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Research Article

Availability of prey and natural habitats are related with temporal dynamics in range and habitat suitability for Asiatic Cheetah

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Abstract

Understanding how species have been affected by recent human mediated landscape transformation is crucial for designing effective conservation strategies. The Critically Endangered Asiatic cheetah (*Acinonyx jubatus venaticus*) has faced a dramatic range decline and currently occurs in very small populations restricted to the mountain deserts of Central Iran. In this study, we aim to quantify temporal changes in ecological requirements and availability of suitable areas for the Asiatic cheetah. Ecological models for historical and contemporary time-periods were built based on historical and contemporary species records and using a set of 11 ecogeographical variables including climate, anthromes and prey availability of each time-period, using maximum entropy modelling. Distance to the prey *Gazella bennettii* was the most important factor related to the occurrence of cheetahs in historical time period, while in contemporary times it was replaced by the climatic factor maximum temperature of the warmest month. Predicted areas of high suitability occur within the borders of Iran. When compared, suitability decreased 72% from historical to contemporary periods causing the current loss of suitability in some protected areas. Our results suggest that the fundamental niche of Asiatic cheetahs has not changed but the realized niche has changed over time. When environmental correlates of species distribution for each time period are analysed in detail, changes in realized niche are likely related to depletion of cheetah's main prey, temperature variation and landscape transformation of its habitats. Conservation measures should start urgently to improve protection for gazelle species (prey) and wildlands (habitat), especially in temperate areas, to ensure the survival of the last Asiatic cheetahs. Further research on cheetah's interaction with other predators and preys, and gene flow dynamics between populations would also benefit its long term conservation.

Introduction

Global biodiversity is threatened by overexploitation, and human-mediated climate and landscape changes (Travis, 2013; Butchart et al., 2010), especially by the expansion of agriculture and grazing (Ceballos and Ehrlich, 2002; Di Marco and Santini, 2015). Major habitat changes occurred during the last century, resulting in the formation of present anthropogenic biomes or anthromes (Ellis et al., 2010). Such changes can impact biodiversity and mammals in particular have been reported as vulnerable to them (Turvey and Fritz, 2011).

Understanding temporal changes in the availability of suitable habitats is critical for the conservation of large carnivores (Carroll et al., 2003). Given their usually large home-range sizes and low population densities, carnivores are deeply affected by habitat change (Breitenmoser, 1998; Crooks et al., 2011; Ripple et al., 2014) and frequently forced to shift distributions to suboptimal habitats when disturbed (Ordeñana et al., 2010). Knowledge on habitat selection patterns throughout time is of particular importance for large carnivores that have been declining during the last century. Such knowledge may reinforce conservation strategies of currently small and endangered populations (Woodroffe, 2000).

The Cheetah (*Acinonyx jubatus Schreber*, 1775) is a large carnivore that was deeply affected by habitat changes induced by human activities over the past century. Habitat transformation and fragmentation, illegal hunting, and reduction in prey availability have caused local population extinction across Africa and Asia and dramatically reduced its distribution (Marker and Dickman, 2004; Durant et al., 2014, 2015). In Asia, the Asiatic cheetah ranged from Sinai to India but presently is restricted to the arid parts of Iran (Nowel and Jackson, 1996; Jowkar et al., 2008). Habitat loss and degradation, poaching, capture of wild adults for game hunting, pastoralism competition, and importantly prey depletion have affected cheetah in Iran (Asadi, 1997; Durant et al., 2015). These threats have increased in the last 30 years, especially prey loss and habitat degradation (Ziaie, 2008). The present population persists in the central mountain deserts (Jowkar, 1999) and has reached critically low levels, population size was estimated to be less than 120 individuals in 2008 (CACP, 2008) and currently it has been estimated to be less than 50 individuals (Khalatbari et al., 2017). As such, the Asiatic cheetah is among the most globally threatened felids, being listed

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as "Critically Endangered", included in Appendix I of CITES (Jowkar et al., 2008).

Habitat requirements of cheetahs in time and space make them vulnerable to land use changes that can shift habitat suitability and threaten cheetah's survival (Ray et al., 2005; Muntifering et al., 2006; Ahmadi et al., 2017). Preliminary relationships between cheetah occurrence and abiotic factors in Africa identified slope, temperature, precipitation and land cover type as playing important roles in cheetah distribution (Broekhuis, 2007; Pettorelli et al., 2009), while topographic features, water supplies and habitat type have been related with the species distribution in Iran (Firouz, 1999; Jowkar, 1999; Ziaie, 2008; Sarhangzadeh et al., 2015; Ahmadi et al., 2017). Thus, the conversion of semi-natural habitats and wild lands into croplands and rangelands that occurred in Iran since the 1900s (Tab. S1; quantified from Ellis et al., 2010) is probably related to cheetah decline. Additionally, prey availability plays an important role in felid's (Trainor et al., 2014; Sandom et al., 2017a,b) as well as cheetahs' distributions (Durant et al., 1988; Broomhall et al., 2003; Bissett and Bernard, 2007). Predominant prey items of cheetahs in Asia were gazelles and antelope (Divyabhanusinh, 1984; Mallon, 2007); particularly in Iran, cheetahs' main prey is Goitered Gazelle (*Gazella subgutturosa*) and Indian Gazelle (*Gazella bennettii*) (Lay, 1967; Firouz, 1999). Other ungulates such as *Ovis orientalis* and *Capra aegragus* have been referred as sub-optimal prey (Asadi, 1997; Ziaie, 2008), although important locally (Nazeri et al., 2015). Both gazelles species were abundant along their past range, but habitat transformation and hunting activities have dramatically reduced their population size and distribution during last 30 years (Mallon, 2008a,b) to the point that currently they are mostly restricted to protected areas (Yusefi et al., 2006; Ziaie, 2008). Severe decline of Asiatic cheetah population has been reported to be the consequence of this decline of gazelle's population (Karami, 1992; Nowel and Jackson, 1996; Asadi, 1997; Firouz, 1999; Mallon, 2007). There is little quantitative information about environmental factors affecting cheetah populations in Iran (Sarhangzadeh et al., 2015; Ahmadi et al., 2017) and no information on how human landscape modifications and prey availability reduction affected its range decline. In Iran, the cheetah has been considered as a legally protected species since 1959 (Firouz, 1976), however the percentage of suitable protected habitats for the species has not been quantified. Such data are basal while designing measures for cheetah conservation (Hannah et al., 2005; Preston et al., 2008).

In this study, we aim to identify distributional range drivers and suitable habitats for the Asiatic cheetah in Iran, as well as changes they have faced in the available suitable spaces throughout the last century. For these purposes, we relate species distribution with human mediated habitat changes (anthromes), topographic and climate variables and prey availability in two timeframe periods, historical (1900s) and contemporary (2000s), and projected the historical models to the contemporary environmental conditions in order to answer the following questions: 1) which environmental factors are mostly related to the distribution of cheetahs in historical and contemporary times? 2) Which are the suitable areas for species occurrence in historical and contemporary times? 3) How has the extension of suitable areas for the species changed over time? 4) What percentage of the contemporary suitable habitats is covered by the current network of Iranian protected areas? Given the documented range decline of cheetahs, the identification of distributional range drivers in each time period is crucial to understand how human activities are related with the species range and to support the implementation of local conservation options for Asiatic cheetahs.

Methods

Study area

The study area is located in Southwest Asia, including Iran and parts of the neighbouring countries (Fig. 1), following the currently known distribution of the species (Jowkar et al., 2008). Limits were based on a buffer of 200 km around the observation points to include a larger environmental variability in the ecological models (see below) and to infer potential suitable areas for the species outside of known presence areas.

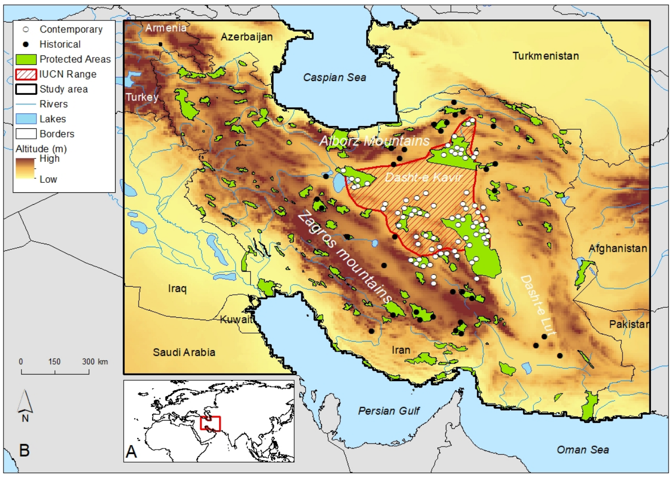

Figure 1 – (A) Location of the study area in south-west Asia; (B) Study area, protected areas, the IUCN distribution range of the Asiatic cheetah and distribution of the observation points in the historical (black dots) and contemporary (white dots) times.

Species observations

A total of 519 observations from the period 1966–2015 were collected from: a) field guides (Harrington and Darehshuri, 1977; Ziaie, 2008); b) published references (Firouz, 1999; Darvish Sefat, 2006; Karami et al., 2015); c) unpublished observations of live specimens, of specimens found dead, and of specimens observed by camera-trap photos in protected areas between 2001 and 2009 by the Conservation of the Asiatic Cheetah Project of Iran (CACP) and local offices of the Department of Environment of Iran (DoE); and d) ad-hoc observations of specimens made by game guards. Given the documented range decline of Asiatic cheetahs in the last decades (Asadi, 1997; Firouz, 1999; Ziaie, 2008), observations were divided into two time periods: historical dataset (N=519, all observations) accounting for the historical range and a subset of these data (N=463) depicting the contemporary range. The contemporary range was estimated using the locations where there was an observation in the past 25 years (i.e. 1991–2015; 70% of observations since 2000). The historical range was estimated using the locations where there were references to cheetah occurrence in the past period and that recent surveys did not find any records or species signs (Cheraghi et al., 2006; Ghodousi et al., 2006; Yusefi et al., 2006), as well as the contemporary dataset to account for spatial biases of sampling in historical times (Martínez-Freiría et al., 2016). Therefore, the dataset to infer the historical range spans from 1966 to 2015, comprising the contemporary dataset.

Both datasets, particularly the historical one, were obtained from an uneven sampling scheme and thus, they could bias ecological models (Merow et al., 2013; Yackulic et al., 2013). Also, in the contemporary dataset some observations were collected in protected areas which were frequently patrolled and subject of field surveys. Therefore, we tried to minimize the impacts of sampling biases in the development of ecological models: 1) in the contemporary dataset we used observational data collected during fieldwork campaigns specifically designed to detect the species, which were representative of the location of extant cheetah populations throughout Iran (Fig. S2); and 2) in both datasets, observations were spatially rarefied taking into account the distance among them (5 classes; from 20 to 70 km) and the topographic heterogeneity of the study area as proxy for its environmental variability (see Merow et al., 2013). We used the SDMtoolbox 2.0 (Brown et al., 2017) for ArcMap 10.1 for this purpose. The final datasets included 78 and 112 observations for the historical and the contemporary times, respectively (see Fig. 1).

Environmental factors

Based on the available knowledge about species' ecology and distribution (Nowel and Jackson, 1996; Marker et al., 2003; Broekhuis, 2007; Pettorelli et al., 2009), 11 ecogeographical variables (hereafter EGV)

Table 1 – Environmental factors used for modelling the habitat suitability of the cheetah, depicting units and range of variables in historical (<1990) and contemporary (>1990) periods. Distances present the Euclidean distances for each grid cell to the closest habitat type or prey availability source.

EGV	Units	Historical	Contemporary
Annual Precipitation	mm	49–744	44–731
Max Temperature of Warmest Month	°C	22.5–45.65	23.5–46.5
Slope	degrees	0.0–6.6	0.0–6.6
Distance to Dense Settlements	degrees	0.0–6.307	0.0–3.605
Distance to Villages	degrees	0.0–5.203	0.0–3.005
Distance to Croplands	degrees	0.0–4.859	0.0–2.926
Distance to Rangelands	degrees	0.0–2.730	0.0–1.850
Distance to Seminatural	degrees	0.0–2.090	0.0–3.254
Distance to Wildlands	degrees	0.0–2.899	0.0–5.765
Distance to *G. bennettii*	degrees	0.0–11.101	0.0–11.305
Distance to *G. subgutturosa*	degrees	0.0–3.500	0.0–6.692

that are likely to influence the cheetah's distribution were selected for ecological modelling (Tab. 1). These included: 1) two climatic variables, annual precipitation and maximum temperature of the warmest month for each time-period. To account for probable climate changes occurring in our study area during our species observational records periods, we created two bioclimatic datasets: the historical (1966–1990) and the contemporary (1991–2015) following Martínez-Freiría et al. (2016). The monthly climate data for the period 1966–2015 (CRU TS4.00; Harris et al., 2014) was downloaded from the Climatic Research Unit portal (http://www.cru.uea.ac.uk/). The monthly data represents 10 year periods with 0.5 arc-degrees of spatial resolution. We further averaged the data to the periods of interest (1966–1990 and 1991–2015) and downscaled to 0.0833 degrees of resolution. The spatial downscaling was performed for each bioclimatic dataset using a thin-plate spline interpolation with altitude as covariable, similar to other global climate data (Hijmans et al., 2005). This process was performed in R with packages `fields` and `rgdal`. Two bioclimatic variables for each period were constructed with the averaged and downscaled monthly data using the `dismo` package on R software (R Core Team, 2015); 2) one topographical factor, slope, derived from altitude variable (USGS, 2006) using the Slope function from ArcGIS; 3) two prey availability variables, consisting of Euclidean distances to historical and contemporary ranges of main prey of cheetahs in Iran, *G. bennettii* and *G. subgutturosa*. In order to reduce the number of variables and thus, reduce models complexity (Radosavljevic and Anderson, 2014), we decided to use a set of biologically relevant variables potentially affecting cheetah's range reduction, therefore among all potential prey items we selected those whose distribution range in the last century has reduced significantly (Mallon, 2008a,b). Historical ranges for both prey species were adapted from IUCN species range distribution polygons, whereas contemporary ranges consists of all localities where confirmed observations of gazelle's presence were recorded during last 25 years (Darvish Sefat, 2006; Karami et al., 2015; Bureau of the Habitat and Protected Areas, unpublished Data); and 4) two sets of Euclidean distances to six anthrome levels derived from 19 anthrome classes of the 1900s and 2000s periods (Ellis et al., 2010; Tab. S1). Distance variables were shown to be valuable in ecological modelling exercises (Brito et al., 2009; Vale et al., 2016). Finally, in order to account for ecological needs of cheetahs (e.g. home range varies from 150 to 195 km^2, Broomhall et al., 2003), grid cell size of all EGVs used to perform ecological models was changed to 0.0833 degrees ($\approx$10 km) using the mean value of neighbouring pixels.

Ecological niche-based models

The nature of our observations (i.e. coming from different sources) and the biological characteristics of the cheetah (i.e. large home ranges and low detection probability; Broomhall et al., 2003; Marker et al., 2008; Andresen et al., 2014) precluded the use of ecological models based on presence/absence data. For these reasons, ecological models were developed using the Maximum Entropy approach on the presence-only software Maxent 3.3 (Phillips et al., 2006). This modelling technique was reported to have high performance in many ecological modelling studies (Elith et al., 2006; Hernandez et al., 2006) and for specialist species, such as cheetah (Richmond et al., 2010). Two models were developed for each time period: historical (1966–1990) and contemporary (1991–2015) using associated variables from the corresponding time period, excepting slope, which was the same for the two models.

We were aware of major assumptions and requirements of Maxent to obtain reliable ecological models (see Royle et al., 2012; Merow et al., 2013; Merow and Silander, 2014) and thus, (1) we followed a test-calibration process of Maxent parameters before running the final models, addressing models complexity (i.e. feature types and regularization value; see Vale et al., 2016) and retaining parameters (see below) with the highest performances (i.e. based on AUC values; see Warren and Seifert, 2011); and (2) we selected models output in raw format, as it expresses relative occurrence rate (ROR) which is independent of the prevalence (parameter unknown for the Asiatic cheetah). Models were built for the historical (hereafter Historical) and contemporary (hereafter Contemporary) time periods, and the historical model was projected to contemporary time (hereafter Projection) to predict currently available suitable habitats. The final models for each period included a total of 50 model replicates run with random seed and a different random 70% training / 30% testing data partition in each run. Observations for each replicate were chosen by bootstrap, allowing sampling with replacement. Models were run with linear, quadratic and product features with regularization multiplier of 1, as these parameters showed the highest performance. Area Under the Curve (AUC) of the Receiver Operating Characteristics (ROC) plot was taken as measure of models fitness (Fielding and Bell, 1997).

The weight of each EGV for describing the species distribution was determined by its average percentage's contribution to the models. The relation between occurrence of cheetahs and EGVs was determined by the visual examination of response curves profiles from univariate models (Phillips et al., 2006) and the average gain was assessed with training and test data using a jackknife analysis. EGVs were excluded one at a time to create different models with the remaining variables. Then, several univariate models were created using each individual variable, and in addition a model was created using all variables (Torres et al., 2010).

To convert models of continuous presence probability to binary predictions (i.e. absence/presence squares) we followed Guillera-Arroita et al. (2015), selecting values between 10^{th} and 90^{th} percentiles of the ROR distribution as presence squares. In the GIS, binary Historical and Projection were compared to quantify the temporal dynamics of available suitable areas, while binary Projection and Contemporary were compared to quantify potential changes in the realized niche. Finally, binary models and projection were intersected with the current network of protected areas of Iran (Bureau of the Habitat and Protected Areas, 2016) to quantify percentages of the protected suitable areas in both time periods. Kappa statistic was used to compare suitability maps between different time periods (Visser and de Nijs, 2006).

Results

Overall the quality of historical and contemporary models was acceptable and evaluated as fitted with low standard deviations for training and testing datasets (Tab. 2).

Environmental factors related to species occurrence

In the historical model, the most important environmental factors related to cheetah distribution were two prey related-variables (distance to *G. bennettii* and distance to *G. subgutturosa*), one anthrome (distance to croplands), and one topographic (slope); distance to *G. bennettii* was the most important factor (Tab. 2). In the contemporary model, maximum temperature of the warmest month became the most important factor and distance to *G. bennettii* became the second most important factor followed by one anthrome (distance to wildlands). The importance of maximum temperature of the warmest month and distance to dense settlements increased from historical to contemporary models (Tab. 2). Jackknife analyses suggested that distances to *G. bennettii*

Table 2 – Number of training and test samples, and average and standard deviation of training and test AUC, AUC standard deviation, and percentage of contribution of each variable for the contemporary and projection models.

	Historical	Contemporary
N Training - Test	78–33	112–48
Training AUC (±SD)	0.970 ± 0.004	0.920 ± 0.006
Test AUC (±SD)	0.964 ± 0.009	0.905 ± 0.015
AUC Standard Deviation	0.008	0.014
% contribution (±SD)		
Annual Precipitation	3.493 ± 1.247	1.917 ± 0.927
Max Temperature of Warmest Month	6.978 ± 2.145	36.040 ± 3.328
Slope	7.448 ± 2.543	5.879 ± 1.697
Distance to:		
Dense Settlements	1.428 ± 1.023	6.046 ± 2.498
Villages	2.474 ± 0.955	2.558 ± 0.921
Croplands	10.000 ± 2.160	2.477 ± 1.238
Rangelands	2.151 ± 1.021	6.115 ± 2.875
Seminatural	1.086 ± 1.117	1.780 ± 1.110
Wildlands	6.145 ± 2.170	9.725 ± 2.294
G. bennettii	50.240 ± 4.272	25.690 ± 2.078
G. subgutturosa	8.550 ± 2.263	1.770 ± 0.574

and to wildlands were the two most important variables in both models (Fig. S3).

Response curve profiles for the most important variables in both historical and contemporary models showed that cheetahs are highly dependent to availability of their two main prey species, especially to *G. bennettii* (Fig. 2). Availability of both prey species decreased from Historical to Contemporary, as can be noticed in response curve profiles (Fig. 2A, 2B), as well as in the range of these variables for both time periods (Tab. 1). Ranges delimited by temperature for Historical and Contemporary were slightly different: areas between 27 °C to 45.5 °C were selected in the historical period, but in the contemporary one it slightly shifted to warmer areas with 29 °C to 46.5 °C (Fig. 2E). Regarding anthromes, cheetahs selected wildlands and areas close to them in both historical and contemporary periods. Response curve profiles are similar (Fig.2C), but availability of wildlands has decreased over time (Tab. 1). They apparently selected areas close to croplands but keeping a certain distance from them.

Although Cheetahs select areas far from croplands in historical times (Fig.2D), this variable lost importance in contemporary times (Tab. 1).

Predicted occurrence

Suitable areas for the cheetah in both models were mostly identified within the borders of Iran and these areas were predicted as larger in extension for the historical model in comparison to the contemporary model and more fragmented for the projection model in comparison to contemporary model (see Fig. S4). Kappa statistics indicated poor spatial agreement in the predictions of suitable areas when comparing historical and projected models (k=0.296) and projected and contemporary models (k=0.386). The binary historical model predicted 36.6% of the study area as suitable for the species, including 100% of total observations for this period. This area covers the central plateau of Iran (excluding mountains, Hyrcanian forests and hot and humid northern shores of Persian Gulf and Oman Sea) and some areas in neighbouring countries of Turkmenistan, Afghanistan, and Pakistan (Fig. 3). The contemporary model predicted an extremely smaller area compared to the historical model as suitable area for species (13% of the study area), including 94% of total observations for this period. This area is mostly continuous, except in south of Touran national park and protected area, and in some other patchy areas located close to Afghanistan border, from Sistan region to Hormozgan, and in the north shores of Persian Gulf. Areas predicted by projection model were more fragmented than contemporary model covering 10% of the study area, including 52% of total observations for this period. Predicted areas included three fragmented habitats separated by harsh deserts and salty plains (Fig. 3).

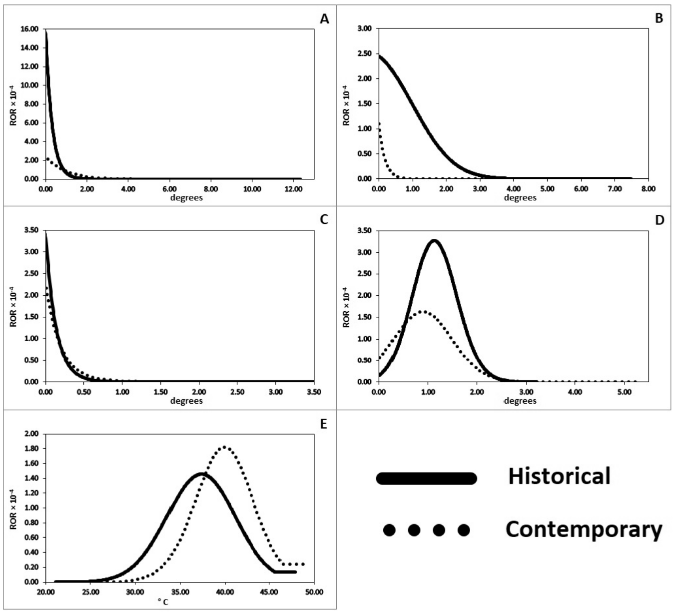

Figure 2 – Response curves for the most related environmental factors to the historical and contemporary distribution of the Asiatic cheetah (see Tab/ 2 for details). Curves depict average relative occurrence rate (ROR) from 50 model replicates. A. Distance to *G. bennettii*, B. Distance to *G. subgutturosa*, C. Distance to wildlands, D. Distance to croplands and E. Maximum temperature of the warmest month.

Predicted suitable areas within the study area have decreased 72% from Historical to Projection and 22% from Contemporary to Projection (Fig. 3). Reductions from Historical to Projection occurred in most of the historical suitable habitats, in the east, south and centre of the country. These reductions produced the division of suitable habitats into three patches (Fig. 3). Reduction from Contemporary to Projection is mainly evident in the core areas. About 16%, 23% and 24% of the suitable predicted habitats were located inside protected areas, respectively, by the Historical, Contemporary and Projection. When comparing Historical model and its projection, 3864 pixels were identified as permanently suitable, 10956 pixels lost their suitability, and 258 pixels gained suitability. Comparing the Projection and Contemporary, 2148 pixels were identified as permanently suitable, 1974 as underestimated suitable habitats (suitable pixels in the Projection that are classified as unsuitable in Contemporary), and 3140 as overestimated suitable habitats (unsuitable pixels in the Projection that are classified as suitable in the Contemporary).

Discussion

By using ecological modelling, this study identified and quantified environmental factors related to the Asiatic cheetah distribution, inferring potential suitable areas for its occurrence in Iran and adjacent territories. The development of this study in two time frame periods allowed estimating potential range shifts during the last century. Importantly, inferences which might have implications for future research, as well as for conservation and management of cheetahs in Iran, can be retrieved from this study.

Temporal changes in ecogeographical correlates

Our results agree with previous knowledge on ecological requirements of African and Asian populations of cheetahs (Durant et al., 1988; Jowkar, 1999; Broomhall et al., 2003; Broekhuis, 2007; Pettorelli et al., 2009; Sarhangzadeh et al., 2015; Ahmadi et al., 2017), as they recognize similar sets of variables (e.g. prey availability and wildlands) affecting their distribution. However, our study found distinct weights in environmental correlates of species distribution for each time period, suggesting that fundamental niche of Asiatic cheetahs has not changed, but the realized niche changed due to decline in prey availability and loss of wildlands over time. This shift could be interpreted by cheetahs

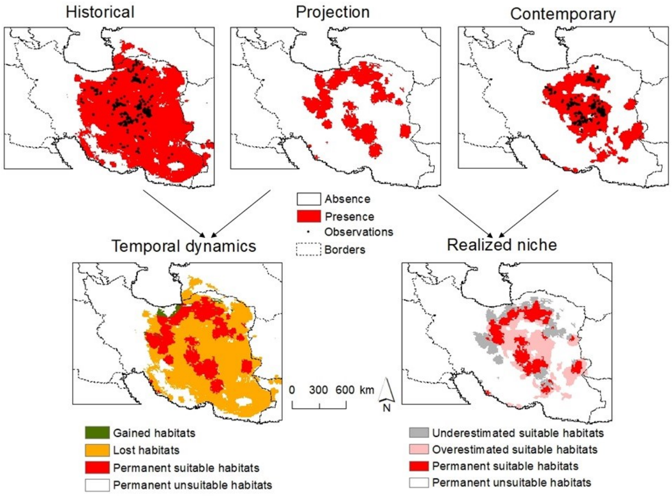

Figure 3 – Historical, contemporary and projection of suitable habitats and dynamics of habitat suitability from historical to contemporary time periods for the Asiatic cheetah.

using suboptimal habitats that are warmer and dryer in the contemporary period (Fig. 2).

Two gazelle species, *G. bennettii* and *G. subgutturosa*, were considered predominant prey for cheetahs in south-western Asia (Lay, 1967; Nowel and Jackson, 1996; Firouz, 1976; Mallon, 2007). Their severe population decline and range regression (Mallon, 2008a,b) has been suggested as the main factor affecting cheetahs' historical reduction in Asia (Lay, 1967; Firouz, 1999; Mallon, 2007). Similarly, our results suggest that cheetahs were historically mainly dependent on occurrence of *G. bennettii* (Tab. 2) and the profiles of the response curves of both gazelles are similar in contemporary period which reveal similar trends of cheetah occurrence rate with increasing distances to prey availability (Fig.2). Major increase in occupation of preferred habitats by humans or livestock (Tab. S1; quantified from Ellis et al., 2010) has probably forced cheetahs to use suboptimal habitats to avoid human disturbance (Pettorelli et al., 2009) following their prey (Andresen et al., 2014).

Campaigns to improve habitats (e.g. protecting *Artemisia* vegetation; Khosravi et al., 2016) and protect coexisting species to gazelles (e.g. *Equus hemionus onager*; Nazeri et al., 2015), as well as protection and re-introduction programmes of remaining populations of both gazelles (Khosravi et al., 2017) should be conducted to favour the viability of current cheetah populations and to allow re-colonization of former suitable areas by cheetahs (Khalatbari et al., 2017). Rehabilitation of cheetahs' main prey is also important because lack of gazelles might push cheetahs to search for suboptimal prey, such as wild sheep (*Ovis orientalis*), wild goat (*Capra aegagrus*), and hares (Yusefi et al., 2006; Ziaie, 2008; Farhadinia and Hemami, 2010), or even livestock (Hunter et al., 2007; Farhadinia et al., 2012). The later may increase local conflicts with humans (CACP, 2008), and ultimately impact cheetahs negatively. There is urgent need in increasing public awareness, especially for shepherds and livestock owners via educational programs and other management measures dedicated to avoid non-natural causes of cheetah death.

In the contemporary time, a climate factor (maximum temperature of the warmest month) became the most important variable influencing cheetah's distribution. According to response curves, cheetahs prefer warm habitats, avoiding very hot deserts. However, comparison of response curves for both time periods suggests that they are now forced to select areas with higher temperature. Climate change is predicted to happen at faster velocities in flat, desert areas (Loarie et al., 2009), thus it is probable that cheetahs will lose further parts of their habitat in the near future. Increasing conservation efforts to recover rangelands and prey population in temperate suitable areas could be considered as a solution to provide suitable habitats for cheetah in the future in anticipation of an in increasing aridity in current cheetah habitats (Khalatbari et al., 2017).

The historical model predicted that cheetahs have preference for being close to wildlands and avoiding dense human settlements, such preferences have increased from historical to contemporary periods while decrease in availability of wildlands in contemporary time has forced cheetahs to contract their ranges and to live closer to humans. Consequently, road mortality is likely to increase (Yusefi, 2004) From a total of 29 cheetahs found killed in the last 16 years, 13 were roadkills (CACP, 2010 and CACP unpublished records), an important figure when the total population size in Iran was estimated to be less than 50 individuals (Khalatbari et al., 2017). Putative corridors between subpopulations have been identified (Moqanaki and Cushman, 2016; Mohammadi and Kaboli, 2016; Khosravi et al., 2018). The establishment of wildlife crossing in the areas where roads are intersecting these corridors should be considered. These potential connections should be evaluated with molecular markers following a landscape genetics approach to predict functional connectivity and prioritize putative corridors.

Taken together, our results suggest that the ecological preferences of cheetahs remained stable from historical to contemporary periods while the availability of areas with environmental traits selected by cheetahs have changed.

Temporal changes in habitat suitability

Our binary models predicted different extensions of suitable areas for cheetahs in Iran and a reduction of 72.19% in suitable area from Historical to Projection. These reductions occurred in most of the former predicted distribution, and possible causes for such reductions can be grouped in three factors: 1) reductions of prey availability, mostly in the east and south and 2) increasing temperature in the harsh deserts of Dasht-e Kavir and Dasht-e Lut and 3) increasing human population and wildland loss, affecting marginal areas in the foothills of eastern Zagros and of southern, eastern and north-eastern Alborz. One of the lost marginal areas in the east and northeast of Alborz foothills was known to be used as a corridor between populations of Iran and Turkmenistan (Misonne, 1959). Management actions for recovering these habitats should be developed as a way to recover suitable habitats which are acting as stepping stone for the species (Ahmadi et al., 2017).

In both models the predicted suitable areas were more widespread than the area covered by observational data probably due to low cheetah density (Marker et al., 2008). Increase in the percentage of observations located outside of predicted suitable areas emphasizes that cheetahs are now occupying more suboptimal habitats.

Changes in realized niche

There were grid cells classified as suitable in the projected model and as unsuitable in the contemporary model, and vice-versa. These spatial disagreements were taken as an indication of model overestimation or underestimation, respectively. Underestimation indicates areas predicted by Projection as suitable but field surveys do not confirm species presence. In theory, these may correspond to habitats that could be occupied by cheetahs in future if the population size and range expands. However, current conditions do not allow the species to occupy them, probably intense human activities and/or competition with other large carnivores (Durant, 2000; Rostro-García et al., 2015). Overestimation indicates areas where the species is currently known to be present but Projection failed to identify them as suitable. Such disagreement may be related to key variables related to the ecological niche of species missing from the ecological modelling exercises. Most likely, refuge availability or predation on other prey items should be included in future developments of this work (Broomhall et al., 2003; Pettorelli et al., 2009).

Coverage by protected areas

From a total of 272 areas classified as "under protection" (10.8% of the country), 14 areas were dedicated to cheetah conservation. Given the contraction of suitable habitats through time, increase in the percentage of suitable habitats covered by protected areas, suggests that suitable habitats are becoming more restricted to protected areas. However, given that protection of cheetahs should not be limited to protected areas (Durant et al., 2017) maximizing conservation efforts for improving the situation of the cheetah in Iran should be tackled by developing monitoring and management programs, as well as habitat and prey restoration initiatives inside and outside of the protected areas (i.e. effective control of livestock grazing and limiting number of their guarding dogs).

Conclusions and future research

The Asiatic cheetah has lost almost all of its range in Asia. With known small populations remaining only in Iran, it is now on the verge of extinction. Our study has revealed new insights into the ecological requirements, suitable areas and conservation needs of the Asiatic cheetah. Still there are knowledge gaps on relevant biological and ecological aspects of the species for designing effective conservation and management plans. These include studies on: 1) probable species occurrence in areas predicted by ecological models as suitable but unconfirmed by field research; 2) prey-predator relationships, including geographical variation in prey preferences and modelling other potential preys; 3) interspecific competition with other large carnivores, such as leopard (*Panthera pardus*), hyena (*Hyaena hyaena*) and wolf (*Canis lupus*), that are usually sympatric to cheetah but ecological interactions are poorly understood (Hunter et al., 2007); 4) vulnerability to global warming (e.g. Fordham et al., 2013); and 5) spatial connectivity and gene flow among populations, by using molecular markers and landscape analyses at fine scales. Conservation actions to protect remaining individuals and to recover prey population (Khalatbari et al., 2017) should start immediately to ensure the survival of the last Asiatic cheetahs.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Anthrome levels and changes in the percentage of coverage by each level from 1900 to 2000 in the study area.

Figure S2 Distribution of surveyed area for detecting species presence.

Figure S3 Jackknife results of environmental factors used in the historical and contemporary models.

Figure S4 Average and standard deviation for probability of occurrence of the Asiatic cheetah in historical, contemporary and projection models.