	12.2
Goitered Gazelle	**BIO9**	Mean Temperature of Driest Quarter	**44.7**	**51.5**
	BIO4	Temperature Seasonality	41.1	39.1
	BIO18	Precipitation of Warmest Quarter	14.3	9.4
Jebeer Gazelle	**BIO9**	Mean Temperature of Driest Quarter	**39.8**	**56.5**
	BIO8	Mean Temperature of Wettest Quarter	35	18.5
	BIO19	Precipitation of Coldest Quarter	21.5	24
	BIO4	Temperature Seasonality	3.6	1.1
Cape Hare	**BIO9**	Mean Temperature of Driest Quarter	**95.1**	**91.4**
	BIO18	Precipitation of Warmest Quarter	3.4	5.4
	BIO8	Mean Temperature of Wettest Quarter	1.5	3.2

Note: Contribution measures the total gain of the model by including a particular variable, while permutation importance measures the contribution of each variable to the model.

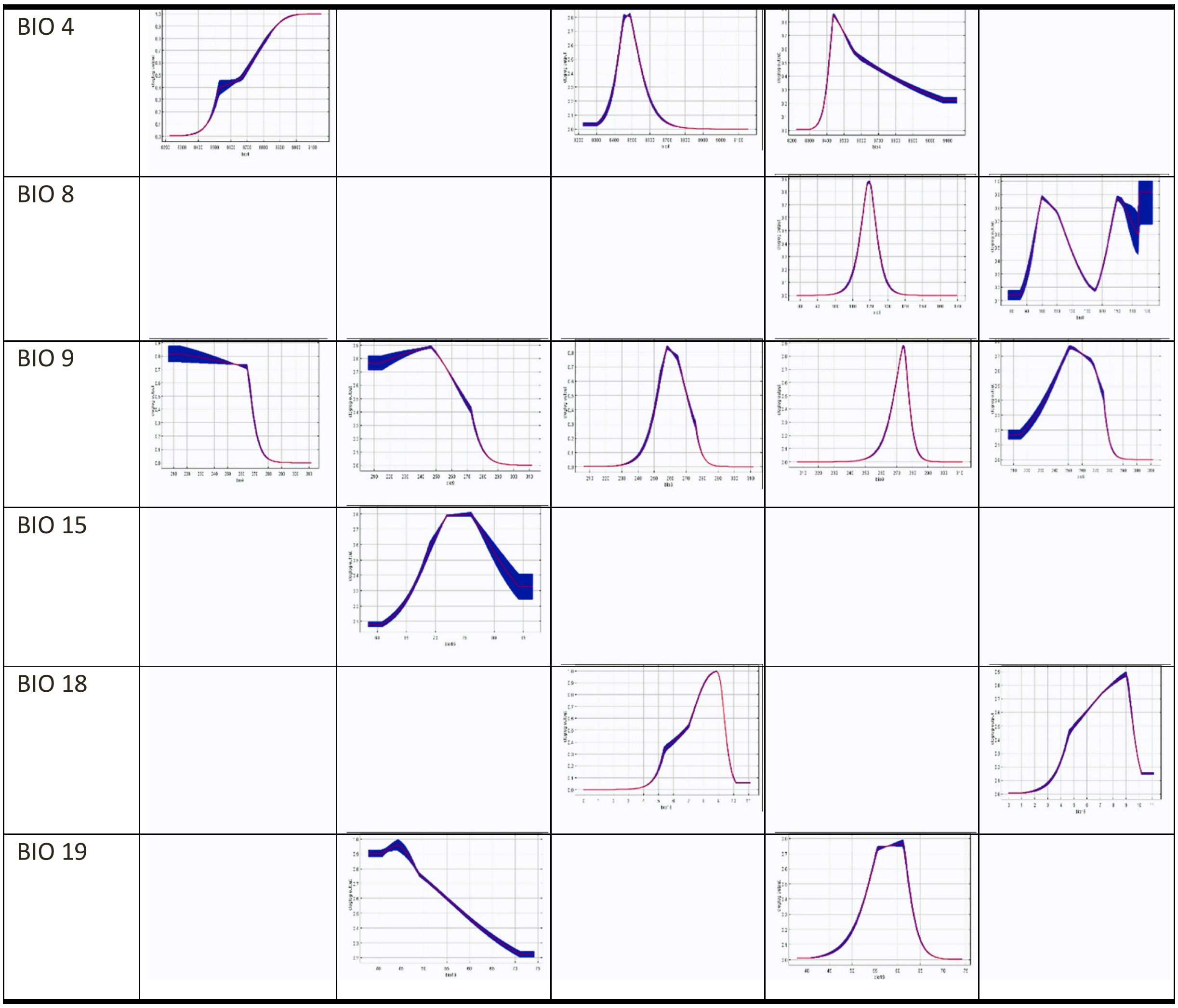


Fig. 2. Response curves for the most important common bioclimatic variables developed for the five Cheetah prey species in Turan Biosphere Reserve. Blue areas describe the range of values, while red lines indicate the average value.

of mean summer temperature, mean temperature of the wettest quarter (spring in TBR), winter precipitation, and temperature seasonality. In contrast, the Cape Hare showed a preference for average summer temperatures, while its presence was also associated, to a lesser extent, with summer precipitation and mean spring temperature (Fig. 2).

Projecting the bioclimatic models across the study area revealed that a minimum of 50% of TBR is bioclimatically suitable for the five prey species. The suitable area was largest for Urial and Cape Hare (74%, 70% respectively), and smallest for Jebeer and Goitered Gazelle (59%, 58% respectively) (Fig. 4).

3.2. Environmental models

Of the five environmental models assessed, four displayed a high level of efficacy, ranging from ’good’ to ’excellent’ with AUC values between 0.83 and 0.94 for test data (Wild goat: 0.94; Urial: 0.85; Goitered Gazelle: 0.83; Jebeer Gazelle 0.90). The only exception was Cape Hare which exhibited an ‘average’ model of an AUC value of 0.73. The number of predictor variables in the best environmental models was four for Urial and Wild Goat, six for Goitered Gazelle and Cape Hare, and eight for Jebeer Gazelle. The models contained predictor variables of all three classes, i.e. vegetation, topography and distance to anthropogenic and natural features (Table 4).

Wild goat preferred high levels and tolerated even extremely high values of relief roughness. Moreover, the species required high levels of the Enhanced Vegetation Index. Also Urial preferred areas with a pronounced terrain relief and occurred mainly in elevations of 1200–2200 m. Goitered Gazelle was most likely to be observed in close vicinity of wells, far from corrals, at low to intermediate road densities (bell-shaped relation) and on northern slopes. The highest probability of presence for Jebeer Gazelle, most important was vicinity to corrals, large distance to farmlands, and intermediate elevation of about 800–1100 m. The Cape Hare strongly preferred areas in close vicinity to wells and streams, elevations of 800–1600 m, and intermediate values of road density (Fig. 3).

Projecting the environmental models across the study area showed that at least 50% of TBR are suitable for the five prey species, with Cape Hare demonstrating the largest potential range, with 46% falling into the categories of ’optimal’ and ’suitable’. This was followed by the Urial and Goitered Gazelle, both accounting for 29%. The suitable habitat of Jebeer Gazelle covered 22%, while the one of Wild Goat made up 17% (Fig. 4, ESM-Fig. 1).

In terms of habitat suitability, the western and eastern mountainous regions, along with their hilly surroundings, as well as the northwest and western plains, were identified as the most suitable areas for all five species (Fig. 4). However, for the Wild Goat specifically, only small patches of the mountainous and rocky regions in the eastern and southeastern TBR were found to be environmentally suitable. The suitable habitats for the Urial exhibited a similar geographical distribution, but were larger in size compared to those of the Wild Goat. In the case of the Goitered Gazelle, there was a substantial overlap between environmentally and climatically suitable sites, with the northern and western plains, and to a lesser extent, parts of the central plains, being deemed the most suitable.

Table 4

Contribution and permutation importance of environmental variables to the distribution models of the five studied species.

Species	Variables	Contribution (%)	Permutation importance (%)
Wild Goat	**Roughness**	**74.1**	**84.9**
	EVI	13.6	13.3
	Eastness	7.3	1
	Distance to farmland	5	0.9
Urial	**Roughness**	**80.4**	**75.9**
	Elevation	9.7	14
	The integrated moisture index (IMI)	5.2	6.9
	Distance to corral	4.7	3.2
Goitered Gazelle	**Distance to well**	**25.7**	**24.5**
	Distance to corral	23.9	24.3
	Road density	21.6	16.9
	Northness	15.2	17.1
	Eastness	7.5	13.9
	Roughness	6.2	3.2
Jebeer Gazelle	**Distance to corral**	**30**	**27.8**
	Distance to farmland	21.9	21.8
	Elevation	18.9	6.5
	Distance to well	9.3	23.3
	Eastness	7.3	11
	Road density	7.3	7
	Northness	3.2	2.2
	Roughness	2	0.2
Cape Hare	**Distance to well**	**50**	**30.5**
	Northness	15.3	18.5
	Elevation	11.8	17.3
	Road density	10.2	9.3
	Roughness	6.4	13.9
	Distance to river	6.2	10.5

Note: Contribution measures the total gain of the model by including a particular variable and permutation importance measures the contribution of each variable to the model.

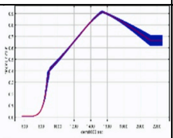
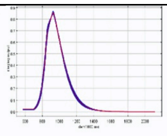
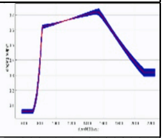
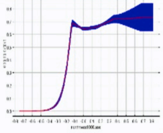
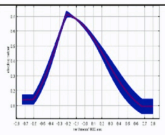
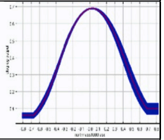
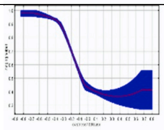
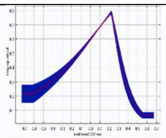
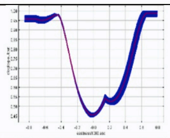
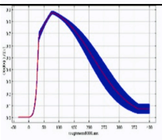
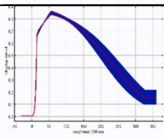
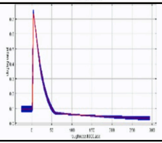
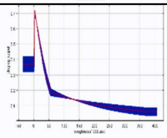
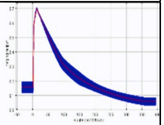
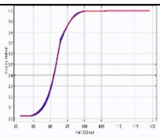
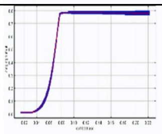
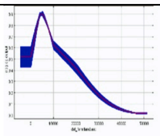
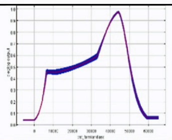
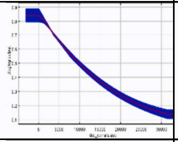
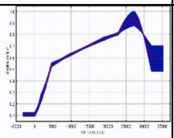
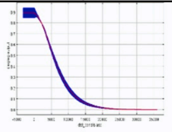
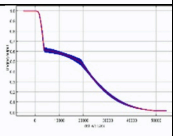
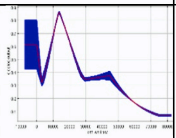
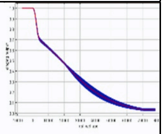
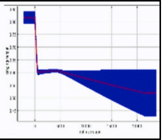
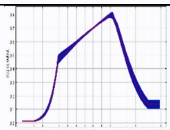
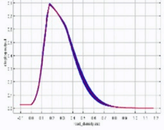
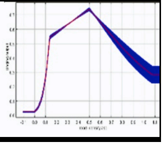
Species	Wild goat	Urial	Goitered gazelle	Jebeer gazelle	Cape hare
Elevation					
Northness					
Eastness					
Roughness					
IMI (integrated moisture index)					
EVI - Enhanced Vegetation Index					
Distance to farmland					
Distance to corrals					
Distance to well					
Distance to river					
Road density					

Fig. 3. Response curves for the most important environmental variables developed for the five cheetah prey species in Turan Biosphere Reserve. Blue areas describe the range of values, red lines the average value.

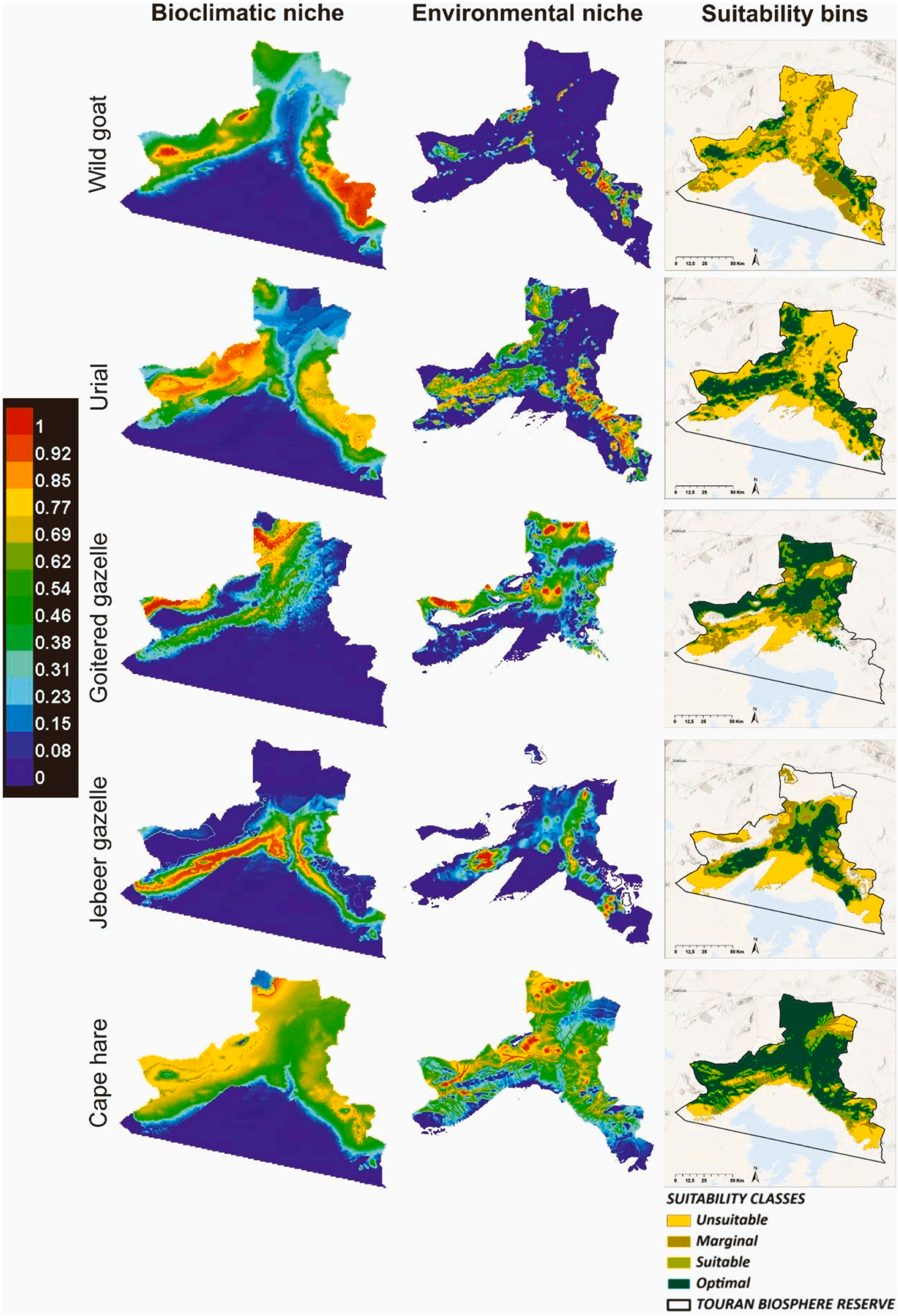


Fig. 4. Overview depicting the bioclimatic niches (left panels), environmental niches (middle panels), and overall habitat suitability in four bins (right panels) for the five prey species of Cheetah.

On the other hand, the Jebeer Gazelle demonstrated high levels of environmental suitability only in small patches of the hilly areas between the mountains and the southern plains, where climatic conditions were also favorable. Lastly, the Cape Hare exhibited larger variations in environmental suitability across the TBR compared to climatic suitability, with several highly suitable areas scattered throughout the northern, central, and western parts (Fig. 4).

3.3. Overall habitat suitability for Cheetah prey species

The map of combined habitat suitability for all five prey species showed that 0.5% of TBR were suitable for all five species, further 5% for four, further 21% for three and further 22% for two species (Fig. 5).

4. Discussion

4.1. Wild Goat

For the Wild Goat, large parts of the mountainous and hilly areas in TBR are climatically suitable. However, only small patches of these areas (17% of TBR) provide a suitable environment for the species. The primary climatic limitation for the species are extremely

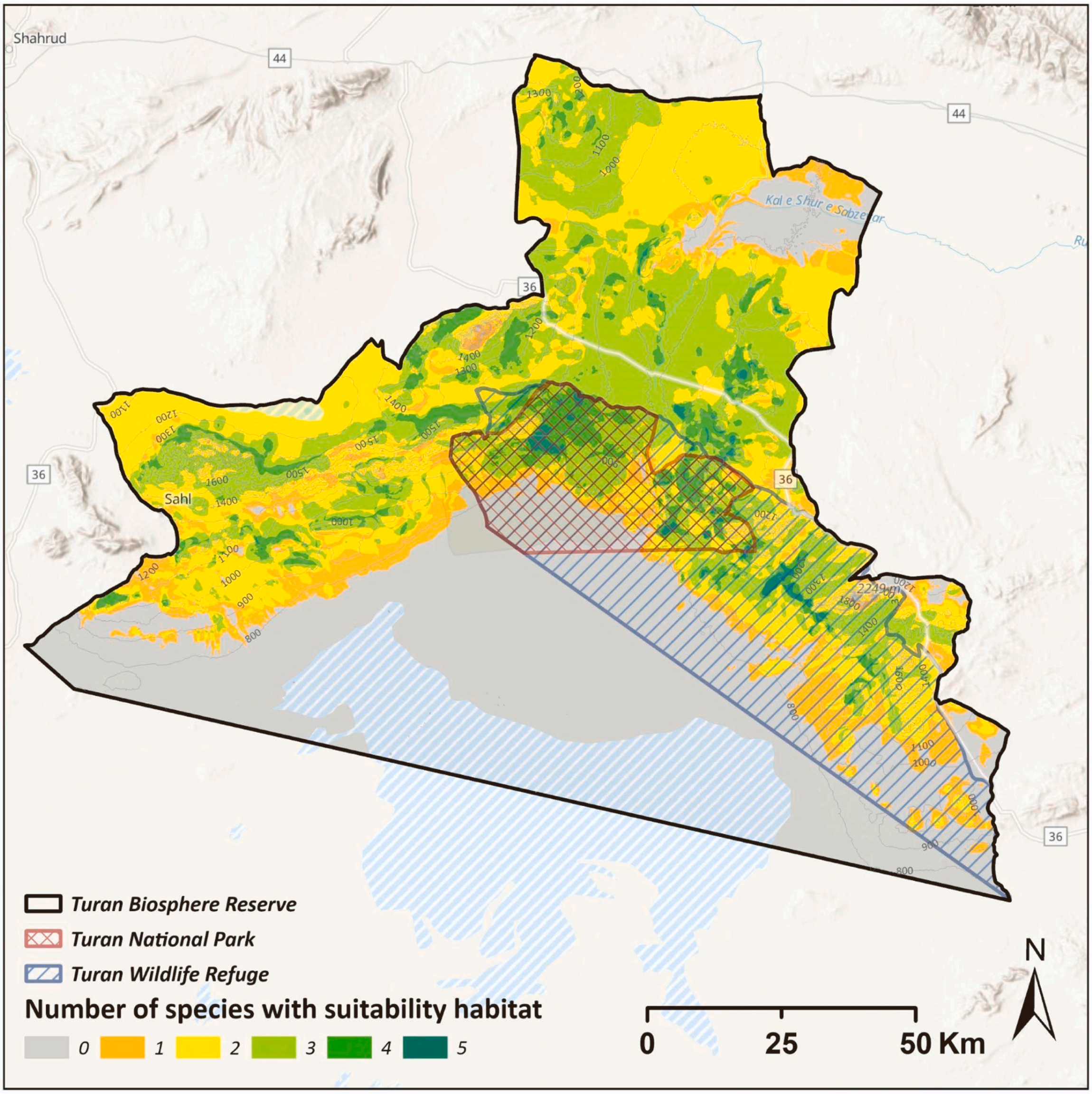


Fig. 5. Overall habitat suitability in TBR for five Cheetah prey species.

high summer temperatures. In terms of environmental constraints, the species does not inhabit flat or vegetation-scarce areas. These findings align with previous studies that have reported a positive correlation between Wild Goat and relief roughness or ruggedness (Madadi et al., 2018; Hosseini et al., 2019) as well as rocky substrates (Esfandabad et al., 2010).

Furthermore, Wild Goat tends to favor habitats with specific vegetation types, such as steppes containing *Artemisia aucheri*, *Astragalus* spp., or *Amygdalus scoparia* (Sarhangzadeh et al., 2013). Currently, the climatically and environmentally suitable mountain habitats for Wild Goats in TBR are surrounded by vast plains at considerable distances. Consequently, Wild Goat populations already face significant habitat fragmentation. With the projected impact of climate change, the eastern mountainous regions of TBR are expected to become less climatically suitable for the species. This could potentially reduce both the available habitat and increase fragmentation levels among the remaining patches. These concerns are particularly troubling as TBR is considered a crucial stronghold for Wild Goat within Iran (Malakoutikhah et al., 2020).

4.2. Urial

In terms of Urial distribution, large portions of the mountainous and hilly areas in the western TBR exhibit suitable climatic conditions. However, environmental constraints limit the extent of suitable habitat to only 29% of the TBR. It is intriguing to note that the western mountainous regions offer higher quality habitat for the Urial from a climatic perspective. Conversely, the eastern mountainous region proves to be the most suitable in terms of environmental variables. The species is primarily limited by climatic extremes, specifically hot summer temperatures and high levels of winter precipitation, within its range. In addition, the distribution of Urial at a local scale is mainly confined to mountainous and hilly areas (Valdez et al., 1998; Safiyan-Boldaji, 2003; Wockner et al., 2003; Bleich et al., 2009; Bashari and Hemami, 2013).

A recent study conducted by Malakoutikhah et al. (2020) analyzed the distribution of Wild Sheep species in Central Iran. Their findings suggest that significant range reductions are expected until 2070 due to climate change. However, they also highlight that the largest stable habitats are located in the northern and northwestern regions, including the TBR. In fact, the TBR has been identified as one of the most crucial areas for the future distribution of the Urial in Iran, particularly its western part, which aligns with our analysis of the most suitable climatic conditions.

4.3. Goitered Gazelle

For the Goitered Gazelle, 29% of the TBR, with a strong focus on the northern and western plains, were found to be suitable in terms of bioclimatic and environmental conditions. The species shows a preference for intermediate climates characterized by moderate temperature, precipitation, and seasonality. The highest probabilities of presence were associated with proximity to wells, significant distance from corrals, and low to intermediate road density. These findings align with a study conducted in Central Iran, which demonstrated that the distribution of the Goitered Gazelle is influenced by temperature seasonality and the climate of the coldest quarter, considered as the most important variable (Khosravi et al., 2016).

Malakoutikhah et al. (2020) estimated that under the current climatic conditions, 19% of Central Iran is suitable habitat for the Goitered Gazelle, including the western and northwestern parts of the TBR. Although the species is projected to lose 60% of its habitats by 2070, the TBR has been identified as one of the most stable habitats in the central region of Iran. It is known that Goitered Gazelles prefer habitats in close proximity to water sources (Hosseini et al., 2016), while actively avoiding areas with human presence, such as corrals, farms, mines, and roads (Hosseini et al., 2016; Ansari, 2017; Hassanvand et al., 2018; Esfandabad et al., 2019). The species also benefits from hilly terrain and light topographic conditions, which provide suitable escape terrain (Farhadinia et al., 2009; Bagherirad et al., 2014). In the Miandasht Wildlife Refuge, located approximately 75 km from the TBR, Goitered Gazelles were observed to prefer grazing in flat plains with accessible escape terrain (Farhadinia et al., 2009). However, in the TBR, it appears that due to the presence of artificial water resources, reduced levels of persecution facilitated by warden stations, and supplemental feeding, the species has primarily the vast northwestern plains, hilly areas, and western plains as its main habitat.

4.4. Jebeer Gazelle

For the Jebeer Gazelle, the central areas and two strips following the foothills towards the southwest and southeast are identified as the most suitable in terms of bioclimatic conditions. In the environmental model, these areas (approximately 22% of the TBR) are also deemed suitable. Climatically, the species displays a preference for an intermediate climate characterized by moderate spring and summer temperatures and winter precipitation. The highest probabilities of presence are associated with low distances to corrals and wells, high distances from farmland, low road density, and intermediate elevation.

Ebrahimi et al. (2019) reported that the most crucial climatic variable determining the presence of the Jebeer Gazelle in Iran is annual precipitation. The species is known to inhabit arid to semi-arid habitats (Groves, 1993) and hyper-arid environments with an annual precipitation ranging between 50 and 250 mm (Akbari et al., 2014). Jebeer Gazelles typically reside in plains but occasionally show a preference for hills and foothills (Akbari et al., 2013; Sarhangzadeh and Akbari, 2019; Morovati et al., 2019). However, this species has also been found in dry scrubland and light forest (Kumar et al., 2020). Interestingly, in the TBR, Jebeer Gazelles exhibited a preference for habitat adjacent to corrals, a pattern that has not been observed in other studies. During particularly dry years, it is likely that Jebeer Gazelles roam around corrals in search of food resources and residual forage from livestock. Moreover, many of these corrals are located in the preferred hillside habitats of Jebeer Gazelles, leading to competition between the gazelles and the livestock. Similar interference between preferred habitat of Jebeer Gazelles and farming has also been reported in the Thar Desert in India

(Dookia, 2009). In addition, most corrals remain unoccupied during the hottest six months of the year. The seasonal effect of corrals on the presence of Jebeer Gazelles and Cheetahs is particularly relevant in northeastern Iran (Farhadinia et al., 2012). In contrast to previous research conducted in Iranian protected areas such as Naybandan Wildlife Refuge, Dare Anjir Wildlife Refuge, and Kavir National Park (Akbari et al., 2013; Sarhangzadeh and Akbari, 2019), which indicated that Jebeer Gazelles preferred habitats near water sources, our study reveals a different pattern. We found that the most suitable habitat for this species in the TBR is actually located far from wells. This unexpected result can potentially be attributed to the higher predation pressure exerted by Cheetahs near wells, as they tend to target Jebeer Gazelles as their primary prey choice (Farhadinia and Hemami, 2010; Zahedian and Nezami, 2019). In addition, Jebeer Gazelles have demonstrated their ability to obtain sufficient water from plants, which might also contribute to their preference for habitats that are further away from water sources. (Akbari et al., 2014).

4.5. *Cape Hare*

As for the Cape Hare, suitable habitats (covering approximately 46% of the TBR) are scattered across large areas in the north, west, east, and central TBR. The highest probabilities of presence are associated with mean summer temperatures ranging from 24 to 27°C. Cape Hares are generally distributed over a wide geographic range in Africa, Asia, and southern Europe (Palacios et al., 2008). Within this range, they inhabit various bioclimatic regions and environmental conditions. In Iran, they reside in most ecosystems of the country, including forests, mountains, deserts, and steppes (Etemad, 1985; Ziaie, 2008). They display adaptability to highly variable climatic and environmental conditions. In the TBR, higher densities of Cape Hare are associated with proximity to wells and streams, altitudes ranging from 800 to 1600 m, and average road density. Given the dry conditions, it is not surprising that Cape Hares prefer areas close to water sources (Ziaie, 2008) to ensure sufficient water, food, and thermal shelter. The presence of Cape Hare close to roads is likely related to seasonal vegetation growth near the roads.

4.6. *Overall prey suitability*

Like the suitable and optimal habitat for individual prey species, the overall map of prey suitability shows that a significant portion of the TBR is suitable for these species, with 48% of available area being suitable for at least two different species and 27% for at least three different species. Suitable habitat areas for three or more prey species are congruent with the distribution of water resources, game warden stations, hand fodder distribution areas, and corrals, indicating the favorable subzones: hilly areas, mainly located at an altitude of 1200–2200 m a.s.l., offering vegetation for livestock grazing in autumn and winter and the first half of spring.

4.7. *Conclusions and conservation recommendations*

In this study, we used a comprehensive field dataset to establish habitat suitability models for the five primary prey species of the Asiatic Cheetah and finally created an overall habitat suitability map of prey species within a central region of the Cheetah's remaining range. Our models indicate that the suitable areas for the prey species in TBR are fragmented, particularly for the Wild Goat and Jebeer Gazelle. Previous studies have confirmed seasonal or vertical movement patterns for the Wild Goat (Esfandabad et al., 2010; Sarhangzadeh et al., 2013), Wild Sheep (Kermani et al., 2020), Goitered Gazelle (Fadakar et al., 2020; Askerove et al., 2021), and Jebeer Gazelle (Torabian et al., 2021).

However, suitable habitat for at least three of the five prey species occurs in a continuum across TBR, which is promising for cheetah conservation given the importance of preserving the most suitable prey species in order to maintain predator populations (cf. Hayward et al., 2007). Therefore, the results of our study can serve as a foundation for conservation management efforts to establish migration corridors both within and outside of TBR, potentially by expanding the existing protected area network. This approach would likely enhance the suitability of TBR and its surrounding areas for the Asiatic Cheetah, which is known to require a vast home range (Ahmadi et al., 2017; Durant et al., 2017) that aligns with the habitats of its prey species (Zahedian and Nezami, 2019). It is possible that recent losses and fragmentation of Cheetah habitat (Durant et al., 2017; Farhadinia et al., 2017) could be halted or even reversed through such conservation measures.

Preserving the mountain habitats in the west and east, as well as the plain areas in the northwest, center, west, and east of the TBR, is paramount for safeguarding cheetah habitats. Consequently, cheetahs are compelled to extensively traverse different areas within the study area to secure necessary food resources. The presence of local road networks, enclosures, and other infrastructure practically impedes this movement, leading to risks such as accidents and hunting.

Considering the impact of roads on habitats suitable for several prey species, especially Goitered Gazelle, it is crucial to integrate this aspect into conservation management plans. This is particularly relevant due to the occurrence of road kills as a mortality factor in Cheetah habitats in Iran and the negative effect of roads on habitat connectivity (Nezami, 2018).

The proximity of suitable habitats containing three or more prey species to springs and corrals underscores their strong reliance on these resources, which also signify the vulnerability of the cheetah and its prey species to environmental changes, particularly climate change and drought. Conservation management strategies for prey species, particularly Goitered Gazelle, Jebeer Gazelles, and Cape hare, should therefore consider the locations of corrals, farmland, roads, and wells. In addition to restricting livestock grazing and preventing poaching in the short term, a comprehensive plan should be developed to relocate corrals away from areas that are highly suitable for these species and to increase public awareness about the Cheetah and its prey species.

Much suitable habitat for three or more species is outside the borders of the wildlife refuge and Turan National Park. Redrawing the boundaries of these areas, especially expanding the size of Turan National Park and applying strong protection strategies could assist in better protection of TBR.

CRediT authorship contribution statement

Stefan Dullinger: Conceptualization, Methodology, Supervision, Writing – review & editing. **Stefan Schindler:** Writing – review & editing, Writing – original draft, Validation, Supervision, Conceptualization, Data curation, Formal analysis, Investigation. **Parvin Safiyan-Boldaji:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Kostas Poirazidis:** Conceptualization, Formal analysis, Investigation, Methodology, Software, Validation, Writing – original draft, Writing – review & editing. **Mahmoud-Reza Hemami:** Conceptualization, Supervision, Writing – review & editing. **Dietmar Moser:** Conceptualization, Supervision, Writing – review & editing. **Christoph Plutzar:** Conceptualization, Methodology.

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.

Acknowledgments

We are grateful for the technical support of the Department of Environment of Iran. Our special thank goes to the game guards and local people who were a great help in surveying the species distribution in the Turan Biosphere Reserve.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02937.

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