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All roads lead to Iran: Predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah

E. M. Moqanaki[1]* & S. A. Cushman[2]

1 Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney, Oxfordshire, UK
2 Rocky Mountain Research Station, USDA Forest Service, Flagstaff, AZ, USA

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Correspondence
*Current address: Iranian Cheetah Society, P.O. Box 14155-8549, Tehran, Iran.
Email: ehsan.moqanaki@gmail.com

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Abstract

Effective conservation solutions for small and isolated wildlife populations depend on identifying and preserving critical biological corridors and dispersal routes. With a worldwide population of ≤70 individuals, the critically endangered Asiatic cheetah *Acinonyx jubatus venaticus* persists in several fragmented nuclei in Iran. Connectivity between nuclei is crucial for the survival of this subspecies, but detailed information to guide conservation actions is lacking. We developed a resistance surface that predicted cost of cheetah movement as functions of topographical complexity, human development, surface water and landscape protection level. We predicted alternative models for the landscape connectivity of Asiatic cheetahs, considering the combination of relative landscape resistance and different dispersal ability scenarios. We predicted that core connected habitat patches are concentrated in three sub-regions, and within these sub-regions, populations were predicted to be broken up into two to eight isolated patches, depending on the dispersal ability scenario. Despite the achievements of recent conservation initiatives, long-term survival of the Asiatic cheetah in Iran is threatened by the combination of its small population size and fragmented distribution. We propose that conservation of the Asiatic cheetah urgently requires integrated landscape-level management to reduce mortality risk, protect core areas and corridors, and ultimately establish stepping-stone populations to integrate this fragmented population.

Introduction

Extinction risk in wildlife populations is influenced by environmental factors, intrinsic traits and exposure to anthropogenic threats (Cardillo *et al.*, 2005). Small and isolated populations are particularly at risk of imminent extinction due to demographic stochasticity, environmental catastrophes, Allee effect and loss of genetic diversity (Traill *et al.*, 2010). Effective conservation solutions in an increasingly fragmented world (Purvis, Jones & Mace, 2000; Ceballos & Ehrlich, 2002) are tied closely to correctly identifying and preserving population core areas and corridors protecting key dispersal routes (Sawyer, Epps & Brashares, 2011; Hand *et al.*, 2014).

Many mammalian carnivores are threatened and persist in increasingly isolated and shrinking populations (Ripple *et al.*, 2014). Understanding factors affecting animal movement is crucial for landscape-scale conservation planning of endangered carnivore populations, as in many cases only arrival of dispersers may prevent or reverse local extinctions (Beier, 1995; Baguette *et al.*, 2013; Elliot *et al.*, 2014). Mapping potential corridors and predicting landscape connectivity is currently a topic of intense focus in carnivore conservation (Zeller, McGarigal & Whiteley, 2012), in which connectivity models are applied to landscape resistance surfaces to estimate the expected rate and pattern of animal movement through a landscape as a function of landscape features (Cushman *et al.*, 2013a). Landscape resistance is defined as the physiological cost or behavioral avoidance of moving through a particular environment (Zeller *et al.*, 2012), and can be related to the reduction in survival of the target animal. Resistance can be estimated by parameterizing environmental factors across a cost or resistance gradient to animal movements (Cushman *et al.*, 2013*a*). Once landscape resistance is estimated, then population connectivity can be predicted using approaches such as factorial least-cost path analysis (Cushman, McKelvey & Schwartz, 2009), or cumulative resistant kernels (Compton *et al.*, 2007; Cushman & Landguth, 2012).

With a rough population estimate of 60–100 individuals (Hunter *et al.*, 2007), the critically endangered Asiatic cheetah *Acinonyx jubatus venaticus* now only occurs in Iran (Jowkar *et al.*, 2008). Historically, cheetahs were distributed throughout south-west and central Asia as far east as India

(Nowell & Jackson, 1996; Mallon, 2007). However, Asiatic cheetah sub-populations declined to extinction across most of their range in the nineteenth and early twentieth centuries, mainly due to overexploitation of prey and direct killing (Heptner & Sludskii, 1972; Nowell & Jackson, 1996; Mallon, 2007). In Iran, cheetahs apparently started recolonizing parts of their former range in the early 1960s after receiving legal protection and with the recovery of wild ungulates (primarily gazelles *Gazella subgutturosa* and *G. bennettii*; but see Farhadinia *et al.*, 2008), in the newly established network of protected areas (Firouz, 1974; Darehshuri, 1978). A decade of ineffective law enforcement after the collapse of the government in 1979 and during the Iran–Iraq War, negatively affected the Iranian cheetah population (Asadi, 1997). Cheetahs apparently survived this period in the eastern-central arid and hyper arid deserts, where the human population density is extremely low (Karami, 1992; Farhadinia, 2004).

Existing cheetah population remnants are aggregated around the edge of the central Iranian plateau (Farhadinia, 2004), mainly within protected areas, some of which are separated by hundreds of kilometers (Hunter *et al.*, 2007). Unfortunately, most cheetah reserves are surrounded by dense transportation infrastructure and road mortalities are a serious threat (Hunter *et al.*, 2007; Farhadinia *et al.*, 2014). The majority of these reserves do not host more than a handful of mature individuals (Supporting Information Table S1), turning connectivity among reserves into a critical factor to ensure the long-term viability of this cheetah population.

There has been virtually no formal research on cheetah movement behavior in relation to landscape features in Iran. In the absence of empirical data on the factors driving cheetah dispersal, landscape connectivity modeling can estimate the importance of different dispersal routes to guide cheetah conservation efforts and future research. Our main objective in this study was to evaluate the effects of different landscape features and anthropogenic disturbance on cheetah movement and connectivity across the current cheetah range in Iran. The results of this study provide sufficient information to: (1) identify the key core areas, linkages, and potential areas for mitigating mortality risk, (2) improve future landscape planning decision-making processes by balancing cheetah conservation and human needs, and (3) establish stepping stone populations to enhance viability of the last meta-population of Asiatic cheetah in existence in the wild.

Methods

Study landscape

Our analysis covered the full geographic range of cheetahs in Iran (28–38° N, 50–59° E), including all places where at least one confirmed record of cheetah presence has been documented since 2001 (Supporting Information Table S1; Fig. 1). This 587 500 km^2-landscape is characterized by desert and xeric shrubland biomes (Freitag, 1986). Human population density is generally low, and major populated areas exist only on the northern and western edges where some large cities are located. Extensive road and national railway networks exist within this landscape, including main lines to Iran's capital Tehran. In addition to the cheetah reserves (Supporting Information Table S1), the study area includes several additional protected areas and No-Hunting Areas managed by Iran Department of Environment which collectively cover *c*. 18% of the analysis area (Fig. 1).

Source locations

Given the lack of high-quality dispersal data, we selected source locations to model population connectivity at a uniform density across the probable extent of the landscape occupied by cheetahs (e.g. Riordan *et al.*, 2016; Supporting Information Table S1). There is no consensus about the size of the Iranian cheetah population, but recent findings suggest that the total population is less than 70 individuals (Farhadinia *et al.*, 2014). We therefore considered a conservative scenario, and used the lower bound of estimates proposed by Jourabchian & Farhadinia (2008) for cheetah reserves (Supporting Information Table S1). Specifically, we modeled a population size of 50 Asiatic cheetahs spread into 14 reserves (Fig. 1). We defined source locations for connectivity modeling as 10 sets of 50 randomly distributed locations throughout these reserves, allocating simulated cheetahs to each reserve according to that reserve's expected minimum population size (Supporting Information Table S1). As our main objective was to examine the variability in the landscape permeability, rather than abundance or habitat preference, the distribution of source points across the study landscape is more important than actual number of points (Riordan *et al.*, 2016).

Environmental data

We selected landscape predictors related to habitat use and movement of cheetahs (Marker *et al.*, 2008; Houser, Somers & Boast, 2009; Cozzi *et al.*, 2013; Welch *et al.*, 2015): topographic complexity, surface water, human development and landscape protection level (Table 1). All GIS data were resampled to 500 m in order to maintain a consistent grain size for our subsequent analyses. Data preparation was performed in QGIS 2.6.1 (QGIS Development Team, 2014) and ArcInfo Workstation (ESRI, 2010).

We used bilinear interpolation to resample topographical slope (Table 1) from 90-m to 500-m pixel size and then used an inverted Gaussian function, as described in Cushman *et al.* (2006), to assign minimum resistance of 1 at 15% average slope within a 500-m pixel with resistance rising with a standard deviation of 20% slope to a maximum of 10. This function assigned low resistance to moderately rough areas, moderate resistance to areas that are flat, and high resistance to areas with very steep average slope within a 500-m pixel because that Asiatic cheetahs show a preference for hilly terrain, eroded foothills and dry watercourses (Hunter *et al.*, 2007), but are thought to be absent from extensive sand plains (Heptner & Sludskii, 1972), and likely avoid areas of extremely rough topography.

Resistance due to landscape protection level and roads were represented as categorical functions (e.g. Cushman

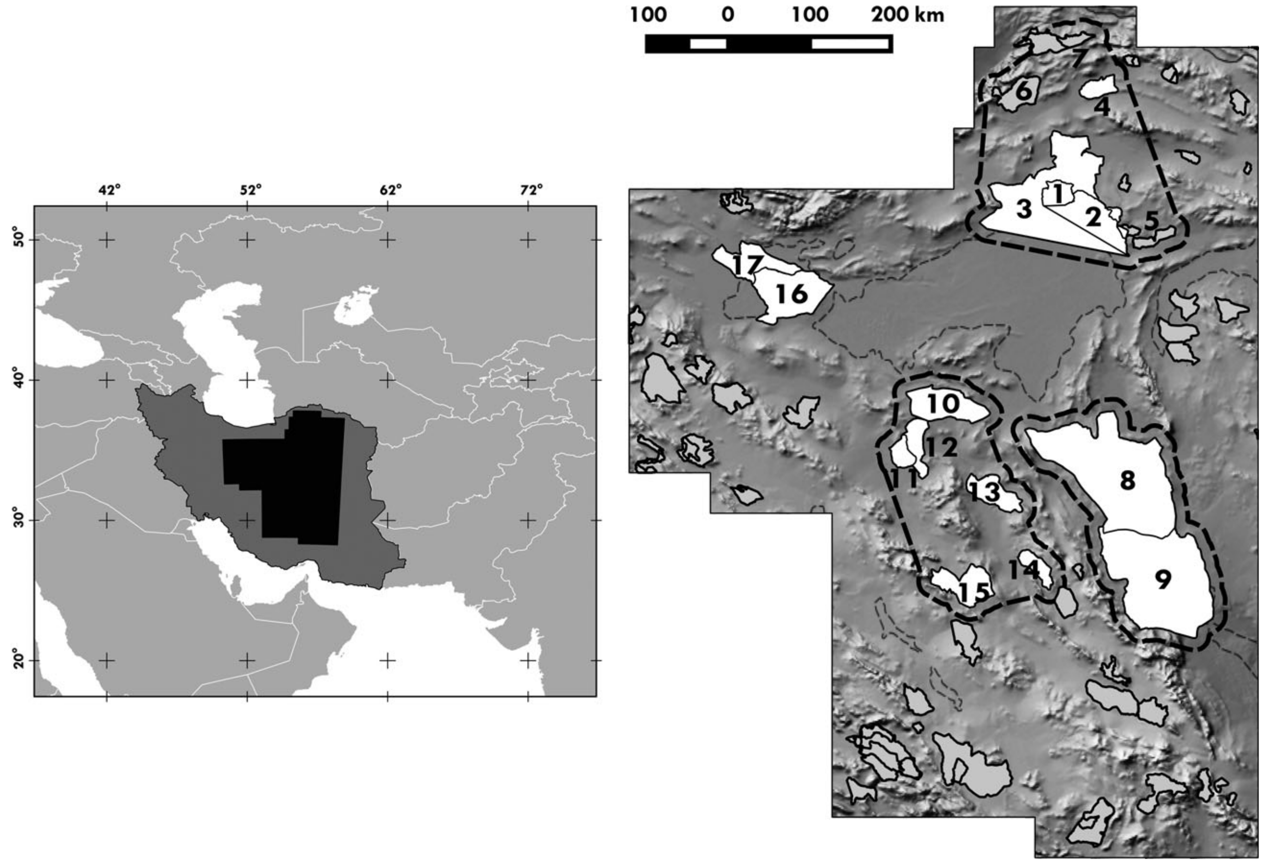

Figure 1 Location of the study landscape in Iran showing cheetah reserves with source locations (white polygons) and other protected areas (gray polygons). Dashed lines display the three perceived cheetah nuclei, or core populations, where dispersal routes between reserves are thought to exist (after Farhadinia *et al.*, 2014): (a) Northern nucleus: 1. Touran NP, 2. Touran WR, 3. Touran PA, 4. Miandasht WR, 5. Dorouneh PA, 6. Khosh Yeilaq WR, 7. Qorkhod PA; (b) Eastern nucleus: 8. Naybandan WR, 9. Darband-e Ravar WR; (c) Central nucleus: 10. Abbas Abad WR, 11. Siah-Kouh NP, 12. Siah-Kouh PA, 13. Dare-Anjir WR, 14. Bafq PA, 15. Kalmand PA. 16. Kavir NP and 17. Kavir PA are the only cheetah reserves outside the perceived nuclei. NP: National Park, WR: Wildlife Refuge, PA: Protected Area. See Supporting Information Table S1 for the perceived or minimum population size of cheetahs in key reserves.

et al., 2006; Table 1). We considered landscape protection level and availability of prey, known to be highly correlated with presence of protected areas (Farhadinia *et al.*, 2013), to be crucial for facilitating Asiatic cheetah movement. Iranian protected areas are classified into four broad categories with strict (thus lower resistance) to low protection and law enforcement (Table 1). We did not consider No-Hunting Areas, as these areas are often subject to various anthropogenic disturbances similar to unprotected lands. Because of lack of data on traffic volume, we considered only road type, assigning high resistance to major roads and lesser resistance to minor roads (Table 1). We also assigned high resistance values to lakes and wetlands (Table 1).

The available layers for current human population density are coarse and outdated for Iran. Therefore, we used nighttime satellite imagery data (Table 1) as proxy for human development and population density (e.g. Elvidge *et al.*, 2007). We used a linear function to transform the layer for year 2013 to assign a minimum resistance value of 1 at 0 light and 100 at maximum with intermediate values scaled linearly in between (e.g. Cushman *et al.*, 2006; Table 1).

Resistant kernel and factorial least-cost path analysis

We combined two connectivity modeling approaches. The first is the resistant kernel (Compton *et al.*, 2007). The resistant kernel computes the cost-distance kernel from each source location, scaling it such that the volume of the kernel reflects the population density at that location, and summing all kernels to create a cumulative resistant kernel surface which reflects the expected frequency of dispersal through all locations in the landscape. The resistance layer is used as weights in the dispersal function, such that the expected density of dispersing individuals is down-weighted by the cumulative cost from the source, following the least-cost route (Compton *et al.*, 2007). The initial expected density was set to one for each source cell. The predicted density in each

Table 1 Metadata and classification of resistance values in the resistance layers used in the analysis

Variable and description	Assigned resistance values	Lower effect	Higher effect
Roughness			
An inverted Gaussian function of slope[a]	Minimum value of 1 at 15% average slope within a 500-m pixel, and rises with a standard deviation of 20% slope to maximum of 10	Same optimal and standard deviation, but maximum resistance of 5	Same optimal and standard deviation, but maximum resistance of 20
Roads[b]			
Primary road: primary highway, trunkroad and motorway	100	50	200
Secondary road: highways that connect smaller towns, subdivisions, and neighborhoods	50	25	100
Tertiary road: residential and local roads	20	10	40
Railroad: railway network	50	25	100
No road	1	1	1
Water[c]			
Surface water including terminal basins, salt lakes and seasonal wetlands	50	25	100
Human development[d]			
Night-time light emission imagery as a proxy of human development[c]	A linear function with minimum value of 1 at 0 light and 100 at maximum with intermediate values scaled linearly in between	Same linear function with minimum 1 and maximum 50	Same linear function with minimum 1 and maximum 200
Protection level[e]			
National Park (IUCN Category II): strict protection, human disturbance is minimum, good populations of ungulates	1	0.5	2
Wildlife Refuge (IUCN Category IV): intermediate protection level, often good populations of ungulates	2	1	4
Protected Area (IUCN Category V): lower protection level, human disturbance varies, local ungulate populations exist but with different status	5	2.5	10
Unprotected land: includes No-Hunting Areas, minimum to no law enforcement, highest level of human disturbances, ungulate populations are either non-existent or very small and sparse	20	10	40

[a]Derived from Digital Elevation Model (DEM) produced by the USGS/NASA Shuttle Radar Topographic Mission (http://srtm.csi.cgiar.org) at 3-arc second resolution (approximately 90 m at the equator).
[b]OpenStreetMap: http://www.openstreetmap.org. Downloaded on 28 August 2015.
[c]Derived from GlobCoverV2.3 at 300-m resolution, ESA Globcover Project: http://www.esa.int/due/ionia/globcover.
[d]Data provided by the defense meteorological satellite program (DMSP) operational linescan system (OLS) at NOAA National Geophysical Data Center: http://ngdc.noaa.gov/eog/dmsp/downloadV4composites.html.
[e]Data provided by Iran Department of Environment as of May 2013.

surrounding cell is predicted density relative to the maximum at a source cell. The model calculates the expected relative density of each pixel of the landscape, given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape (Compton *et al.*, 2007; Cushman, Chase & Griffin, 2010). The resistant kernel approach to connectivity modeling has several advantages over most corridor prediction approaches: (1) it is spatially synoptic and provides prediction and mapping of expected dispersal rates for every pixel in the study extent (Compton *et al.*, 2007); (2) scale dependency of dispersal ability can be directly included in the resistant kernel approach (Cushman *et al.*, 2010); and (3) resistant kernel modeling is computationally efficient (Cushman, Landguth & Flather, 2013b). The second approach is a factorial implementation of least-cost path analysis (e.g. Cushman *et al.*, 2009, 2010). The factorial least-cost path analysis method is based on computing the least-cost paths across the resistance surface between all pairs of source points, and then summing these paths to produce a spatially synoptic map of least-cost path density across the population (e.g. Cushman *et al.*, 2009; Cushman, Lewis & Landguth, 2014). We implemented both of these methods using the UNIversal CORridor network simulator, UNICOR (Landguth *et al.*, 2012), which is a Python-based connectivity modeling tool explicitly designed to efficiently implement resistant kernel and factorial least-cost path connectivity analyses, which are not widely available in other connectivity modeling software.

To account for uncertainties regarding movement behavior data of Asiatic cheetahs, we analyzed four distance thresholds in the resistant kernel analyses (100 000, 200 000, 300 000 and 400 000 cost units, which represent movement abilities of 100, 200, 300 and 400 km, respectively, through optimum low resistance habitat). In the context of this analysis, we treat these distances as hypothetical maximal dispersal distances, and therefore they represent limits to connectivity between populations. We did not use a distance threshold in the factorial least-cost path modeling in order to produce a broad-scale map of the optimal long-range linkages among cheetah populations (e.g. Cushman *et al.* 2013c).

Analyzing connectivity

The analyses described above produced four cumulative-resistant kernel maps (i.e. one for each dispersal ability scenario). These maps indicate the distribution of connected populations and the spatial variation in expected densities of dispersers (Cushman *et al.*, 2010). We used FRAGSTATS v4.2 (McGarigal *et al.*, 2002), the most widely used landscape pattern analysis software, to calculate four landscape metrics quantifying the extent and fragmentation of the cheetah population across dispersal abilities: (1) the percentage of the landscape (PLAND), which quantifies the extent of the study area that is predicted to be connected by dispersal; (2) correlation length (FRAGSTATS metric GYRATE_AM), which provides a measure of the expected distance that one can move through connected habitat before reaching the edge when dropped in a random place and moving in a random direction; (3) largest patch index (LPI), which is the extent of the largest patch of connected habitat as a proportion of the size of the study area; and (4) number of isolated patches of habitat predicted to be reachable by cheetahs (NP), which provides an intuitive measure of the degree of fragmentation of the population. These class-level metrics quantify the impact of each dispersal scenario on the extent and fragmentation of connected habitat patches (McGarigal *et al.*, 2002) and have been frequently used in this manner in past connectivity assessment studies (e.g. Cushman & Landguth, 2012; Cushman, Landguth & Flather, 2012; Elliot *et al.*, 2014; Hand *et al.*, 2014; Cushman *et al.*, 2015).

The factorial least-cost path corridors network uniting all source cells was not spatially analyzed with FRAGSTATS, but was used to visually interpret the pattern of broad-scale potential connectivity across the Iranian cheetah meta-population to identify areas optimally suited for habitat protection, restoration or establishment of stepping stone populations through reintroductions. In addition, we identified all locations where major roads cross the predicted corridor routes between the cheetah core patches, and mapped the 29 strongest corridor road crossing locations.

Sensitivity analysis to evaluate uncertainty in resistance parameters

The resistance levels set for landscape variables (Table 1) were assigned based on knowledge of the ecology of the species and information from other carnivores in other ecosystems. To account for the uncertainty in these parameters, we conducted a sensitivity analysis, recalculating resistant kernel and factorial least-cost path analyses, but varying the resistance assigned to each parameter at a lower (half that of the original resistance layer) and higher (twice that of the original resistance layer) resistance (Table 1). This resulted in a total of 36 additional UNICOR kernel analyses (two for each variable, at the lower and higher resistance for that variable, holding resistance of the other variables constant at their original levels, across the four levels of dispersal ability: 100 000, 200 000, 300 000 and 400 000 cost units). We calculated the FRAGSTATS metrics for each of these and produced a boxplot for each metric, reflecting the effects of uncertainty in resistance levels on the extent, largest patch index, and number of isolated patches of connected habitat.

We also evaluated the sensitivity of the factorial least-cost path network by recalculating it eight times, two for each variable, at the lower and higher resistance values for that variable, holding resistance of the other variables constant at their original levels. We calculated the absolute relative difference between the factorial least-cost path density maps for each variable at the lower and higher resistance values [abs(variable1highR – variable1lowR)/variable1highR] to determine the sensitivity of changing resistance value of each variable on the factorial least-cost path network.

Results

After applying resistant kernels and factorial least-cost path analyses, we predicted connected cheetah habitat patches (i.e. areas with kernel values above zero) to be concentrated in three sub-regions in the study area: (1) north-central (the “northern nucleus”); (2) southern (“central” plus “eastern” nuclei); and (3) north-western (i.e. Kavir NP and PA). These three core populations were predicted to be broken up into a total of eight isolated patches if dispersal of Asiatic cheetahs is limited to 100 km (Fig. 2a). We predicted that if cheetahs are able to disperse 200–300 km in this landscape, the cheetah population consists of three isolated patches (Fig. 2b and c). Only with a dispersal ability of 400 km or larger, would the north-western core area be predicted to be connected to one of the two core patches (i.e. to the southern patch; Fig. 2d). However, we observed that the north-central core remained isolated even at high cheetah dispersal abilities. Overall, we predicted relatively weak internal migration rates within all the three core patches, due to the very small size

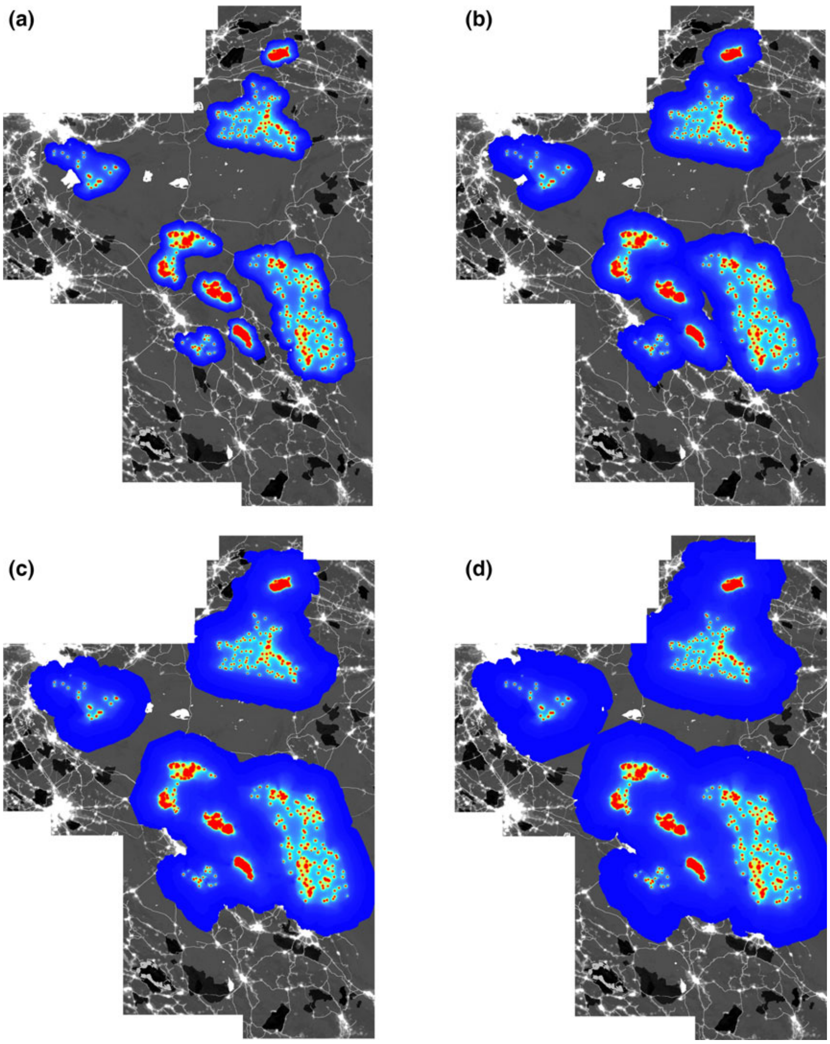

Figure 2 Resistant kernel predicted connectivity for the Asiatic cheetah population in Iran from 10 random draws of 50 points at a uniform density within protected areas that have recently confirmed to contain cheetahs (i.e. cheetah reserves), with four different distance thresholds: (a) 100 000; (b) 200 000; (c) 300 000; and (d) 400 000 cost units. Connectivity (intensity of pixel use) is shown on a color scale from red to blue, with red indicating greater amounts of movement.

of the cheetah population believed to exist in each subregion, and the relatively high resistance to movement outside of existing protected areas (Fig. 2a–d).

PLAND ranged from 19.93% to 56.24% of the study landscape across dispersal scenarios (Table 2). NP was predicted to decrease sharply with dispersal abilities of ≥200 km, and GYRATE_AM of connected habitat was predicted to increase with increasing dispersal abilities (Table 2). The LPI increased almost linearly with increasing dispersal ability (Table 2). GYRATE_AM showed large increases at dispersal abilities >100 km, with values increasing by 53% between dispersal ability scenarios of 100 and 200 km.

A factorial combination of long-distance least-cost corridors predicted by the UNICOR model is shown in Supporting Information Fig. S1, indicating the best predicted routes to connect the three core populations. The predicted corridors were produced without considering dispersal thresholds, so they are not functional in the sense that cheetahs would be expected to use them. Expected dispersal distances are depicted by the extent of the cumulative resistant kernel maps (Fig. 2a–d), and the factorial least-cost map (Supporting Information Fig. S1) extends far beyond the extent of the cumulative kernel maps, even at the largest dispersal ability simulated. We predicted strong corridors between north-central and southern core areas, yet the predicted corridor to the north-western core patch is generally weak (Supporting Information Fig. S1). We identified all locations where major roads cross the predicted corridor routes between the north-central and southern core patches, and mapped the 29 strongest corridor road crossing locations (Fig. 3; Supporting Information Table S2).

Table 2 FRAGSTATS results across the landscape resistance with four levels of dispersal ability for the Asiatic cheetah in Iran

FRAGSTATS	Dispersal ability (cost units[b])			
Metric[a]	100 000	200 000	300 000	400 000
PLAND	19.93	33.19	44.57	56.24
NP	8	3	3	2
LPI	19.93	20.53	26.04	39.86
GYRATE_AM[c]	63323.37	118804.69	129817.96	188094.67

[a]PLAND (percentage of landscape in connected habitat): quantifies how much of the study landscape is predicted to be connected or core habitat for the target species; NP (number of individual patches of connected habitat); LPI (largest patch of connected habitat index): reports the extent of the largest patch of connected or core habitat, as a proportion of the size of the study extent; GYRATE_AM (FRAGSTATS metric of correlation length of connected habitat): provides a measure of the average distance an organism can move within a patch before encountering the patch boundary from a random starting point.

[b]Equivalent to meters that can be moved through ideal (optimum low resistance) habitat, i.e. 1 resistance.

[c]GYRATE_AM gives a global measure of the connectivity of the landscape which is a more relevant functional measure of habitat availability than basic measures such as patch size, nearest neighbor distance, or percentage of the landscape in occupied habitat (McGarigal *et al.*, 2002).

Sensitivity analysis

Results of the sensitivity analysis are shown in Figures 4 and 5 and Supporting Information Figs S2 and S3. Varying resistance parameters for each landscape feature across a range from half to twice the value in the originally estimated resistance surface had only modest effects on the predicted extent, pattern and intensity of connectivity across the study area using resistant kernel analysis, across predicted dispersal thresholds (Figs 4 and 5). The one exception was for the variable "protection level" (Table 1). Specifically, varying resistance in all other parameters had little effect on the extent or fragmentation of connected habitat, while doubling resistance of unprotected areas resulted in roughly a 30% decrease in extent of the landscape connected by dispersal (Fig. 4a), and even larger decreases in the extent of the largest connected patch (Fig. 4b), and correlation length of connected habitat (Fig. 4d). Conversely, cutting the resistance of unprotected areas in half resulted in equivalent magnitudes of increased connectivity. Figure 5 shows changes in the area predicted to be connected by dispersal at the high and low resistance levels for protection level across the four dispersal abilities. The figure shows that connectivity is highly sensitive to dispersal ability and at any given dispersal ability is substantially greater when resistance of unprotected areas is relatively low compared to that of protected areas.

The factorial least-cost path predictions of the location and strength of the corridor network were largely insensitive to variation in resistance parameters. Specifically, varying resistance value for each variable from half to twice its maximum resistance did not change the locations of the factorial least-cost path network considerably (Supporting Information Fig. S2). The one moderate exception was for the variable protection level. Specifically, the mean relativized absolute difference in the predicted least-cost path density maps produced for the resistance layer when protected areas were given half, and when they were given twice, the original maximum resistance was 13.6 times greater than the next most sensitive variable (topographical roughness), indicating that, like for the resistant kernel predictions, factorial least-cost path corridor network is most strongly affected by the resistance of unprotected areas (Supporting Information Fig. S3). However, the locations and relative strength of the least-cost path network was qualitatively similar between the two parameterizations of resistance due to protection level, indicating that predictions of least-cost path routes are robust to uncertainty in relative resistance.

Discussion

We found that the cheetah population in Iran is structured into three main patches that are predicted to be mutually isolated from one another even at large dispersal abilities. Our factorial least-cost path analysis identified optimal routes between these sub-populations that could guide restoration and reintroduction efforts to provide linkage and stepping stone populations to re-establish connectivity across the cheetah meta-population in Iran. This information could enable conservationists and managers to evaluate the optimality and effectiveness of different landscape conservation strategies (Cushman *et al.*, 2013*c*).

Reliable spatially explicit predictions of population connectivity are limited by uncertainty about species distributions, influence of landscape features on animal movement and poor knowledge of species' dispersal abilities (Sawyer *et al.*, 2011; Cushman *et al.*, 2013*b*). However, even in the absence of detailed empirical data for a focal species, it can be useful to model range-wide population connectivity to develop hypotheses for further testing and to identify results that are robust to different dispersal abilities and patterns of landscape resistance (Hand *et al.*, 2014; Riordan *et al.*, 2016). Novel analytical tools used here aid researchers in addressing a number of conservation-oriented questions (Landguth *et al.*, 2012; Cushman *et al.*, 2013a). In addition, researchers should use sensitivity analyses to evaluate uncertainty in both dispersal ability of the target species (e.g. Elliot *et al.*, 2014; Hand *et al.*, 2014) and uncertainty regarding landscape resistance parameterization. Results of any connectivity analyses are dependent on accurate data of target species' distribution, dispersal distance and relative landscape resistance to movement (Sawyer *et al.*, 2011; Cushman *et al.*, 2013*b*). Therefore, although our results must be interpreted as hypotheses requiring verification by further research, implications of our results are substantial to help prioritizing further research and conservation actions.

The Asiatic cheetah is highly mobile, with single males, male coalitions, and females with cubs documented to move between multiple reserves in consecutive years (Farhadinia *et al.*, 2013; Gholikhani & Behnoud, 2015). For example,

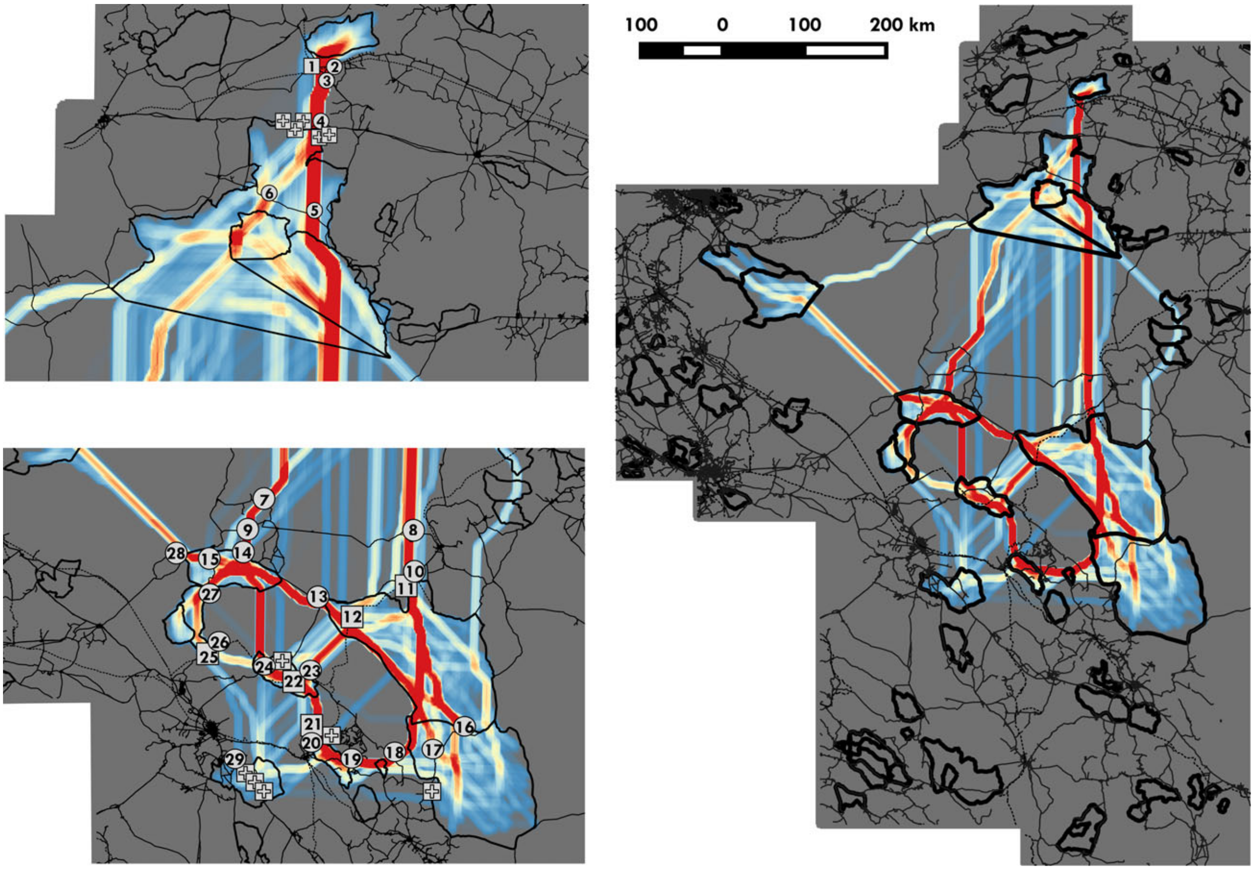

Figure 3 Key fracture zones for the Asiatic cheetah in Iran as overlay of the cumulative factorial least-cost path corridor and transportation networks map. The color ranges from red (high predicted movement rate) to blue (low predicted movement rate). The 29 highways and railroads intersecting the strongest corridors between the core patches are labeled in gray circles (intersecting highways) and rectangles (intersecting railroads). Roads are shown in dark lines and railroads in dashed lines, and protected areas as dark polygons. See Supporting Information Fig. S1 and Table S2 for details.

Farhadinia *et al.* (2013) reported an adult female cheetah moved a minimum of 150 km (calculated as a straight line between camera trap stations) multiple times between two reserves in the southern core habitat patch during 2009–2013. Her three cubs later formed a male coalition and ranged across multiple reserves in this region (Farhadinia *et al.*, 2013). Another male cheetah has been documented in Dare-Anjir Wildlife Refuge (WR) (Fig. 1), around 215 km from where the animal was first detected three years ago (Gholikhani & Behnoud, 2015). Recently, this male has been photographed in Naybandan WR about 9 months after its first detection in Dare-Anjir WR (ICS, 2015). Discovery of a dead adult male cheetah in vicinity of Touran Protected Area, about 52 km away from his natal range (ICS, 2016), confirms such movements between multiple reserves in the north-central core patch as well. The biological drivers of long-distance movement of Asiatic cheetahs are not yet understood, but low availability and density of ungulate populations might be a trigger (Farhadinia *et al.*, 2013). Given this limited empirical knowledge of cheetah dispersal distances in Iran, we feel the range of dispersal abilities we simulated encapsulates the expected range of dispersal, with evidence suggesting our 200 km scenario likely most closely reflects actual cheetah dispersal in this population.

Our analysis predicted that the main source of fragmentation in the study area is the relatively high resistance outside protected areas leading to isolated occupied patches and large areas where cheetahs are likely to only occur at very low frequency. The dominant effect of land-use, in particular the relative resistance of unprotected areas compared with protected areas, was robust to the sensitivity analysis, suggesting that protected area status has a large contribution to population connectivity and that the relative resistance of the surrounding matrix of unprotected land is the most important driver of connectivity. A similar result was seen in Elliot *et al.* (2014) who found that while vegetation, roads and human population all affected connectivity, protected area status was the most important predictor of the occurrence and dispersal of African lions *Panthera leo*, with very high resistance to movement in unprotected areas.

Our results also predict that road and railway networks may act as partial barriers increasing isolation of the core

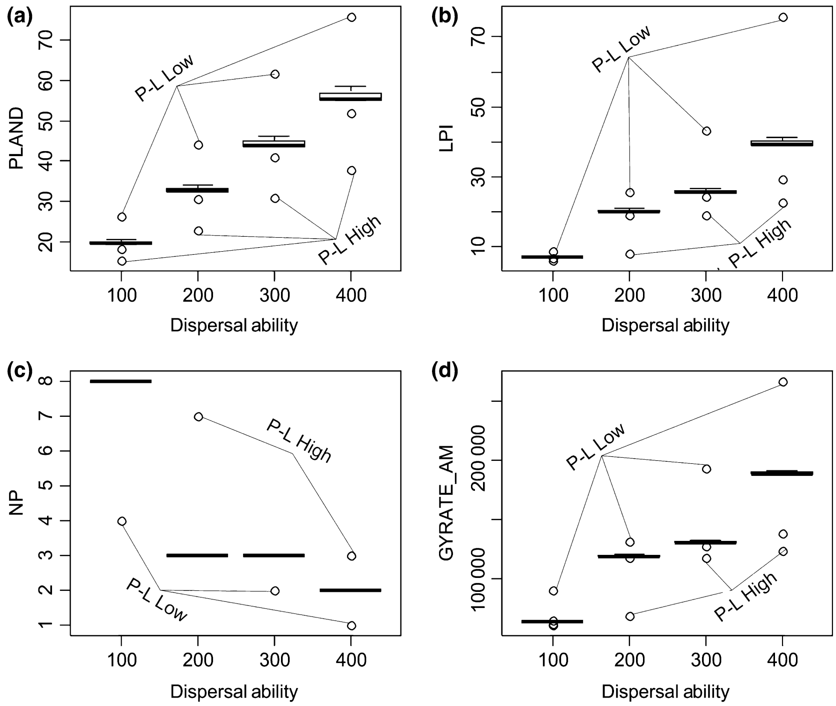

Figure 4 Boxplots showing variability in FRAGSTATS metrics calculating extent and fragmentation of connected habitat across all combinations of dispersal ability (100 000; 200 000; 300 000; 400 000 cost units) and relative resistance (−50%, as estimated, + 100%) across all landscape variables (topographic complexity, human development (including roads and human footprint), and landscape protection level). In all cases, there was very little variability as a function of relative resistance, except for "protection level" (P-L), in which connectivity was much higher when resistance was relatively low outside protected areas (P-L Low) compared to when resistance was relatively high (P-L High) outside protected areas. See Table 2 for explanation of FRAGSTATS metrics "PLAND", "LPI", "NP", and "GYRATE_AM".

populations, aside from having a direct impact on cheetah's survival. Similar to Cushman *et al.* (2009) and Mateo-Sánchez, Cushman & Saura (2014), we used factorial least-cost path analysis to identify locations where major roads cross the predicted corridor routes between the north-central and southern core patches. These intersections are potential barrier locations, and locations of potentially elevated cheetah mortality risk due to traffic collisions (Cushman *et al.*, 2013*c*). Between 2001 and 2014, at least 11 Asiatic cheetah individuals have been killed in road accidents (Farhadinia *et al.*, 2014; Fig. 3). This represents a very high risk for such an extremely small population, and road mortalities have been documented to be the largest threat to viability of other small populations of large felids, such as the Florida panther *Puma concolor coryi* (Schwab & Zandbergen, 2011). All cheetah vehicle collisions occurred on the roads intersecting dispersal routes predicted in this study (Fig. 3), which is anecdotal validation of our connectivity predictions (Cushman *et al.*, 2013c). In addition, the match between observed mortalities and predicted important highway crossings provide a way to prioritize locations for management actions to mitigate mortality risk (e.g. Cushman *et al.*, 2013c). Given the low likelihood that large-scale road risk mitigation efforts will be undertaken in Iran in the near future, it is essential to identify and employ less expensive and locally feasible techniques to minimize the risk of cheetah-vehicle collisions.

The connectivity maps (Supporting Information Fig. S1; Fig. 3) highlight areas that likely support infrequent, but critical, movements between cheetah populations in Iran. Presently, no protected areas are designated along the potentially important dispersal routes between the north-central and southern core patches (Fig. 3). The network of least-cost paths provides guidance on the optimal places to position stepping stones (i.e. new protected areas) between these three predicted core populations, which may offer connectivity between the extant populations. Specifically, ideal stepping stone locations would be areas that are on major predicted least-cost path connectivity routes (Fig. 3), but outside of current resistant kernel population centers (Fig. 2). Candidate locations are No-Hunting Areas already designed between a number of cheetah reserves in Yazd Province, and presently unprotected landscape between Miandasht WR and Touran Complex in the north-central core patch, and between Kavir Complex in the north-west through Semnan Province to the north-central core patch, and southward to Abbas Abad WR and Siah-Kouh Complex in Esfahan Province (Figs 1 and 3). We believe protecting the core populations should be highest priority for cheetah conservation in Iran, but it is also critically important to protect corridors between patches. Our analyses support the hypothesis that the north-western core patch might be functionally isolated (e.g. Farhadinia *et al.*, 2014). If the current size of cheetah

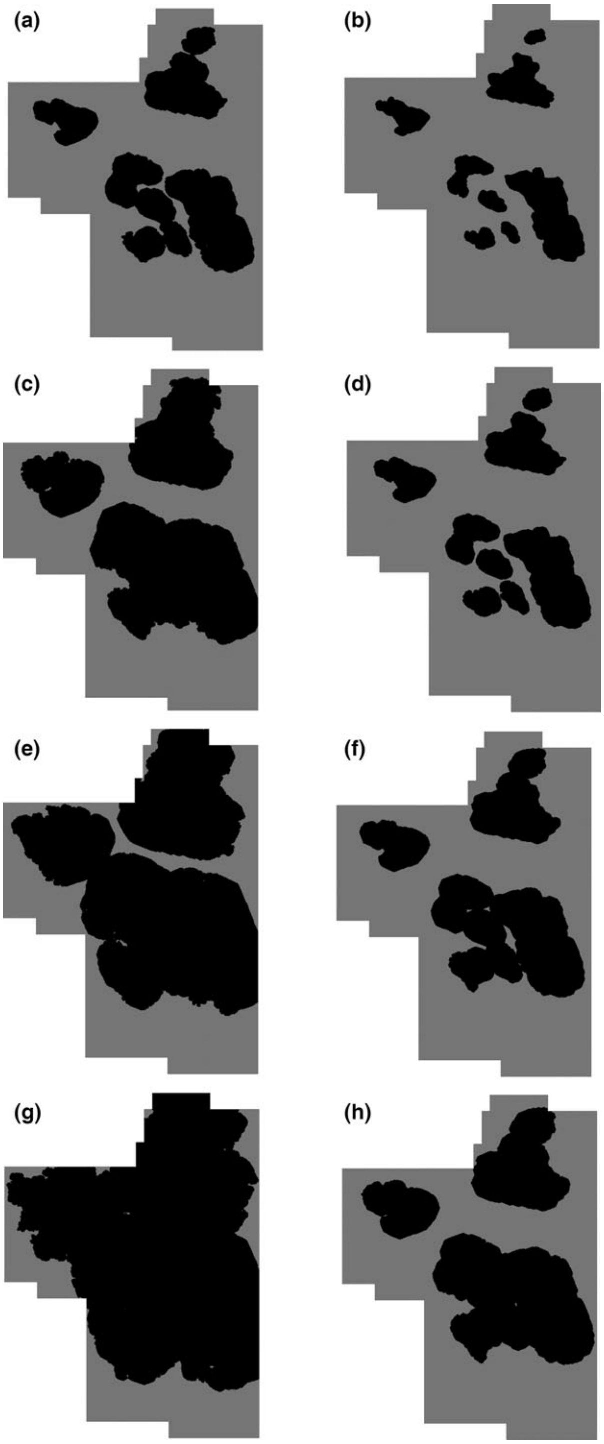

Figure 5 Plots of area predicted to be connected by cheetah dispersal across the four dispersal abilities (a,b: 100 000; c,d: 200 000; e,f: 300 000; and g,h: 400 000 cost units) for resistance surface setting resistance of unprotected areas to ½ that in the original parameterization (a,c,e,g) and two times that in the original parameterization (b,d,f,h).

populations in these core habitats are as small as believed (Supporting Information Table S1), it is likely that the northwestern core patch will go extinct in the near future and is unlikely to be recolonized through natural dispersal.

The key factor affecting cheetah numbers in Iran is believed to be the disappearance of ungulates through illegal hunting and anthropogenic loss of habitat (Farhadinia, 2004; Hunter *et al.*, 2007; Breitenmoser, Alizadeh & Breitenmoser-Würsten, 2009). However, viable populations of ungulates are presently persisting in the majority of cheetah reserves (Jourabchian & Farhadinia, 2008; CACP, unpubl. data). Thus, conservation efforts should focus on protecting and expanding ungulate populations, both in the core areas identified as most important in this study, as well as candidate stepping stones. In addition, although cheetahs are strictly protected under Iranian law, direct persecution by nomadic pastoralists is still a significant threat (Hunter *et al.*, 2007; Farhadinia *et al.*, 2014). In our scenarios of high dispersal ability and relatively low resistance, much of the landscape in the study area was predicted to be connected by dispersal. A similar result was found by Kramer-Schadt *et al.* (2004) who simulated Eurasian lynx *Lynx lynx* dispersal in Germany with an individual-based model that combined cost-weighted dispersal with context specific mortality risk. Their results indicated that most suitable patches could be interconnected by movements of dispersing lynx. But, when realistic mortality risks were applied, most patches become isolated. Thus, their results suggested that patch connectivity is limited not so much by the distribution of dispersal habitat, but by the high mortality of dispersing individuals and argued that effective conservation must focus more on reducing mortality rather than solely investing in habitat restoration. In the present context, it is important for future work to explore the interactions of landscape connectivity and mortality risk in affecting population size and connectivity of Asiatic cheetah populations in Iran. Individual-based spatially explicit simulation models such as CDPOP (Landguth & Cushman, 2010) offer a powerful framework to evaluate the interactions between mortality risk and movement, and quantify the relative importance of mortality and connectivity on viability and identify the key locations to mitigate mortality risk as well as connectivity.

Our analyses were based on landscape resistance parameters and dispersal abilities estimated based on cheetah ecology. We utilized uncertainty analysis to evaluate the sensitivity of results to both sets of parameters, and found, as in Cushman *et al.* (2012) and Hand *et al.* (2014), that dispersal ability had a much larger effect than variation in estimates of landscape resistance. However, errors in estimating landscape resistance can have a large impact on predictions of population connectivity (e.g. Cushman *et al.*, 2014). Therefore, it is important for the results we identified here to be tested, validated and refined using empirical methods, such as landscape genetics (e.g. Cushman *et al.*, 2006) or path-level modeling based on GPS telemetry (e.g. Cushman & Lewis, 2010; Elliot *et al.*, 2014). This is particularly true since connectivity is mediated by juvenile dispersal, and dispersing animals often utilize the landscape very differently than resident adults, with often less avoidance of areas with relatively high risk and low habitat suitability (e.g. Palomares *et al.*, 2000; Elliot *et al.*, 2014).

In response to the global extinction crisis, the scientific community has put significant effort to understand and quantify extinction risk, and to bridge the gap with policy-makers and governments for effective conservation of endangered wildlife populations. However, in many cases, the conservation targets are simply to maximize short-term persistence, rather than long-term viability, with compromises resulting from complex political and financial realities (Traill *et al.*, 2010). Despite some uncertainty related to parameterization, we feel that action must be taken with the best information that is available given the extreme vulnerability of the cheetah population in Iran. For the Asiatic cheetah to avoid extinction in its last remnant population, it is likely that several issues must be simultaneously addressed, with protection of core populations, improvement of prey biomass across the range, reintroduction of stepping stone populations, improvement of connectivity and reduction of direct mortality through road-kill and direct persecution likely to each be necessary for population viability.

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References

Asadi, H. (1997). *The environmental limitations and future of the Asiatic cheetah in Iran*. Tehran, Iran: Progress report to IUCN/SSC Cat Specialist Group.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev.* **88**, 310–326.

Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *J. Wildlife. Manage.* **59**, 228–237.

Breitenmoser, U., Alizadeh, A. & Breitenmoser-Würsten, Ch. (2009). *Conservation of the Asiatic cheetah, its natural habitat and associated biota in the I.R. of Iran*. Terminal evaluation of the project, Tehran, Iran: CACP, 73 pp.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Edmonds, O.R.P., Sechrest, W., Orme, D.L. & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241.

Ceballos, G. & Ehrlich, P.R. (2002). Mammal population losses and the extinction crisis. *Science* **296**, 904–907.

Compton, B., McGarigal, K., Cushman, S.A. & Gamble, L. (2007). A resistant kernel model of connectivity for vernal pool breeding amphibians. *Conserv. Biol.* **21**, 788–799.

Cozzi, G., Broekhuis, F., McNutt, J.W. & Schmid, B. (2013). Comparison of the effects of artificial and natural barriers on large African carnivores: implications for interspecific relationships and connectivity. *J. Anim. Ecol.* **82**, 707–715.

Cushman, S.A. & Landguth, E.L. (2012). Multi-taxa population connectivity in the Northern Rocky Mountains. *Ecol. Model.* **231**, 101–112.

Cushman, S.A. & Lewis, J.S. (2010). Movement behavior explains genetic differentiation in American black bear. *Land. Ecol.* **25**, 1613–1625.

Cushman, S.A., McKelvey, K.S., Hayden, J. & Schwartz, M. (2006). Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *Am. Nat.* **168**, 486–499.

Cushman, S.A., McKelvey, K.S. & Schwartz, M. (2009). Using empirically derived source destination models to map regional conservation corridors. *Conserv. Biol.* **23**, 368–376.

Cushman, S.A., Chase, M. & Griffin, C. (2010). Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In *Spatial complexity, informatics, and wildlife conservation*: 349–367. Cushman, S.R. & Huettmann, F. (Eds). New York: Springer.

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. *Divers. Distrib.* **6**, 844–854.

Cushman, S.A., McRae, B., Adriansen, F., Beier, P., Shirley, M. & Zeller, K. (2013a). Biological corridors and connectivity. In *Key topics in conservation biology 2*: 384–404. Macdonald, D. & Willis, K.J. (Eds). New York: Wiley.

Cushman, S.A., Landguth, E.L. & Flather, C.H. (2013b). Evaluating population connectivity for species of conservation concern in the American Great Plains. *Biodivers. Conserv.* **22**, 2583–2605.

Cushman, S.A., Lewis, J.S. & Landguth, E.L. (2013c). Evaluating the intersection of a regional wildlife connectivity network with highways. *Mov. Ecol.* **1**, 1–12.

Cushman, S.A., Lewis, J.S. & Landguth, E.L. (2014). Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. *Diversity* **6**, 844–854.

Cushman, S.A., Elliot, N.B., Macdonald, D.W. & Loveridge, A.J. (2015). A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. *Landscape Ecol.* 1–17. (Online DOI:10.1007/s10980-015-0292-3)

Darehshuri, B.F. (1978). Threatened cats of Asia: Asiatic cheetah. *Wildlife.* **20**, 396–397.

Elliot, N.B., Cushman, S.A., Macdonald, D.W. & Loveridge, A.J. (2014). The devil is in the dispersers: predictions of landscape connectivity change with demography. *J. Appl. Ecol.* **51**, 1169–1178.

Elvidge, C.D., Safran, J., Tuttle, B.T., Sutton, P., Cinzano, P., Pettit, D., Arvesen, J. & Small, C. (2007). Potential for global mapping of development via a Nightsat mission. *GeoJ* **69**, 45–53.

Farhadinia, M.S. (2004). The last stronghold: Cheetah in Iran. *Cat News* **40**, 11–14.

Farhadinia, M.S., Jourabchian, A., Eslami, M., Hosseini, F. & Nezami, B. (2008). Is food availability a reliable indicator of cheetah presence in Iran? *Cat News* **49**, 14–18.

Farhadinia, M.S., Akbari, H., Mousavi, S.-J., Eslami, M., Azizi, M., Shokouhi, J., Gholikhani, N. & 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.S., Eslami, M., Hobeali, K., Hosseini-Zavarei, F., Gholikhani, N. & Tak Tehrani, A. (2014). *Status of Asiatic cheetah in Iran: A country-scale assessment. Report to People's Trust for Endangered Species*. Tehran: Iranian Cheetah Society.

Firouz, E. (1974). Environmental and nature conservation in Iran. *Environ. Conserv.* **3**, 33–42.

Freitag, H. (1986). Notes on the distribution, climate and flora of the sand deserts of Iran and Afghanistan. *P. Roy. Soc. Edinb. B.* **89**, 135–146.

Gholikhani, N. & Behnoud, P. (2015). 215 km in the heart of the desert. *Yuznameh* **21**, 3 [in Persian].

Hand, B.K., Cushman, S.A., Landguth, E.L. & Lucotch, J. (2014). Assessing multi-taxa sensitivity to the human footprint, habitat fragmentation and loss by exploring alternative scenarios of dispersal ability and population size: a simulation approach. *Biodivers. Conserv.* **23**, 2761–2779.

Heptner, V.G. & Sludskii, A.A. (1972). Mammals of the Soviet Union. Vol II, Part 2 (Hyaenas and Cats). Moscow: Vyssha Shkola [in Russian]. English translation edited by R.S. Hoffmann (1992). Washington DC: Smithsonian Institute and the Natural Science Foundation. 784 pp.

Houser, A., Somers, M.J. & Boast, L.K. (2009). Home range use of free-ranging cheetah on farm and conservation land in Botswana. *S. Afr. J. Wildl. Res.* **39**, 11–22.

Hunter, L., Jowkar, H., Ziaie, H., Schaller, G., Balme, G., Walzer, C., Ostrowski, S., Zahler, P., Robert-Charrue, N., Kashiri, K. & Christie, S. (2007). Conserving the Asiatic cheetah in Iran: launching the first radio-telemetry study. *Cat News* **46**, 8–11.

Iranian Cheetah Society (ICS). (2015). *Multiple cheetah movements between the key reserves*. Available from: http://www.wildlife.ir/en/2015/10/11/just-released-multiple-cheetah-movements-between-the-key-reserves/ (accessed 20 October 2015).

Iranian Cheetah Society (ICS). (2016). *New cheetah death highlights the importance of identifying and preserving biological corridors*. Available from: http://www.wildlife.ir/en/2016/02/06/new-cheetah-death-highlights-the-importance-of-identifying-and-preserving-biological-corridors/ (accessed 21 February 2016).

Jourabchian, A. & Farhadinia, M.S. (2008). *Final report on Conservation of the Asiatic cheetah, its Natural Habitats and Associated Biota in Iran*. Tehran: CACP [in Persian with English summary].

Jowkar, H., Hunter, L., Ziaie, H., Marker, L., Breitenmoser-Würsten, C. & Durant, S. (2008). *Acinonyx jubatus* ssp. *venaticus*. The IUCN Red List of Threatened Species 2008: e.T220A13035342.

Karami, M. (1992). Cheetah distribution in Khorasan province. *Iran. Cat News* **16**, 4.

Kramer-Schadt, S., Revilla, E., Wiegand, T. & Breitenmoser, U. (2004). Fragmented landscapes, road mortality and patch occupancy: modelling influences on the dispersal of the Eurasian lynx. *J. Appl. Ecol.* **41**, 711–723.

Landguth, E.L. & Cushman, S.A. (2010). CDPOP: A spatially explicit cost distance population genetics program. *Mol. Ecol. Resour* **10**, 156–161.

Landguth, E.L., Hand, B.K., Glassy, J., Cushman, S.A. & Sawaya, M.A. (2012). UNICOR: a species connectivity and corridor network simulator. *Ecography* **35**, 9–14.

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

Marker, L., Dickman, A., Mills, M.G.L., Jeo, R.M. & Macdonald, D.W. (2008). Spatial ecology of cheetahs on north-central Namibian farmlands. *J. Zool.* **274**, 226–238.

Mateo-Sánchez, M.C., Cushman, S.A. & Saura, S. (2014). Connecting endangered brown bear subpopulations in the Cantabrian Range (north-western Spain). *Anim. Conserv.* **17**, 430–440.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002). *FRAGSTATS: spatial pattern analysis program for categorical maps*. University of Massachusetts, Amherst. Available from: www.umass.edu/landeco/research/fragstats/fragstats.html (accessed 16 September 2015).

Nowell, K. & Jackson, P. (1996). *Wild Cats. Status survey and conservation action plan*. Gland: IUCN.

Palomares, F., Delibes, M., Ferreras, P., Fedriani, J.M., Calzada, J. & Revilla, E. (2000). Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. *Conserv. Biol.* **14**, 809–818.

Purvis, A., Jones, K.E. & Mace, G.M. (2000). Extinction. *Science* **22**, 1123–1133.

Riordan, P., Cushman, S.A., Mallon, D., Shi, K. & Hughes, J. (2016). 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., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014). Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484.

Sawyer, S.C., Epps, C.W. & Brashares, J.S. (2011). Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *J. Appl. Ecol.* **48**, 668–678.

Schwab, A.C. & Zandbergen, P.A. (2011). Vehicle-related mortality and road crossing behavior of the Florida panther. *Appl. Geogr.* **31**, 859–870.

Traill, L.W., Brook, B.W., Frankham, R.R. & Bradshaw, C.J. (2010). Pragmatic population viability targets in a rapidly changing world. *Biol. Conserv.* **143**, 28–34.

Welch, R.J., Bissett, C., Perry, T.W. & Parker, D.M. (2015). Somewhere to hide: home range and habitat selection of cheetahs in an arid, enclosed system. *J. Arid Environ.* **114**, 91–99.

Zeller, K., McGarigal, K. & Whiteley, A.R. (2012). Estimating landscape resistance to movement: a review. *Landscape Ecol.* **27**, 777–797.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Asiatic cheetah dispersal corridors and habitat connectivity for the resistance map in Iran calculated by factorial least-cost path modeling in UNICOR. Warmer colors show greater amounts of movement, i.e. stronger corridors.

Figure S2. (a) Mean density of least-cost path network across all combinations of resistance values, including the original parameterization and cutting maximum resistance value in half and doubling maximum resistance value for each individual variable. (b) Coefficient of variation in density of least-cost path network across all combinations of resistance values, ranging from 0 in dark blue to 2.3 in dark red.

Figure S3. Comparison of the location and strength of predicted least-cost path network connecting all source points for: (a) resistance map where resistance of unprotected areas was half that in original parameterization, and (b) resistance of unprotected areas was twice that in original parameterization, and all other variables resistance is at original parameterization.

Table S1. The perceived (2004 and 2008 expert estimates) or minimum (2014 survey) population size of Asiatic cheetahs in key cheetah reserves in Iran. We selected source locations at a uniform density across 14 reserves with permanent records of cheetah presence since 2001 (shown in bold letters) to model cheetah population connectivity in Iran. We based our modeling scenario on a minimum population size of 50 cheetahs based on the lower bound of 2008 expert estimates.

Table S2. The strongest corridor road crossing locations identified as potential barrier locations, and locations of potentially elevated Asiatic cheetah mortality risk due to traffic collisions in Iran. See Fig. 4 for location of each barrier and the text for details.