DOI: 10.1111/ddi.12560

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Combining landscape suitability and habitat connectivity to conserve the last surviving population of cheetah in Asia

Mohsen Ahmadi[1] | Bagher Nezami Balouchi[2,3] | Houman Jowkar[3] | Mahmoud-Reza Hemami[1] | Davoud Fadakar[1] | Shima Malakouti-Khah[1] | Stéphane Ostrowski[4]

[1]Department of Natural Resources, Isfahan University of Technology, Isfahan, Iran

[2]Department of Natural Resources and Environment Sciences, University of Environment, Karaj, Iran

[3]Conservation of Asiatic Cheetah Project (CACP), I.R. Iran Department of Environment, Teheran, Iran

[4]Wildlife Conservation Society (WCS), Bronx, NY, USA

Correspondence
Mohsen Ahmadi, Department of Natural Resources, Isfahan University of Technology, Isfahan, Iran.
Email: m.ahmadi@na.iut.ac.ir

Funding information
DoE of the Islamic Republic of Iran; Global Environmental Facilities (GEF); United Nations Development Program (UNDP); Wildlife Conservation Society (WCS)

Editor: Piero Visconti

Abstract

Aim: The Asiatic cheetah, *Acinonyx jubatus venaticus*, a critically endangered large felid, has disappeared from vast tracks of its historical range across south-western Asia. It is currently confined to the arid ecosystems of central Iran for which little is known about its distribution and habitat linkages. We proposed the first evaluation of Asiatic cheetah's distribution and developed models of landscape suitability and connectivity to inform future conservation planning.

Location: Central Iran.

Methods: We analysed presence data of a 14-year-long cheetah monitoring programme according to environmental and anthropogenic factors, and generated an ensemble model of habitat suitability based on seven species distribution models (SDMs). We then used the concept of circuit theory and landscape connectivity prioritization (LCP) on resultant core habitats and landscape suitability to evaluate potential linkages between core areas.

Results: Core habitats, that is, the areas hosting the largest continuous suitable habitats for Asiatic cheetahs, covered approximately 49,144 km^2 (*c.* 6.3% of the study area). Availability of prey species, avoidance of human-dominated areas and their infrastructures, and rough landscapes covered with sparse vegetation were the most predictive factors of the core habitats for the last cheetah population in Asia. Although relatively vast, the area of potential core habitats available to cheetahs appeared to be fragmented with limited connectivity between the northern and southern parts of this distribution.

Main conclusions: Our approach highlights the importance of distribution models to recognize, at a coarse-scale level, a spatial population structure and habitat suitability characteristics for a large carnivore surviving at very low density. We have identified specific areas of suitable habitat where developing new landscape protection and adaptive conservation management; and improving the safety of important linkages between core habitats are likely to promote the conservation of the last surviving population of cheetah in Asia.

KEYWORDS
arid environment, cheetah conservation planning, circuit theory, ensemble model, Iran, species distribution model

1 | INTRODUCTION

Apex predators play a fundamental role in many ecosystems as keystone species and are also important flagship species for conservation (Ford et al., 2014; Ripple et al., 2014), but they are among the most controversial and challenging groups of species to be conserved in the face of human development in modern world (Chapron et al., 2014). While conservation of large carnivores seems an effective strategy for protecting habitat necessary for their prey and associated species (Kunkel, Atwood, Ruth, Pletscher, & Hornocker, 2013; Sergio et al., 2008), large carnivores management strategies and their conservation implications face many challenges. For example, it is difficult to dedicate to them spatially extensive heterogeneous landscapes to fulfil their broad ecological requirements and range-wide home ranges (Chapron et al., 2014; Ripple et al., 2014; Santini, Boitani, Maiorano, & Rondinini, 2016). In many cases, they require action on a scale that is seldom seen in terrestrial conservation, including coordinated trans-boundary initiatives (Farhadinia et al., 2015; Rabinowitz & Zeller, 2010). Also identifying and preserving connectivity among large carnivore's heterogeneous habitats appears crucial for the maintenance of functional ecological linkages, and vital to their long-term survival (Crooks, Burdett, Theobald, Rondinini, & Boitani, 2011; Dickson, Roemer, McRae, & Rundall, 2013; Santini, Saura, & Rondinini, 2016).

The Asiatic cheetah (*Acinonyx jubatus venaticus*; Griffith, 1821) is a critically endangered large feline now confined to the arid landscapes of central Iran and is thought to number <100 individuals (Hunter et al., 2007). Similar to the critically endangered Saharan cheetah (*A. j. hecki*), also living in desert habitats, the Asiatic cheetah is wide ranging and occurs at very low density compared to cheetahs in more productive habitats (Belbachir, Pettorelli, Wacher, Belbachir-Bazi, & Durant, 2015; Farhadinia et al., 2013). Although the Asiatic cheetah has been regularly reported from a number of protected areas scattered across central Iran (Hunter et al., 2007; Moqanaki & Cushman, 2016), it does not seem to be confined to these sites and has been documented to move long distances, over large stretches of deserts between distant areas (Farhadinia et al., 2013). Overall, habitat suitability criteria for the Asiatic cheetah are poorly understood, and as a corollary, the extent of environmental, biological and anthropogenic factors affecting the connectivity within this habitat and the proportion of suitable habitat receiving some level of protection are unknown. These uncertainties hinder the implementation of effective land use planning across its vast landscape to maintain connectivity between suitable habitats and mitigate conflicts with humans.

The deteriorating situation of the Asiatic cheetah requires conservation measures that are supported by accurate information on its distribution patterns and dispersal possibilities (Hunter et al., 2007). Species distribution models (SDMs) have been used in many studies to better understand habitat suitability criteria for large carnivores (Almasieh, Kaboli, & Beier, 2016; Brito, Acosta, Álvares, & Cuzin, 2009; Farhadinia et al., 2015) and have enabled to prioritize large carnivore's conservation actions (Farhadinia et al., 2015; Rabinowitz & Zeller, 2010; Sanderson, Redford, et al., 2002). Nonetheless most range-wide priority-setting attempts to achieve conservation goals for carnivores have been confronted with the difficulty of addressing corridors and habitat connectivity (Rabinowitz & Zeller, 2010). To ensure that populations of large carnivores are conserved within a sustainable habitat complex, it is necessary to have a connected network of protected areas or functional conservation networks (Crooks et al., 2011), which aim to increase connectivity and promote dispersal of large mammals between core habitats or/and population units (Almasieh et al., 2016; Rabinowitz & Zeller, 2010).

Recently, the concept of habitat permeability and landscape connectivity prioritization (LCP) has proved a powerful approach for wildlife conservation planning (e.g., Carroll, McRae, & Brookes, 2012; Dickson et al., 2013; Visconti & Elkin, 2009). Functional connectivity allows biologists to take into account the effect of compositional structure of the landscape on ecological and evolutionary processes of species dispersal, gene flow and population dynamics (Carroll et al., 2012; McRae & Beier, 2007). Furthermore, identifying patches requiring extra protection improves the maintenance of ecological integrity and enables conservation planning to prompt long-term population viability (Saura & Pascual-Hortal, 2007; Visconti & Elkin, 2009). This approach may prove appropriate for the Asiatic cheetah, which shows exceptionally high degree of mobility across patchily dispersed strongholds, all vulnerable to habitat deterioration (Farhadinia et al., 2013).

This study, which is based on all reliable Asiatic cheetah presence data compiled over the past 14 years, is the first attempt to understand the global distribution patterns of the species in Iran. Recently, Moqanaki and Cushman (2016) proposed a landscape connectivity model among the Iranian conservation areas (CAs) for the Asiatic cheetah. However, their results were limited by the facts that they did not use data on cheetah presence, they considered CAs as the only cheetah strongholds across the landscape and did not use habitat suitability and patterns of distribution along the environmental gradients outside CAs. In the current study, we present an approach that combines SDM, circuit and graph theories to (1) identify habitat suitability and the remaining core habitats for cheetahs, (2) evaluate the most important environmental factors influencing their distribution, (3) assess landscape permeability among core habitats and (4) prioritize core habitats and linkages based on their contribution to maintain long-term connectivity.

2 | METHODS

2.1 | Study area

The central plateau of Iran covers approximately 780,000 km^2 of land limited by the Alborz and Zagros mountain chains to the north and west/south-west, respectively, and the international border with Afghanistan and the Sistan-Baluchistan desert to the east and south-east, and is administered by nine provinces (Figure 1). The area is characterized by a warm arid climate and is composed of vast flat drylands with patchily distributed mountainous areas. It is part of the Irano-Turanian floristic region in which xerophytic plant taxa of *Artemisia* sp., *Stipa* sp. and *Salsola* sp. dominate (Manafzadeh, Salvo, & Conti, 2014). Starting in the early 1970s, the Department of Environment (DoE) of Iran has been creating and administrating an expanding network of CAs with the aim to protect and manage the faunal, floral and

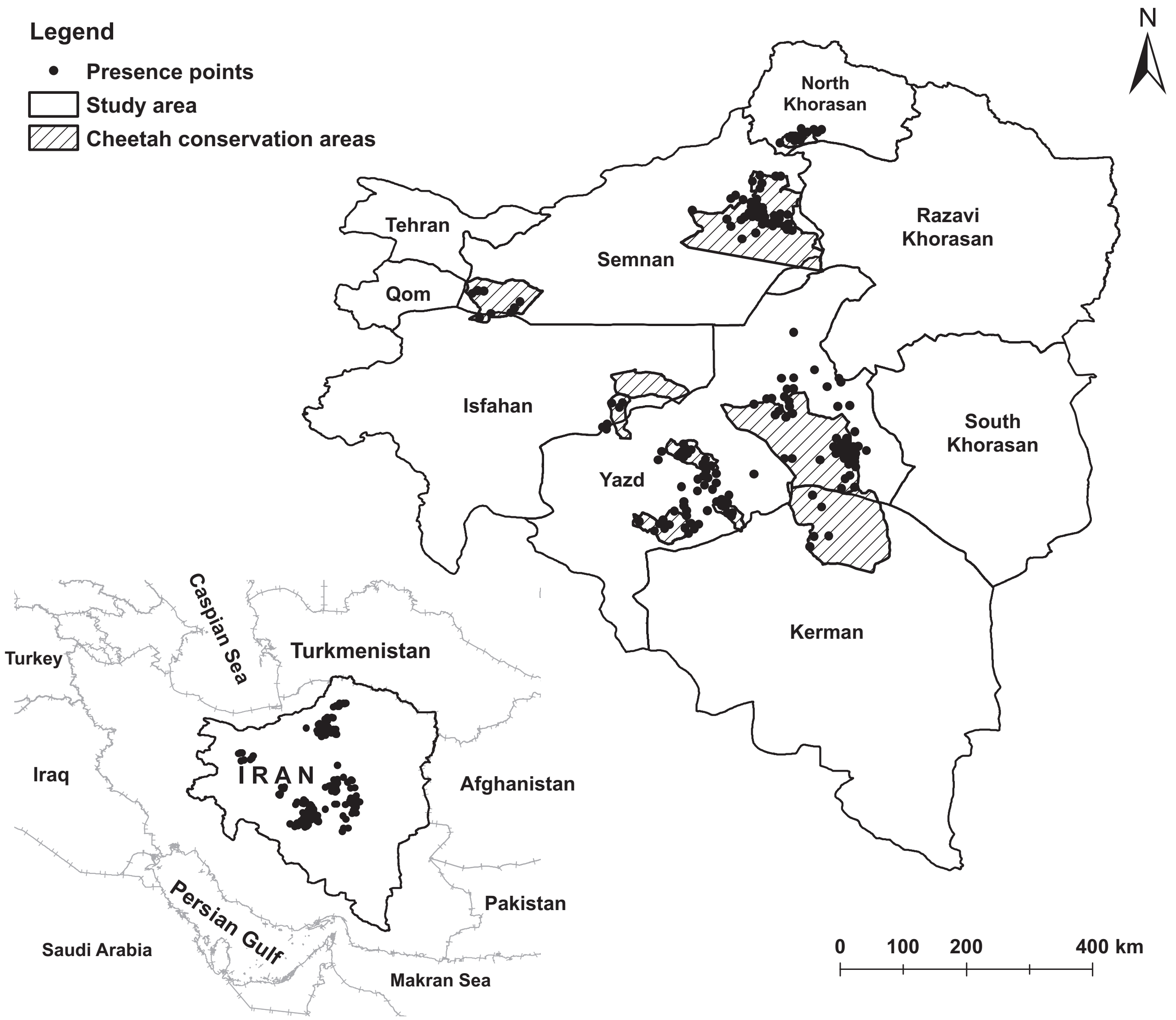

FIGURE 1 Documented cheetah presence locations in the nine provinces of the central plateau of Iran between 2001 and 2014. Cheetah conservation areas are those with specific management aiming at conserving cheetahs

geological diversity of Iran (Makhdoum, 2008). Ten CAs created in the central plateau, including three National Parks, five Wildlife Refuges and two Protected Areas (corresponding to management categories II, IV, and V, respectively, of the IUCN protected areas categories system), have been implementing since 2001 targeted conservation efforts to protect the Asiatic cheetah, its habitat and prey.

2.2 | Asiatic cheetah locations

The "Conservation of the Asiatic Cheetah Project" (CACP) of DoE has compiled cheetah occurrence information via a country-scale monitoring programme, extending from 2001 to 2014. The preliminary data subset used in the study included the totality of the 680 presence locations of this compilation, corresponding to direct observations (i.e., field patrols of guards, 485 presence points) and camera trap photographs (195 presence points) of free-ranging cheetahs, because this information might have suffered spatial biases in sampling effort, resulting in over-fitting of spatial models in areas with clumping of presence points (Dormann et al., 2007; Kramer-Schadt et al., 2013). We performed a spatial filtering procedure to account for spatially biased records (Kramer-Schadt et al., 2013). We ran a Global Moran's *I* test to evaluate the spatial autocorrelation of the presence data across the study area. We then filtered presence points to only single points within a 5 km-distance from others, which resulted in 205 unique locations with decreased spatial autocorrelation, upon which we based the SDM approach.

2.3 | Environmental variables

We selected 10 environmental and anthropogenic variables likely to affect the distribution of the cheetah (Pettorelli, Hilborn, Broekhuis, & Durant, 2009; Farhadinia & Hemami, 2010; Burton, Sam, Balangtaa, & Brashares, 2012; Andresen, Everatt, & Somers, 2014; Table 1). Land cover classes including low canopy rangelands, moderate canopy rangelands, shrublands and barelands (see Table 1 for list of variables and descriptions) were extracted from maps developed by the Iranian Forests, Ranges and Watershed Management Organization (IFRWO). To provide continuity for the extracted categories (Franklin, 2010), we calculated the proportion of each cover type within a 5 × 5 km grid by running the ArcMap Neighborhood statistic tool.

To take into account the anthropogenic effects in our modelling approach, we used the human footprint model developed by Sanderson, Jaiteh, et al (2002) which integrates data on population density and the presence of infrastructures including road networks, land transformation and human access. Because of the coarse precision of the human footprint model, we also included the density of villages in the study area estimated from a kernel density function applied to village point layer obtained from a topographic military map of Iran (1:25,000). Using the Shuttle Radar Topography Mission (SRTM) elevation model (http://srtm.csi.cgiar.org), we also considered altitude and topographic roughness (i.e., standard deviation of altitude of all raster cells within a grid of 5 × 5 km) in the modelling method as the most important variables affecting physiographic heterogeneity.

To account for the availability of the main cheetah prey species; the goitered gazelle (*Gazella subgutturosa*), Jebeer gazelle (*G. bennettii*), wild sheep (*Ovis orientalis*) and Persian ibex (*Capra aegagrus*) (Farhadinia & Hemami, 2010; Harrison & Bates, 1991), we used distributional data compiled in the "Atlas of Mammals of Iran" (Karami, Ghadirian, & Feizollahi, 2013) at a 25 × 25 km grid scale. We overlaid shape files of these four preys' distribution to obtain a composite map of presence. We then calculated distance to areas hosting prey species by running ArcMap Spatial Analyst Tools.

All the explanatory variables were prepared in ARCGIS 9.3 (Esri, 2010) at a grid size of 1 × 1 km. Before starting the modelling work, we calculated Pearson correlation coefficients to test for multicollinearity among predictors, but detected no high correlation (more than 0.7) between any pair of explanatory variables.

TABLE 1 Environmental variables used in species distribution modelling for evaluating Asiatic cheetah distribution in arid ecosystems of central Iran

Variable	Description
Prey availability	Overlaid shape file of the distribution of main prey species
Low canopy rangeland	Sparse vegetation with density ≤ 25%
Mod canopy rangeland	Mixture of grassland–scrubland with density ≥ 25%
Shrubland	Patches covered by scrubs–shrubs with canopy cover ≥ 10%
Bareland	Uncovered areas including sand dunes and salty lands
Altitude	Elevation above sea level
Roughness	*SD* of altitude of all raster cells within a 5 × 5 km grid
Cropland	Agricultural properties including dry and irrigated farms
Village density	Number of villages within a 5 × 5 km grid
Human footprint	Integrated index of population density, land transformation, human access and presence of infrastructure

2.4 | Distribution modelling approach

To predict cheetah distribution, we used biomod2 package (Thuiller, Lafourcade, Engler, & Araújo, 2009) in R environment v. 3.1.2 (R Development Core Team, 2014). Because different modelling methods can yield widely varying results, using this method allowed us to simultaneously take into account results from multiple modelling approaches and build a consensus model called as "ensemble" model (Araújo & New, 2007; Thuiller et al., 2009). We used three regression-based methods: generalized linear models (GLM), generalized additive models (GAM) and multiple adaptive regression splines (MARS), and four machine learning algorithms: generalized boosting model (GBM), random forest (RF), maximum entropy (MaxEnt) and artificial neural network (ANN) to obtain an integrative prediction of Asiatic cheetah's distribution in the study area. As all these models require background data (e.g., pseudo-absence points), we generated a randomly drawn sample of 5,000 background points from the extent of study area excepting occurrence cells. We calibrated models using the 75% of occurrence points as training data, and evaluated models prediction based on the remaining 25% of data set as test data. Models were evaluated using area under the curve (AUC) of a receiver operating characteristic (ROC) plot and the true skill statistic (TSS) because of their independence from prevalence in the species data (Allouche, Tsoar, & Kadmon, 2006).

Using BIOMOD framework, we estimated the contribution (i.e., importance) of variables in the cheetah's distribution models, and the response of the species distribution to the gradient of explanatory variables was also evaluated based on the response curves derived from GLM, GBM and RF models.

Finally, we implemented the ensemble model by weighted-averaging the individual models proportionally to all their evaluation metrics scores (Thuiller et al., 2009). In addition to obtaining final cheetah's distribution model, we also intended to find the most suitable areas as core habitats for cheetahs and evaluate habitat connectivity among them. For this reason, instead of a binary classification of presence/absence from the final ensemble model, we overlaid presence/absence map of the seven aforementioned models using a map algebra procedure. Using stacked binary map of presence/absence models, we obtained a composite map of suitable/unsuitable areas with raster values of 0–7 in which 0 score indicates areas being unsuitable in all models and 7 represents areas identified as suitable by all models and categorized as core habitats. To identify habitat patches with minimum areas capable of sustaining cheetahs, we focused on patches larger than 1,700 km^2. We selected this threshold value based on preliminary telemetry results (H. Jowkar, personal communication, 2007) and the estimated mean home-range size of the Saharan cheetah, a subspecies living in a comparable arid ecosystem (i.e., 1,583 km^2; Belbachir et al., 2015).

2.5 | Cheetah habitat connectivity

To evaluate the connectivity within cheetah's suitable habitats in the vast desert of central Iran, we used the concept of circuit theory and CIRCUITSCAPE software (McRae & Shah, 2009). Through identifying multiple alternative pathways, this method provides a detailed exploration of potential linkage and connectivity variability (Walpole, Bowman, Murray, & Wilson, 2012). Circuit theory treats cells in a landscape as electrical nodes connected to neighbouring cells by resistors, with resistance values determined by the cells' landscape resistance/conductance values (McRae, Dickson, Keitt, & Shah, 2008). Furthermore, using this method, we identified "pinch points" as areas where current densities are high and alternative pathways are not available (see McRae et al., 2008 for more details). We used core habitats as source patches, and the ensemble distribution model as a measure of conductance (i.e., conductance of each raster point for movement).

2.6 | Landscape connectivity prioritization

For LCP, we focused on the probability of connectivity (PC) index, which is among the most well-performing indices in landscape connectivity analysis (Bodin & Saura, 2010; Saura & Pascual-Hortal, 2007). The characteristic that used to derive PC index can refer to different attributes such as patch area (i.e., core habitat in this study), area-weighted habitat quality, carrying capacity or other relevant attributes (Saura & Pascual-Hortal, 2007; Visconti & Elkin, 2009). In this study in addition to typically used patch area, we tested, as a novel

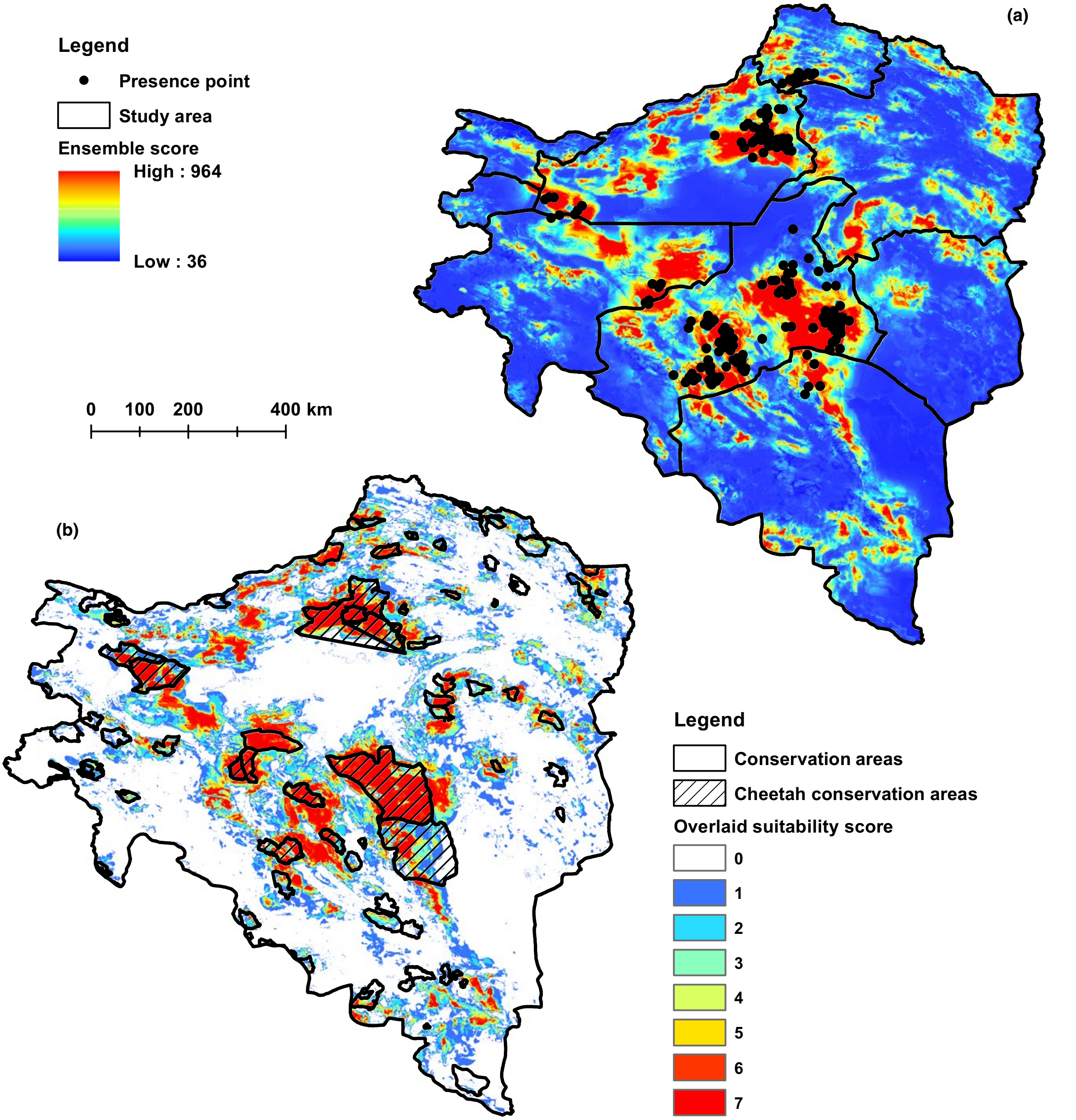

FIGURE 2 (a) Ensemble distribution model of Asiatic cheetah based on weighted-averaging seven species distribution models (SDMs). (b) Stacked binary prediction as an ensemble model based on overlaid suitable/unsuitable distribution models used to identify Asiatic cheetah's core habitats. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Performance of discrimination capacity and accuracy of different algorithms to predict Asiatic cheetah distribution in central Iran

	GLM	GAM	MARS	MaxEnt	GBM	RF	ANN
AUC	0.901	0.837	0.872	0.905	0.913	0.902	0.876
TSS	0.730	0.655	0.652	0.707	0.713	0.727	0.670

AUC, area under the curve of ROC plot; TSS, true statistical skill.
For models description, see "Methods".

procedure, the current values of cheetah's core habitats that were derived from circuit theory as the patch quality characteristic. Moreover, the prioritization of core habitats (i.e., their contribution to overall habitat connectivity) was calculated from the percentage of the variation in PC (dPC) caused by the removal of each individual patch from the landscape (Saura & Pascual-Hortal, 2007), both for patch area (dPC A) and patch current (dPC C). A description of the dPC calculations is provided in Appendix S1. We calculated dPC values at two dispersal distances of 50 km and 150 km using conefor 2.6 software (Saura & Torné, 2009). conefor needs distance-probability values corresponding to dispersal ability of the targeted species. Although there is little information on Asiatic cheetah movements, we chose 50 km as a reasonable median dispersal distance and 150 km as a maximum dispersal distance estimated based on camera trap recapture data (Farhadinia et al., 2013). Accordingly, we set distance-probability values of 0.5 and 0.05 for 50 km and 150 km dispersal distances, respectively, as recommended by Saura and Torné (2009).

3 | RESULTS

Our ensemble model indicated a patchily distributed suitable habitat for Asiatic cheetah in the central plateau of Iran (Figure 2). GLM, MaxEnt, GBM and RF distribution models showed excellent predictive performance with respect to AUC metric (i.e., model's discrimination capacity) and GAM, MARS and ANN good performance (Table 2). The prediction accuracy was good (e.g., TSS > 0.6) for all models (Table 2).

The average importance of the variables among the models showed that the prey availability, human footprint, roughness, village density and low canopy rangeland variables contributed the most to the cheetah distribution (Table 3). The response curves produced to evaluate cheetah's response to environmental gradient revealed an almost similar pattern between GLM, GBM and RF (Figure 3), all indicating that the highest probability of cheetahs' presence occurs in areas with highest prey availability. The effect of anthropogenic variables (i.e., human footprint and village density) indicated that with increasing human presence cheetahs' occurrence decreased. Finally taking landscape attributes into account, response curves also depicted a high preference of the Asiatic cheetah for rough landscapes covered by sparse vegetation with avoidance of bare lands (Figure 3).

Overlaying presence/absence distribution maps to obtain an integrated suitability map of all models indicated that 40.5% of the study area was identified as suitable habitat by at least one of the distribution models (i.e., areas with suitability score of 1–7; Table 4). Accordingly, 59.5% of the study area was not identified as suitable by any of the seven distribution models (Table 4). We identified five core habitats that represented areas of highest environmental suitability for the species in Iran (Figure 4). We also included an additional core habitat in North Khorasan Province (see Figure 1). Although this patch of habitat has an area smaller than the estimated mean home-range size for Asiatic cheetah, it hosts a documented population of cheetahs, possibly as a result of an unusually abundant population of gazelles (Farhadinia et al., 2012). Accordingly, we estimated that the current core habitats for cheetahs in Iran stretch over 49,144.5 km^2 or approximately 6.3% of the central plateau.

Connectivity analysis using a circuit theory based approach revealed that while there is strong permeability within southern and northern populations, the connectivity between these two distribution patches is limited (Figure 4), as a result of low landscape suitability between them (Figure 2). Moreover, our cumulative current map highlighted the existence of several pinch points across the predicted linkages, which, as landscape bottlenecks, may contribute to constrain cheetah's movements.

Landscape connectivity prioritization analysis showed a different pattern of patch prioritization depending on whether using the extent of core habitats or circuit current as patch characteristics. Based on the extent of core habitats, core habitats 5, 6 and 4 were the most important patches for sustaining connectivity, respectively (Table 5). However, with respect to circuit current as patch characteristics, core habitats ranking was 6, 4 and 5, respectively (Table 5). Nonetheless, we found that for both patch area and patch circuit current the connectivity ranking of core habitats correlated positively with their characteristics, and was independent of the dispersal distances.

TABLE 3 Mean and standard deviation (*SD*) of the contribution of environmental variables in seven Asiatic cheetah's distribution models in central Iran. Contribution values were calculated based on the difference in Pearson correlation scores between general model and randomized (e.g., permuted) models for each variable

Variables	Mean	*SD*
Prey availability	0.521	0.091
Human footprint	0.223	0.056
Roughness	0.169	0.102
Villages density	0.110	0.056
Low canopy rangeland	0.083	0.030
Bareland	0.056	0.048
Altitude	0.033	0.038
Cropland	0.031	0.026
Shrubland	0.016	0.024
Mod canopy rangeland	0.013	0.015

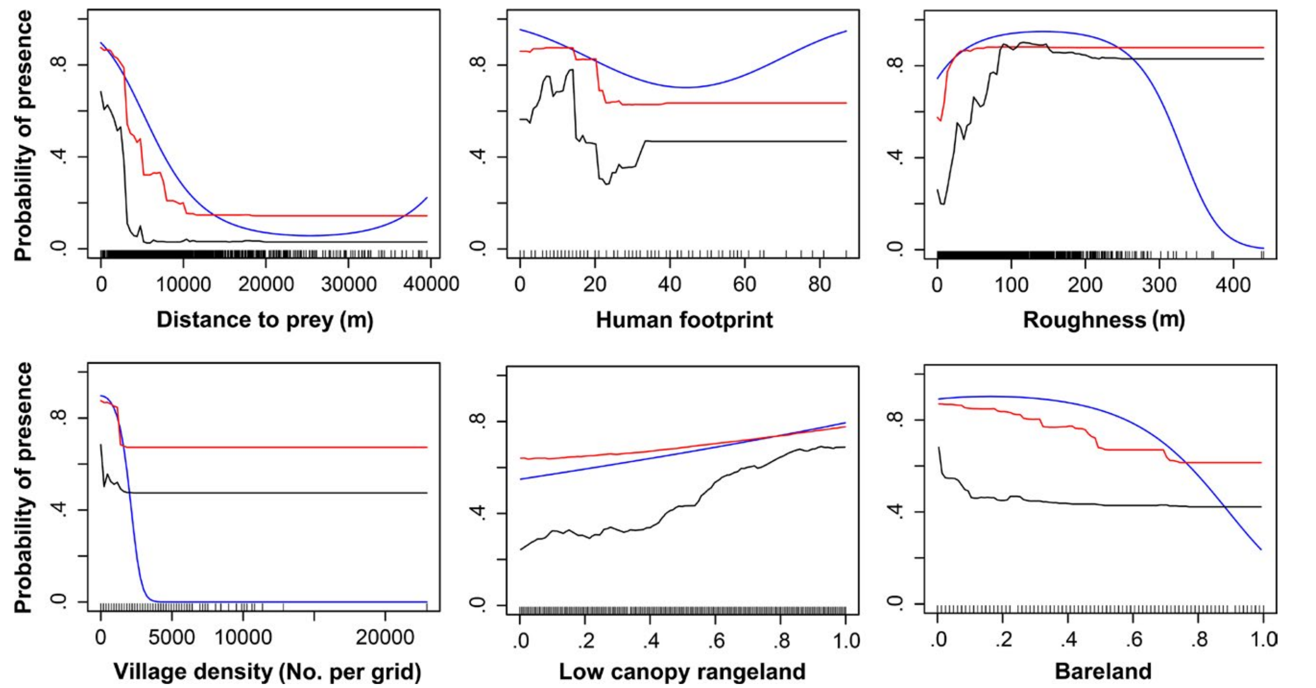

FIGURE 3 Response curves of Asiatic cheetah's distribution to the gradient of the most important predictors for habitat suitability. Results shown are for GLM (blue line), GBM (red line) and RF (black line) models. For description of variables, see Table 1. Human footprint (ratio of 100), low canopy rangeland and bareland (for both ratios of 1) are adimensional variables. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Surface and proportion of suitable/unsuitable habitats for the Asiatic cheetah in central Iran

Category	Suitability score	Area (km^2)	Proportion of study area	Protected by all CAs in km^2 (%)	Protected by cheetah's CAs[a] in km^2 (%)
Unsuitable habitat	0	464,466	59.5		
Suitable habitat	1–7	316175.7	40.5	73,818.86 (23)	51,512.65 (16)
Core habitat	7	49,144.5	6.3	30,759.16 (63)	26,130.45 (53)

[a]Conservation areas (CAs) for cheetahs are protected areas with specific management aiming at conserving cheetahs.

4 | DISCUSSION

Setting priority actions for species conservation should be primarily conducted based on reliable, detailed and spatially explicit understanding of the species requirements, and available conservation options (Rabinowitz & Zeller, 2010; Sanderson, Redford, et al., 2002). In the present study, we propose the first combined evaluation of habitat suitability and connectivity for the Asiatic cheetah, an apex predator that suffered considerable contraction of its distribution range for at least the past 100 years (Harrison & Bates, 1991). We used the most complete compilation of recent locations collected for this cheetah subspecies and a sophisticated ensemble modelling approach that accounts for SDMs-specific uncertainty (Araújo & New, 2007; Thuiller et al., 2009). The stacked binary prediction as the ensemble model achieved 100% sensitivity, which means that all cheetah presence locations were correctly predicted as suitable by the overlaid suitability maps. Although such an approach is likely to decrease the model's specificity (i.e., correctly predicted pseudo-absence), here estimated at 65%, it minimized the omission of potentially suitable areas for cheetahs. Decreasing the omission error compared to the commission error seems an acceptable choice in the case of a species on the brink of extinction and requiring generous and immediate conservation efforts.

The comparison of SDMs results revealed that GLM has the highest TSS value (Table 2), confirming the efficiency of this simple regression-based model to correctly classify out-of-sample data when doing extrapolations (Franklin, 2010; Merow et al., 2014). However, machine learning methods (MaxEnt, GBM and RF), that have good propensity for interpolation, showed the best performance based on discrimination capacity (i.e., AUC) values (Table 2), a result supported by comparative examinations of SDMs (Elith & Graham, 2009; Elith et al., 2006).

The present study confirms that availability of prey species is a fundamental criterion of landscape suitability for cheetah in Iran. Habitat selection for areas with high prey abundance has been largely reported for other large felids including the African cheetah (*A. j. jubatus*) in South Africa (Rostro-García, Kamler, & Hunter, 2015). Relative availability of natural

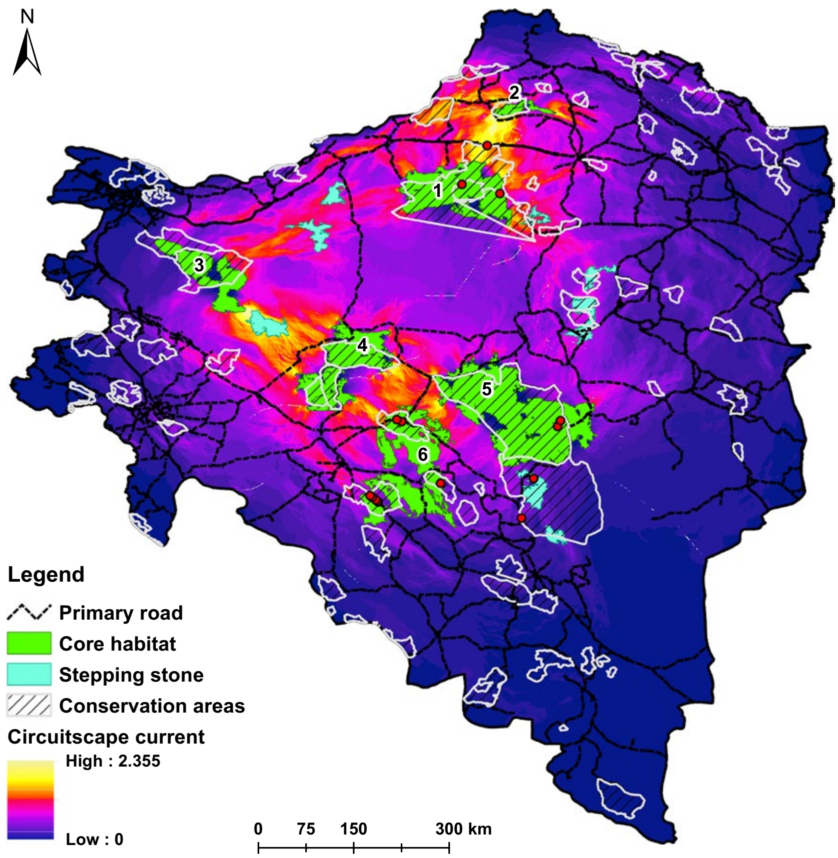

FIGURE 4 Habitat permeability between the six Asiatic cheetah's core habitats based on circuit theory. Stepping stone areas are proposed temporary strongholds between core areas for moving cheetahs. Hatched conservation areas (CAs) are those with specific management aiming at conserving cheetah. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 5 Patch characteristics and results of landscape connectivity prioritization (LCP) to identify the most important core habitats for maintaining landscape connectivity within Asiatic cheetah distribution range. Patches (or core areas) are identified by species distribution modelling using BIOMOD method, and the current is derived from CIRCUITSCAPE software. The values of 50 km and 150 km correspond to assumed median and maximum dispersal distance of the species. dPC A and dPC C are the percentage of PC index value loss for patch area and patch current, respectively. The geographical location of patches is shown in Figure 4

			50 km		150 km	
	Area (km^2)	Circuit current	dPC A	dPC C	dPC A	dPC C
Patch 1	8093.58	2.25	9.65	20.83	7.98	17.95
Patch 2	766.084	1.62	0.57	11.82	0.38	10.63
Patch 3	4560.55	1.43	5.52	9.97	3.73	7.69
Patch 4	7278.62	2.27	25.56	36.21	21.30	34.26
Patch 5	17,491.84	2.07	65.89	35.01	66.17	32.36
Patch 6	10,953.92	2.35	45.26	39.79	45.03	39.81

prey versus livestock has also been shown a good predicator of landscape suitability for cheetahs in Botswana (Winterbach, Winterbach, Boast, Klein, & Somers, 2015). The Asiatic cheetah mainly relies on medium-sized ungulate prey, with a preference for the Jebeer and goitered gazelles (Farhadinia & Hemami, 2010; Farhadinia et al., 2012), two species that have suffered severe declines in population size and distribution in Iran since the 1970s (Mallon, 2007). Therefore, the high dependency on prey identified by our distribution model may provide support for the hypothesis that the Asiatic cheetah is likely to be ecologically constrained in its last stronghold in Asia due to the decline of its favoured prey species.

Cheetahs in Iran are scattered predominantly through low canopy rangelands (e.g., sparse vegetation with density <25%; Table 3) in relatively rough terrains. The high contribution of topographic roughness in the current distribution of the Asiatic cheetah is in contrast with what has been documented for sub-Saharan African cheetahs, which live in flat to undulating grasslands, savannas and shrublands and only occasionally in montane areas (e.g., see Andresen et al., 2014; Rostro-García et al., 2015). The widespread use by Asiatic cheetahs of the rugged parts of the predominantly flat central plateau of Iran is coherent with the relatively low habitat selectivity of cheetahs compared to other carnivores (Durant et al., 2010), and may reflect in Iran a shift in prey selection. Because cheetahs prefer prey within a body mass range of 23–56 kg (Hayward, Hofmeyr, O'brien, & Kerley, 2006), thus with the decline of Jebeer and goitered gazelles, the wild sheep and Persian ibex, two mid-sized species inhabiting rough areas (Esfandabad, Karami, Hemami, Riazi, & Sadough, 2010), have emerged as the most available wild prey species for cheetahs in Iran (Farhadinia & Hemami, 2010). This possibly resulted in cheetahs increasingly using rough habitats. The hypothesis of a contemporary shift in prey selection is supported by the historical distribution of cheetahs in south-west Asia, which extended largely in accordance with the presence of plain-dwelling gazelles (Harrington, 1977; Harrison & Bates, 1991).

Unsurprisingly the Asiatic cheetah prefers areas without humans and associated activities, supporting the documented trend that conflict with humans is a primary factor decreasing large carnivore survival (Winterbach, Winterbach, Somers, & Hayward, 2013). Major demographic changes have occurred in Iran since the 1930s with a 6-fold increase of the total human population and a doubling of the rural population over the period (Amiraslani & Dragovich, 2011). Even so the last remaining stronghold for cheetahs in the central plateau, hosts the lowest human population densities in Iran (NPHC, 2011), these demographic shifts together with developmental changes have created a situation in which more anthropogenic pressure is being exerted on the cheetah habitat, particularly in relation to an increase in infrastructure and livestock numbers. Livestock overgrazing and desertification have resulted in an intensification of food resource degradation for the main cheetah prey species (Hunter et al., 2007; Karami, Hemami, & Groves, 2002), while guard dogs accompanying livestock herds have proved dangerous predators for cheetahs and their prey (CACP database, unpublished).

Landscapes that retain more connections between patches of otherwise isolated habitat are assumed to be more likely to maintain dispersal pathways for large mammals and increase demographic and genetic population size (Mills & Allendorf, 1996). Although one and half time larger than the Serengeti/Mara/Tsavo landscape in Kenya and Tanzania, which hosts the largest population of cheetahs in Africa, the area of potential core habitats remaining available to cheetahs in Iran appears fragmented with possibly a limited connectivity between the northern and southern populations. Although cheetahs display a high mobility and excellent dispersal abilities (Boast, 2014), better conserved connecting habitats would help the species to persist, recolonize empty habitat patches and exchange individuals and genes among subpopulations (Hanski & Ovaskainen, 2000; Mech & Hallett, 2001). Our connectivity model predicts that linkages between core areas exist, although their functionality for dispersal might be to some extent affected by a lack of protection and the risk of road-kill accidents (Figure 4).

The analysis of patch prioritization revealed that for both patch area (i.e., extent of the core habitats) and patch current (i.e., circuit flows through core habitats), patch prioritization was positively correlated with the patch characteristic regardless of the dispersal ability of the species. We also found that core habitats will have a lower chance of being reached by a cheetah when dispersal distances become larger. These results have been documented in other studies (Saura & Rubio, 2010; Zhao et al., 2014). However, our finding highlights that considering different patch characteristics might results in different pattern of patch prioritization. For example, while core habitats 5 and 6 have highest dPC value based on patch area characteristic, core habitats 6 and 4 are the most important patch when using patch current. Although spatial aggregation of patches and the variance of the patch characteristics determines the appropriateness of the application of metrics for LCP analysis (Visconti & Elkin, 2009), our approach reveals that, using the same metrics and spatial aggregation, including patch characteristics that are intrinsically more related to the movement of the species (e.g., patch circuit current vs. patch area), might provide better understandings of the patch contribution for maintaining landscape connectivity. Using circuit theory allows calculating cumulative current (i.e., landscape permeability) terminating to each of the patch habitats and could potentially be used as habitat characteristic for landscape prioritization.

4.1 | Conservation implications

The present study supports that CAs with dedicated resources to cheetah conservation currently protect only 53% and 16% of cheetah core and suitable habitats, respectively (Table 4). Because of its crucial importance for conservation, the network of CAs and associated conservation resources for cheetahs would therefore benefit from being expanded to achieve more effective conservation coverage of cheetah habitats in Iran. Currently, high priority core habitats 1, 2 and 5 are fairly well covered by CAs, but the protection coverage would deserve being expanded to the south-east of core area 3, the north of core area 4 and between existing CAs in core area 6. In combination, this landscape protection scheme will strengthen the role of core areas 4, 5 and 6 for cheetah dispersal as revealed by the patch prioritization analysis. Also, to ensure the cohesion between core habitats in the north and the south we propose to establish new intermediate CAs located in corridors of suitable habitats between core areas 1 and 3, and 3 and 4 (Figure 4). As featured for other large carnivores (Cushman et al., 2012; Riordan et al., 2015) these areas, as stepping stones, would provide temporary strongholds between core areas for moving cheetahs and reconnect through suitable landscapes the northern and southern parts of the cheetah range.

New CAs in the central plateau of Iran as well as their associated management policies should be developed with the specific objective of cheetah conservation. They should include large extents of habitats favoured by gazelles and support in priority their conservation. In addition, the water and food supplementations actively implemented in CAs during summers and droughts should be implemented to support in priority gazelles in their favoured habitats. Hence, this management policy would less likely support the mountain dwelling Persian leopard which, besides being a predator to cheetahs (Hayward et al., 2006), competes with them on prey resources.

Our connectivity approach showed that linkages within and between adjacent cheetah core habitats still exist across the central plateau of Iran (Figure 3). Unfortunately, these pathways are nowadays dissected by main through roads that carry large volume of traffic, putting cheetahs at risk of car collisions. Of 33 documented cheetah mortalities between 2001 and 2016 due to various causes, at least 14 were killed on roads within or between core areas, making it the major cause of documented mortality for cheetahs in Iran (CACP database, unpublished). By providing an applicable tool to identify with accuracy the most important portions of roads to be secured against cheetah car collisions, the circuits approach together with connectivity metrics could help prioritize mitigation measures, increase their cost-effectiveness and likelihood of success. Our connectivity analysis supports that securing primary roads within core areas and between the core areas 1 and 2, and 3 and 4 would be critical to reduce the risk of cheetah car collisions. Fencing of dangerous stretches of roads particularly in combination with wildlife passages has indeed been suggested as one of the most effective methods to minimize car-collision risk with large mammals (Bissonette & Adair, 2008; Ascensão et al., 2013). Large carnivores differently respond to crossing structures given to taxon- and/or habitat-specific factors (Ng et al., 2004; Clevenger & Waltho, 2005). To our knowledge, anticar-collision methods have not been developed specifically for cheetahs, and therefore, methods and structures used for other large carnivores (e.g., Clevenger & Waltho, 2005) will have to be tested for the Asiatic cheetah and adjusted to the Iranian context.

The value of identifying core habitats and linkage areas for Asiatic cheetah at country scale is to inform targeted land planning and better conservation management. Species distribution modelling in combination with circuit theory and LCP analysis provide a robust representation of most suitable habitats for cheetahs in Iran and offers possible adaptive measures for country-scale management of cheetah habitats. Extending landscape protection over larger stretches of suitable habitat, developing in parallel cheetah-specific conservation actions aiming at increasing the size and distribution of gazelle populations, and improving the safety of important linkages between core habitats are likely to promote the conservation of the last surviving population of cheetah in Asia. In the future, evaluating the long-term persistence of the Asiatic cheetah over its last remaining strongholds in Asia would also require studies on metapopulation dynamics based on patch population growth models.

ACKNOWLEDGEMENTS

We are grateful for the financial and technical support of the DoE of the Islamic Republic of Iran, the Global Environmental Facilities (GEF), the United Nations Development Program (UNDP) representation in Iran, and the Wildlife Conservation Society (WCS). The work of WCS in Iran would not have been possible without the long-standing support of the Flora Family Foundation. Our special thanks go to all contributors to the Conservation of the Asiatic Cheetah Project, and particularly successive managers, to directors of the DoE operations in the provinces covered by this study, to managers of CAs and their staff who were the kingpins of all data collection efforts. We thank anonymous referees for helping to improve an earlier version of the manuscript.

AUTHOR CONTRIBUTIONS

M.A., B.N.B. and S.O. conceived the study; B.N.B., H.J. and S.O. compiled the data; M.A., B.N.B., M.R.H., D.F. and S.M. analysed the data; and M.A. and S.O. led the writing.

REFERENCES

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*, 1223–1232.

Almasieh, K., Kaboli, M., & Beier, P. (2016). Identifying habitat cores and corridors for the Iranian black bear in Iran. *Ursus*, *27*, 18–30.

Amiraslani, F., & Dragovich, D. (2011). Combating desertification in Iran over the last 50 years: An overview of changing approaches. *Journal of Environmental Management*, *92*, 1–13.

Andresen, L., Everatt, K. T., & Somers, M. (2014). Use of site occupancy models for targeted monitoring of the cheetah. *Journal of Zoology*, *292*, 212–220.

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, *22*, 42–47.

Ascensão, F., Clevenger, A., Santos-Reis, M., Urbano, P., & Jackson, N. (2013). Wildlife–vehicle collision mitigation: Is partial fencing the answer? An agent-based model approach. *Ecological Modelling*, *257*, 36–43.

Belbachir, F., Pettorelli, N., Wacher, T., Belbachir-Bazi, A., & Durant, S. M. (2015). Monitoring rarity: The critically endangered Saharan cheetah as a flagship species for a threatened ecosystem. *PLoS One*, *10*, e0115136.

Bissonette, J. A., & Adair, W. (2008). Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation*, *141*, 482–488.

Boast, L. (2014). *Exploring the causes of and mitigation options for human-predator conflict on game ranches in Botswana: How is coexistence possible?* D. Phil thesis, University of Cape Town, Cape Town, South Africa.

Bodin, Ö., & Saura, S. (2010). Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments. *Ecological Modelling*, *221*, 2393–2405.

Brito, J. C., Acosta, A. L., Álvares, F., & Cuzin, F. (2009). Biogeography and conservation of taxa from remote regions: An application of ecological-niche based models and GIS to North-African Canids. *Biological Conservation*, *142*, 3020–3029.

Burton, A. C., Sam, M. K., Balangtaa, C., & Brashares, J. S. (2012). Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. *PLoS One*, *7*, e38007.

Carroll, C., McRae, B., & Brookes, A. (2012). Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. *Conservation Biology*, *26*, 78–87.

Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andrén, H., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*, 1517–1519.

Clevenger, A. P., & Waltho, N. (2005). Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological conservation*, *121*, 453–464.

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*, 2642–2651.

Cushman, S. A., Landguth, E. L., & Flather, C. H. (2012). Evaluating the sufficiency of protected lands for maintaining wildlife population connectivity in the US northern Rocky Mountains. *Diversity and Distributions*, *18*, 873–884.

Dickson, B. G., Roemer, G. W., McRae, B. H., & Rundall, J. M. (2013). Models of regional habitat quality and connectivity for pumas (*Puma concolor*) in the southwestern United States. *PLoS One*, *8*, e81898.

Dormann, C. F., McPherson, J. M., Araujo, M. B., Bivand, R., Bolliger, J., Carl, G., … Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, *30*, 609–628.

Durant, S. M., Craft, M. E., Foley, C., Hampson, K., Lobora, A. L., Msuha, M., … Pettorelli, N. (2010). Does size matter? An investigation of habitat use across a carnivore assemblage in the Serengeti, Tanzania. *Journal of Animal Ecology*, *79*, 1012–1022.

Elith, J., & Graham, C. H. (2009). Do they? How do they? Why do they differ? on finding reasons for differing performances of species distribution models. *Ecography*, *32*, 66–77.

Elith, J., Graham, H. C., Anderson, P. R., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, E. N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*, 129–151.

Esfandabad, B. S., Karami, M., Hemami, M. R., Riazi, B., & Sadough, M. B. (2010). Habitat associations of wild goat in central Iran: Implications for conservation. *European Journal of Wildlife Research*, *56*, 883–894.

ESRI (2010). *ArcGIS 9.3*. Redlands, CA: Environmental Systems Research Institute.

Farhadinia, M. S., Ahmadi, M., Sharbafi, E., Khosravi, S., Alinezhad, H., & Macdonald, D. W. (2015). Leveraging trans-boundary conservation partnerships: Persistence of Persian leopard (*Panthera pardus saxicolor*) in the Iranian Caucasus. *Biological Conservation*, *191*, 770–778.

Farhadinia, M. S., Akbari, H., Mousavi, S. J., Eslami, M., Azizi, M., Shokouhi, J., … Hosseini-Zavarei, F. (2013). Exceptionally long movements of the Asiatic cheetah *Acinonyx jubatus venaticus* across multiple arid reserves in central Iran. *Oryx*, *47*, 427–430.

Farhadinia, M., & Hemami, M.-R. (2010). Prey selection by the critically endangered Asiatic cheetah in central Iran. *Journal of Natural History*, *44*, 1239–1249.

Farhadinia, M., Hosseini-Zavarei, F., Nezami, B., Harati, H., Absalan, H., Fabiano, E., & Marker, L. (2012). Feeding ecology of the Asiatic cheetah *Acinonyx jubatus venaticus* in low prey habitats in northeastern Iran: Implications for effective conservation. *Journal of Arid Environments*, *87*, 206–211.

Ford, A. T., Goheen, J. R., Otieno, T. O., Bidner, L., Isbell, L. A., … Pringle, R. M. (2014). Large carnivores make savanna tree communities less thorny. *Science*, *346*, 346–349.

Franklin, J. (2010). *Mapping species distributions: Spatial inference and prediction*. New York: Cambridge University Press.

Hanski, I., & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature*, *404*, 755–758.

Harrington, F. A. (1977). *A guide to the mammals of Iran*. Tehran, Iran: Department of the Environment.

Harrison, D. L., & Bates, P. J. J. (1991). *The mammals of Arabia*. Kent, Engeland: Harrison Zoological Museum Sevenoaks.

Hayward, M., Hofmeyr, M., O'brien, J., & Kerley, G. (2006). Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): Morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *Journal of Zoology*, *270*, 615–627.

Hunter, L., Jowkar, H., Ziaie, H., Schaller, G., Balme, G., Walzer, C., … Christie, S. (2007). Conserving the Asiatic cheetah in Iran: Launching the first radio-telemetry study. *Cat News*, *46*, e11.

Karami, M., Ghadirian, T., & Feizollahi, K. (2013). *Atlas of the mammals of Iran*. Tehran, Iran: Wildlife Center Publication.

Karami, M., Hemami, M. R., & Groves, C. P. (2002). Taxonomic, distributional and ecological data on gazelles in Iran. *Zoology in the Middle East*, *26*, 29–36.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V., … Wilting, A. (2013). The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions*, *19*, 1366–1379.

Kunkel, K. E., Atwood, T., Ruth, T., Pletscher, D. H., & Hornocker, M. (2013). Assessing wolves and cougars as conservation surrogates. *Animal Conservation*, *16*, 32–40.

Makhdoum, M. (2008). Management of protected areas and conservation of biodiversity in Iran. *International Journal of Environmental Studies*, *65*, 563–585.

Mallon, D. P. (2007). Cheetahs in Central Asia: A historical summary. *Cat News*, *46*, 4–7.

Manafzadeh, S., Salvo, G., & Conti, E. (2014). A tale of migrations from east to west: The Irano-Turanian floristic region as a source of Mediterranean xerophytes. *Journal of Biogeography*, *41*, 366–379.

McRae, B. H., & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19885–19890.

McRae, B. H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, *89*, 2712–2724.

McRae, B., & Shah, V. (2009). *Circuitscape user's guide*. Santa Barbara: The University of California.

Mech, S. G., & Hallett, J. G. (2001). Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology*, *15*, 467–474.

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., McMahon, S. M., Normand, S., … Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography*, *37*, 1267–1281.

Mills, L. S., & Allendorf, F. W. (1996). The one-migrant-per-generation rule in conservation and management. *Conservation Biology*, *10*, 1509–1518.

Moqanaki, E., & Cushman, S. (2016). All roads lead to Iran: Predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. *Animal Conservation*, *20*, 29–41.

Ng, S. J., Dole, J. W., Sauvajot, R. M., Riley, S. P., & Valone, T. J. (2004). Use of highway undercrossings by wildlife in southern California. *Biological Conservation*, *115*, 499–507.

NPHC (2011). *National population and housing census report*. Tehran, Iran: Statistical Centre of Iran Press.

Pettorelli, N., Hilborn, A., Broekhuis, F., & Durant, S. (2009). Exploring habitat use by cheetahs using ecological niche factor analysis. *Journal of Zoology*, *277*, 141–148.

R Development Core Team(2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, *143*, 939–945.

Riordan, P., Cushman, S. A., Mallon, D., Shi, K., & Hughes, J. (2015). Predicting global population connectivity and targeting conservation action for snow leopard across its range. *Ecography*, *39*, 419–426.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*, 1241484.

Rostro-García, S., Kamler, J. F., & Hunter, L. T. (2015). To kill, stay or flee: The effects of lions and landscape factors on habitat and kill site selection of cheetahs in South Africa. *PLoS One*, *10*, e0117743.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild: The human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience*, *52*, 891–904.

Sanderson, E. W., Redford, K. H., Chetkiewicz, C. L. B., Medellin, R. A., Rabinowitz, A. R., Robinson, J. G., & Taber, A. B. (2002). Planning to save a species: The jaguar as a model. *Conservation Biology*, *16*, 58–72.

Santini, L., Boitani, L., Maiorano, L., & Rondinini, C. (2016). Effectiveness of protected areas in conserving large carnivores in Europe. In L. N. Joppa, J. E. M. Baillie, & J. G. Robinson (Eds.), *Protected areas: Are they safeguarding biodiversity?* (pp. 122–133). Oxford: Blackwell Scientific Publications.

Santini, L., Saura, S., & Rondinini, C. (2016). Connectivity of the global network of protected areas. *Diversity and Distributions*, *22*, 199–211.

Saura, S., & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning*, *83*, 91–103.

Saura, S., & Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, *33*, 523–537.

Saura, S., & Torné, J. (2009). Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software*, *24*, 135–139.

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., … Hiraldo, F. (2008). Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 1–19.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD—A platform for ensemble forecasting of species distributions. *Ecography*, *32*, 369–373.

Visconti, P., & Elkin, C. (2009). Using connectivity metrics in conservation planning—When does habitat quality matter? *Diversity and Distributions*, *15*, 602–612.

Walpole, A. A., Bowman, J., Murray, D. L., & Wilson, P. J. (2012). Functional connectivity of lynx at their southern range periphery in Ontario, Canada. *Landscape Ecology*, *27*, 761–773.

Winterbach, H. E., Winterbach, C. W., Boast, L. K., Klein, R., & Somers, M. J. (2015). Relative availability of natural prey versus livestock predicts landscape suitability for cheetahs *Acinonyx jubatus* in Botswana. *PeerJ*, *3*, e1033.

Winterbach, H., Winterbach, C., Somers, M., & Hayward, M. (2013). Key factors and related principles in the conservation of large African carnivores. *Mammal Review*, *43*, 89–110.

Zhao, H., Liu, S., Dong, S., Su, X., Liu, Q., & Deng, L. (2014). Characterizing the importance of habitat patches in maintaining landscape connectivity for Tibetan antelope in the Altun Mountain National Nature Reserve, China. *Ecological Research*, *29*, 1065–1075.

BIOSKETCH

Mohsen Ahmadi is a research associate at the Department of Natural Resources, Isfahan University of Technology, Iran. His primary interest is in methods for evaluating spatial and temporal dynamics of biodiversity and species distribution models, with a special interest in the incorporation of new knowledge into conservation goals.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Ahmadi M, Balouchi BN, Jowkar H, et al. Combining landscape suitability and habitat connectivity to conserve the last surviving population of cheetah in Asia. *Divers. Distrib*. 2017;23:592–603. https://doi.org/10.1111/ddi.12560