A multi-scale, multi-species approach for assessing effectiveness of habitat and connectivity conservation for endangered felids

Mohammad Reza Ashrafzadeh[a,*], Rasoul Khosravi[b], Mohammad Ali Adibi[c], Atie Taktehrani[d], Ho Yi Wan[e], Samuel A. Cushman[f]

[a] *Department of Fisheries and Environmental Sciences, Faculty of Natural Resources and Earth Sciences, Shahrekord University, Shahrekord 8818634141, Iran*
[b] *Department of Natural Resources and Environmental Engineering, School of Agriculture, Shiraz University, Shiraz 71441-65186, Iran*
[c] *Semnan Provincial Office of Department of Environment, Semnan, Iran*
[d] *Iranian Cheetah Society (ICS), 14155-8549 Tehran, Iran*
[e] *School of Public and Community Health Sciences, University of Montana, 32 Campus Drive, Missoula, MT, USA*
[f] *USDA Forest Service Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ, USA*

ABSTRACT

Habitat loss and fragmentation are major threats to global biodiversity. Felids, among the many taxa experiencing population declines and range contraction around the world, are known as ecologically and politically powerful levers in conservation programs. Many felids are wide-ranging, and therefore, identifying and conserving their core habitat patches and corridors is essential for developing an umbrella strategy for protecting co-existing species. We employed a multi-scale, multi-species approach to model habitat suitability and connectivity for six felids across Iran. We identified potential core habitats and corridors of movement. We also quantified the spatial niche overlap to estimate the most important variables of habitat selection within the guild. We evaluated the effectiveness of conservation areas in conserving habitats and connectivity. Our findings revealed that each species' habitat use was influenced in a scale-dependent manner by different sets of environmental variables. Core habitats of felids were mostly located in conservation areas. We identified a number of small core habitats for most felids outside conservation areas. Maintaining corridors and stepping stone habitat patches along corridors may be needed to facilitate movement of individuals, especially between habitat remnants in unprotected areas. Our study highlights the importance of considering multiple spatial scales in management and conservation of carnivores. Our analysis shows that habitat selection and connectivity predictions are both very sensitive to scale, and incorrect scale of analysis can result in incorrect inferences that may lead to dramatically inefficient or ineffective conservation actions.

1. Introduction

Mammalian carnivores are among the most threatened taxonomic groups. They require large and interconnected habitat with abundant prey for long-term persistence and viability (Ripple et al., 2014; Ashrafzadeh et al., 2018). Habitat protection through a network of designated conservation areas (CAs) is a widely used approach towards biological conservation (Coetzee, 2017). However, the effectiveness of CAs in maintaining viable populations and core habitats is often unverified. Moreover, in a landscape where habitat patches are fragmented or isolated, individuals often persist in a meta-population, in which connectivity among subpopulations is crucial for regional viability (Wiens, 2001; Habibzadeh and Ashrafzadeh, 2018). Therefore, identifying and maintaining linkages between habitat patches both among and within CAs is critical in effective conservation of carnivores (Cushman et al., 2018).

Spatial niche partitioning in sympatric species plays a key role in shaping the distribution of carnivore species (Hearn et al., 2018). Quantifying the spatial niche overlap of carnivores is critical to understanding ecological processes, such as competition, prey-predator dynamics and coexistence (Roemer et al., 2009). Felids share similar morphological, phylogenic, and behavioral traits, and are frequently strong intra-guild competitors (Davis et al., 2018; Hearn et al., 2018). The potential for competition between coexisting felids for the same resources is highly influenced by the extent of spatial overlap in their occurrence patterns (Grassel et al., 2015). In highly heterogeneous landscapes where there is a mosaic of habitat patches of different environmental conditions and resources are not limiting for each species,

---

* Corresponding author.
E-mail address: mrashrafzadeh@sku.ac.ir (M.R. Ashrafzadeh).

spatial niche partitioning can facilitate coexistence at broad scales (Wereszczuk and Zalewski, 2015). In a recent study, different spatial patterns of habitat selection were identified among five felids in Central Iran, implying potential spatial niche partitioning (Hemami et al., 2018). While interspecific competition can lead to spatial niche partitioning from fine to broad scales (Lewis et al., 2015), little is known about spatial niche overlap in felids and the environmental variables that may result in niche divergence (e.g. Hearn et al., 2018).

Iranian felids have experienced significant declines over the past century due to multiple factors such as habitat loss and fragmentation, direct persecution, loss of prey, and illegal hunting (Moqanaki et al., 2010; Karami et al., 2016; Farashi et al., 2017; Farhadinia et al., 2018a; Ashrafzadeh et al., 2019). Determining species spatial distribution and habitat requirements is key to prioritize areas for conservation and protection. Animals select different habitat components at multiple hierarchical levels and over a range of spatial and temporal scales (McGarigal et al., 2016). Ecological niche models, which characterize relationships between environmental variables and species occurrences, are widely used to identify regions of high conservation priority (Kabir et al., 2017). When developing ecological niche models, it is crucial to use the appropriate variables and scales (Holland et al., 2004; Araújo and Peterson, 2012; Fournier et al., 2017). However, despite widespread recognition of the importance of scale in geographical, biological, and ecological processes, habitat selection studies often do not incorporate a multi-scale approach (McGarigal et al., 2016; Klaassen and Broekhuis, 2018). Developing multi-scale predictors is essential for increasing the accuracy and performance of ecological niche models and for providing useful inferences for management and conservation planning (Fournier et al., 2017).

Due to limited data on the spatial pattern of habitat and population connectivity for nearly all felids in Iran, and given the widespread fragmentation and isolation of their habitat, it is critical to obtain reliable knowledge about spatial patterns of remaining core habitat areas and the connectivity between them (e.g. Ahmadi et al., 2017; Cushman et al., 2018). Further, it is important to inventory how well these core areas and corridors are protected under current policies. The objective of this study was to model and quantitatively compare landscape connectivity and spatial niche overlap of six felids of high conservation importance in Iran. Using the largest database of felid presence across Iran, we employed a multi-scale optimization approach to describe spatial patterns of core habitats and biological corridors among them, measure spatial niche overlap, and evaluate the importance of CAs in maintaining populations and suitable habitat of Iranian felids. Our results provide key information to assist wildlife managers and policy makers in prioritizing core habitats and efforts for conservation and management.

2. Materials and methods

2.1. Study area

Iran is situated at the crossroad of three zoogeographic regions (Palearctic, Oriental and Afrotropical) and serves as a transition zone between hot to cold and xeric to mesic ecosystems (Yusefi et al., 2019). The country is characterized by a central plateau that is surrounded by mountains, semi-steppes, steppes, and deserts (Fig. 1). A detailed description of the study area is given in Text S1 in Online Resource 1.

2.2. Study species and occurrence data

This study includes six of eight native felids in Iran, including the Asiatic cheetah (*Acinonyx jubatus venaticus*), Persian leopard (*Panthera pardus saxicolor*), caracal (*Caracal caracal*), Eurasian lynx (*Lynx lynx*), Pallas's cat (*Otocolobus manul*), and wildcat (*Felis silvestris*). A detailed description of the studied species is given in Text S1 in Online Resource 1. We collected presence data of the six felids from 2007 to 2018. The

data set contains 948 observations, including 624 direct field observations and 324 camera trap records compiled by our team, Iranian Cheetah Society (ICS) and provincial offices of Iranian Department of Environment (DoE). We used only occurrences that were verified by our team, and other experts at ICS and DoE. See Tables S1 and S2 for details about the number of presences for each species. We evaluated spatial autocorrelation of our data by calculating Moran's I, and used the home range size of each species as a spatial filter to reduce spatial dependence (Brown, 2014). However, no presence locality was needed to be removed because of low spatial autocorrelation and even the closest presences had a separating distance greater than the species home range.

2.3. Predictor variables

We selected a priori 17 variables in five categories, including topography, climate, protection, anthropogenic impact, and land cover, to predict the habitat suitability of study species. These variables have shown to be important to several of the study species (Moqanaki and Cushman, 2017; Khosravi et al., 2018; Hemami et al., 2018). Topographic variables included elevation, slope position, topographic roughness, and compound topographic index (CTI). Elevation was obtained from the Shuttle Radar Topography Mission (SRTM) elevation model (http://srtm.csi.cgiar.org) and other topographic variables were calculated with the Geomorphometry and Gradient Metrics Toolbox (Evans et al., 2014). Climatic variables included Worldclim bioclimatic variables (http://www.worldclim.org/bioclim). Due to high correlations among the variables, we only retained mean annual temperature (Bio1), mean annul precipitation (Bio12), temperature seasonality (Bio4), and precipitation seasonality (Bio15) in the analysis. To consider the importance of CAs in providing suitable habitats for felids, we included a variable that represented the level of habitat protection. There are four types of CAs established for wildlife conservation in Iran, including national park, wildlife refuge, protected area, and no-hunting area. We assigned a value to each region (i.e., national park = 100; wildlife refuge = 80, protected area = 60, and no-hunting area = 40) with higher values representing higher level of legal protection afforded to habitat. For anthropogenic impact, we used the WCS human footprint layer (https://wcshumanfootprint.org/; Sanderson et al., 2002). For land cover, we included seven land use and land cover classes (LULC) including forest, shrubland, grassland–scrubland with a density of ≥25%, sparse rangeland with a density of ≤20%, cropland, urban area, and bareland that is composed of sand dunes and salty lands. We obtained these LULC from the Iranian Forests, Rangeland and Watershed Management Organization (https://frw.ir/02/Fa/default.aspx).

Because different environmental predictors may be related to habitat selection of species at different spatial scales (Wiens, 2001), multi-scale optimization is a useful approach to identify the appropriate scale (McGarigal et al., 2016). In this approach, a range of scales is tested for relationships between the response and predictor variables. We calculated the focal mean values of all variables described above using a moving-window with a circular neighborhood of seven different radii: 1, 2, 3, 4, 5, 6, and 7-km. These scales correspond to areas ranging from 3.5 to 150 km^2, which were more than sufficient to capture the home range of each study species. We used Multiscale Maxent Toolbox (Bellamy et al., 2013) to conduct the focal mean analysis across the spatial scales described above.

2.4. Species niche modeling with random forest

Briefly, we conducted random forest in two steps. In the first step, we ran initial univariate models at each spatial scale described above to identify the scale that showed the strongest relationship between species occurrences and each variable. This approach is robust for optimizing scales and works well with random forest (McGarigal et al., 2016; Cushman and Wasserman, 2018). We ran a total of 119
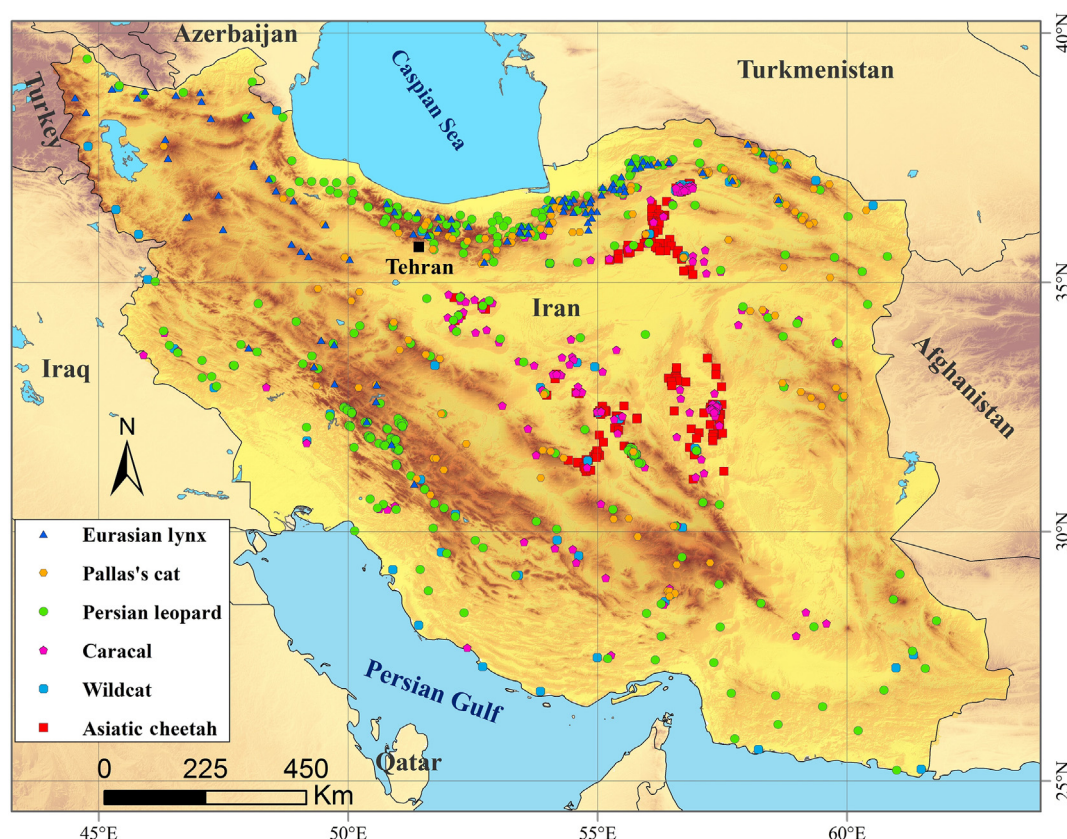
Fig. 1. Location of the study area. Brown-yellow background color represents elevational gradient. Colored filled circles, squares and triangles display the felids' presence localities. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

univariate models per species (17 variables at 7 scales) and used Model Improvement Ratio (MIR; Murphy et al., 2010) to measure the relative predictive performance of each variable at each scale. We retained variables at the scale that had the highest MIR values for further multivariate modeling.

In the second step, we ran a multivariate random forest model using a suite of scale-optimized variables and used MIR to select the best combination of variables in predicting occurrences. The scale-optimized variables were subset using 0.10 increments of MIR value and then random forest model was run using each subset (Murphy et al., 2010). We selected the model that showed the lowest total out-of-bag (OOB) error rate and lowest maximum within-class error as the best variable combination for predicting occurrences of each species. We produced locally weighted smoothing scatterplots (LOWESS) using the top variables for each study species to examine relationships between each predictor variable in the model and predicted outcome. Finally, we created a map of predicted probability of distribution for each species using a matrix of the ratio of majority votes across all bootstrap trees and R package GridAsciiPredict (Crookston and Finley, 2008). We used area under the Total Operating Characteristic curve (Pontius Jr et al., 2007) to assess the performance of the predictions. We used the median value of habitat suitability for presence points to define the highly suitable habitats for each species (Khosravi et al., 2018). All random forest models were conducted using the randomForest R package (Liaw and Wiener, 2002).

2.5. Resistance to movement surface

We converted the random-forest-derived habitat suitability maps into resistance surfaces using an exponential decay function following Wan et al. (2019), because past research has shown that resistance to movement (Keeley et al., 2016) or gene flow (Mateo-Sánchez et al., 2015) is often a negative exponential function of habitat suitability. Resistance values were then rescaled to a range between 1 (for HS = 1) and 10 (for HS = 0) using linear interpolation. The exponential decay function gives low resistance values to most of pixels and only areas with low habitat suitability receive high resistance values.

2.6. Landscape connectivity and corridor network simulation

We conducted cumulative resistant kernel (Compton et al., 2007) and factorial least-cost path (Cushman et al., 2009) analyses in UNICOR (Landguth et al., 2012) to map core habitat patches and corridors for each species. The least-cost paths are buffered based on kernel density estimations using a Gaussian function. The resistance kernels surrounding all individuals are combined through summation to produce an expected density map of dispersing individuals (Compton et al., 2007). Because of scarcity of data regarding maximum dispersal movements of felids in Iran, we tested a range of dispersal abilities on the resistance surfaces in UNICOR (i.e., edge distance = 50,000, 100,000, 150,000, 200,000, 250,000, and 300,000) reflecting dispersal abilities ranging from 50 to 300 km in optimal habitat for each species. It is important to understand that the maximum dispersal distance of species varies depending on many factors, such as limiting factors, resource availability, seasonal patterns, habitat quality, landscape configuration and composition, and behavioral and demographic factors. Using a range of dispersal distances in the analysis allows us to cope with such uncertainty while producing conservative estimates. Further, the dispersal distances described above circumscribe and are comparable to known dispersal distances from empirical studies (e.g., caracal: 95 km (Hamidi et al., 2011), Asiatic cheetah: 217 km (Farhadinia et al., 2016a), Persian leopard: 82 km (Farhadinia et al., 2018c), and Eurasian lynx: 148 km (Samelius et al., 2012)). We simulated a connectivity map at each dispersal ability for each species, depicting the spatial variation
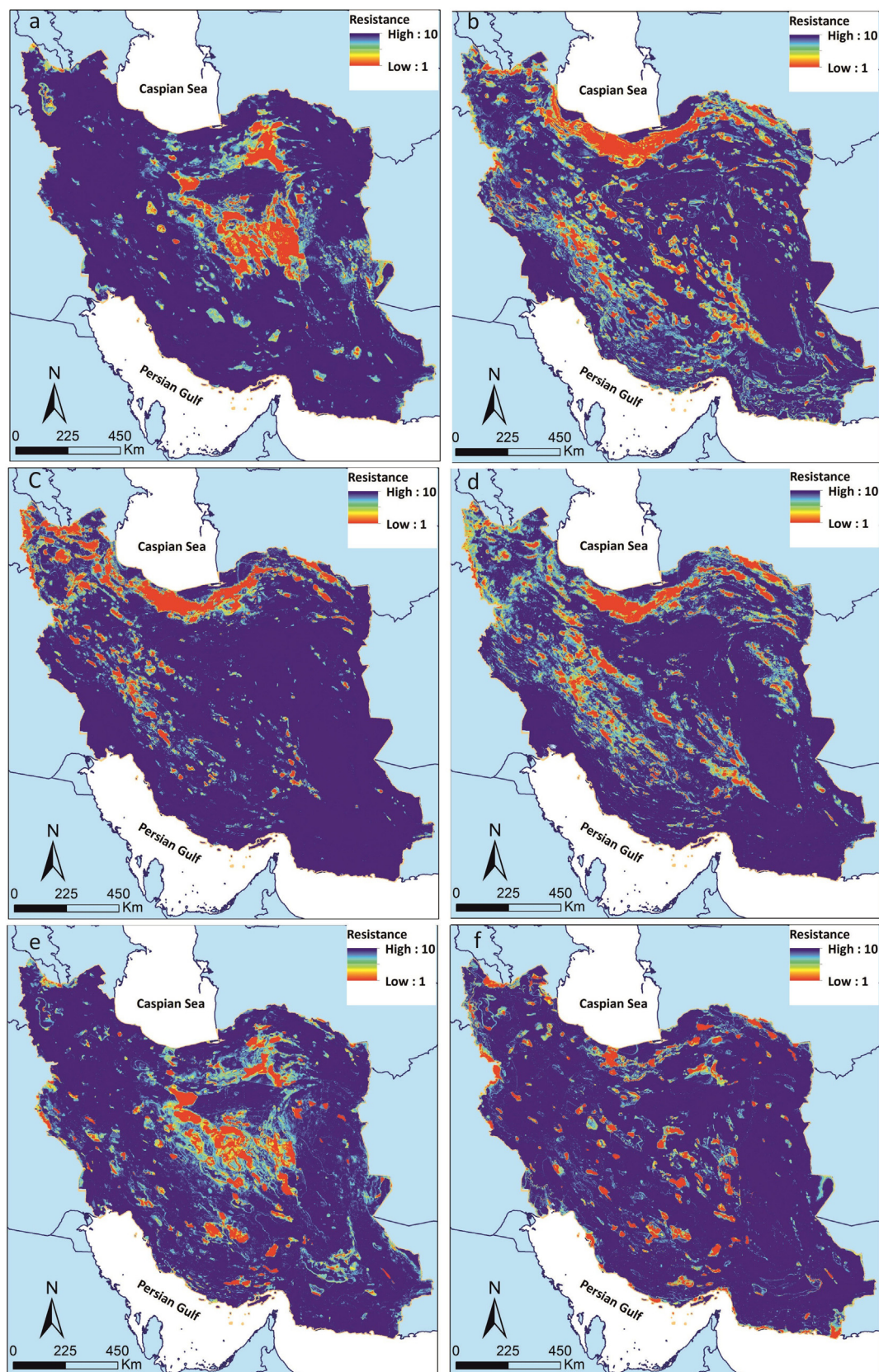
Fig. 2. Landscape resistance surfaces across the study area for (a) Asiatic cheetah, (b) Persian leopard, (c) Eurasian lynx, (d) Pallas's cat, (e) caracal, and (f) wildcat based on exponential decay function. Higher resistance values indicate less probability of dispersing individuals.
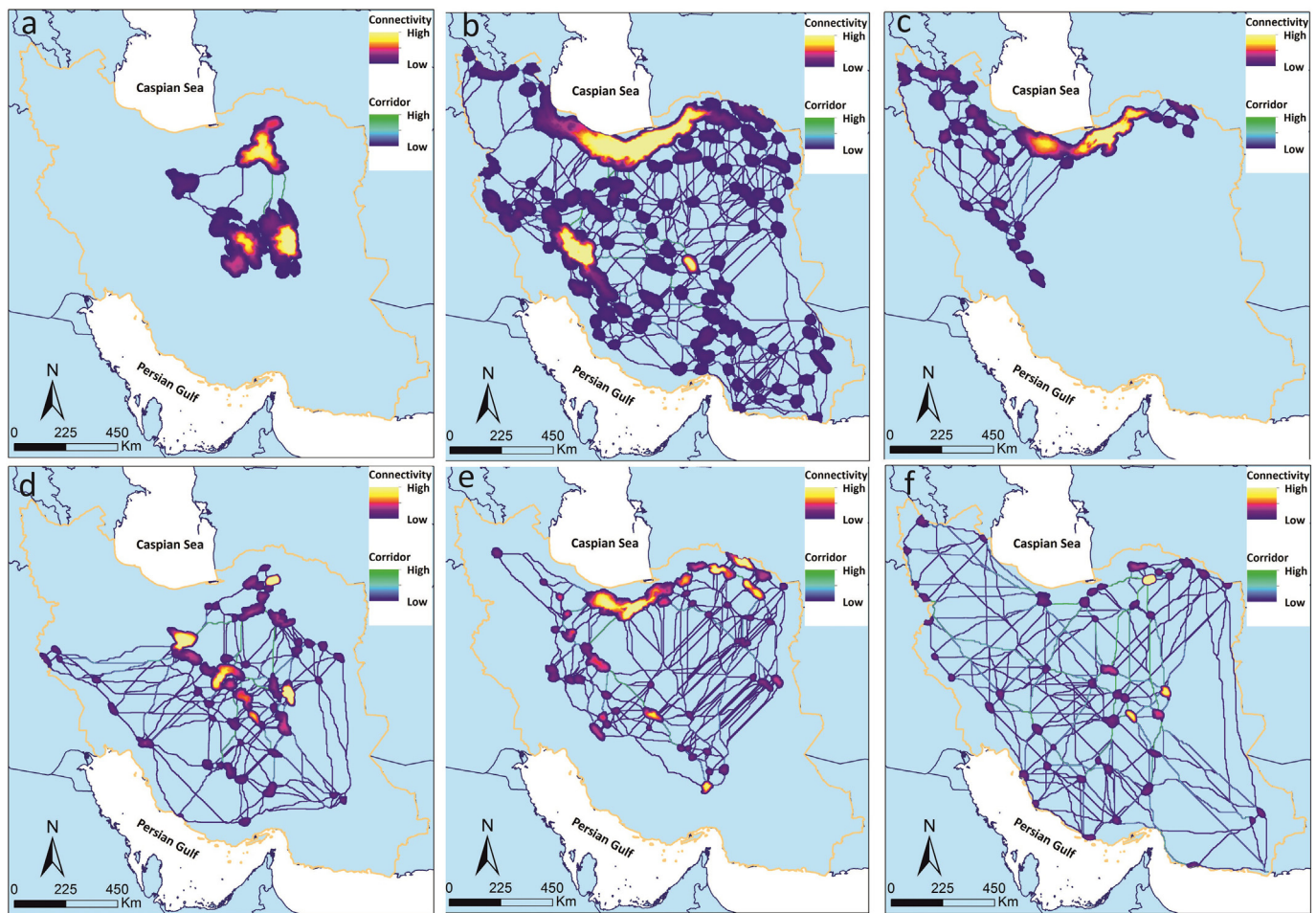
Fig. 3. Resistant kernel connectivity simulations of the six felids under 200-km dispersal ability scenario for (a) Asiatic cheetah, and (b) Persian leopard, under 150-km dispersal ability scenario for (c) Eurasian lynx, and under 100-km dispersal ability senario for (d) caracal, (e) Pallas's cat, and (f) wildcat. The blue and green lines show dispersal corridors, with dark green corresponding to areas that were predicted to be the strongest corridors. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in expected densities of dispersers and distribution of connected corridors and core habitat patches. We used the connectivity maps to identify core habitats for each species. We defined core habitat patches as contiguous patches with resistant kernel values > 10% of the highest recorded for the species (as in Cushman et al., 2013). We intersected the predicted core habitats of all study species to identify areas that are important to multi-species (Cushman et al., 2013).

2.7. Spatial niche overlap

We quantified the spatial niche overlap among study species using the analytical framework proposed by Broennimann et al. (2012) available in the R package ecospat (Di Cola et al., 2017). We used Principal Component Analysis (PCA) to summarize the environmental predictors into a reduced number of uncorrelated principal components (PCs). The first two axes of the PCA were used to represent the spatial niche for each species. The reduced space for each species was defined in a grid of cells. Then, the density of occurrence of each species and also cells with particular environmental conditions was calculated for each cell of the environmental space. Finally, the position of a kernel density of presence points along the principal components for each species was calculated to reflect species spatial ecological niche. Schoener D metric was computed as a niche overlap index for pairwise comparison between species.

2.8. Effectiveness of CAs

To assess the effectiveness of CAs in providing connectivity for felids in Iran, we quantified the extent and percentage of protected areas and corridors for each species that were within CAs.

3. Results

3.1. Univariate scaling

Our univariate scaling analyses revealed that optimized scales vary among study species for a given variable, and among variables for a given study species (Fig. S1; Table S3). There was a relatively broad range of spatial scales selected across all predictors for each species. Univariate scaling revealed that most predictors were strongly related to the species distributions at broad spatial scales (5–7 km; 88% for Asiatic cheetah, 48% for Persian leopard, 42% for Eurasian lynx, 47% for caracal, 53% for Pallas's cat, and 35% for wildcat).

3.2. Multivariate random forest modeling

The final multivariate model included different sets of variables for each species (Figs. S1 and S2). The performance of random forest models varied by species (AUC ranged between 0.62 and 0.82; and OOB error rates ranged between 0.01 and 0.04; Table S1). The most important variables for all study species were bioclimatic variables,

topographic variables, and level of protection (Figs. S2 and S3). The extent of predicted high suitability habitat varied among species. The greatest extent of highly suitable habitat was predicted for the Persian leopard (6.41%) and the lowest was predicted for wildcat (2.88%;Fig. S4). Highly suitable habitats for Persian leopard, caracal, and wildcat were more widely distributed across Iran (Fig. S4). A detailed description of the most important variables for predicting the occurrence of each species and the species response to each variable is given in Text S2 in Online Resource 1.

3.3. Resistance surface

Areas of low resistance to movement for Asiatic cheetah and caracal were concentrated mostly in the northeastern and central parts of Iran. For the wildcat, areas of low resistance were patchier and broadly distributed across study area. For Persian leopard, Eurasian lynx and Pallas's cat, areas of low resistance were mainly concentrated in the northern and northeastern regions (Fig. 2).

3.4. Connectivity network modeling

We present connectivity simulation result for Persian leopard and Asiatic cheetah at the 200-km dispersal ability scenario, for Eurasian lynx at 150-km dispersal ability, and for caracal, Pallas's cat and wildcat at 100-km dispersal ability (Fig. 3). All other scenarios are presented in Figs. S5–S10. Dispersal ability showed a large effect on landscape connectivity strength for all species especially Asiatic cheetah, caracal, Eurasian lynx, and Pallas's cat, with the high dispersal ability producing a much broader connected area than the low dispersal scenarios (Fig. 3). Patterns of landscape connectivity for Persian leopard and wildcat were relatively similar among all dispersal scenarios, with slightly broader extent of landscape connectivity for the high dispersal scenarios.

Under the high dispersal ability scenario (200-km), which was the closest to the empirical dispersal distance (217-km) reported by Farhadinia et al. (2016a) for Asiatic cheetah, central Iran was identified to have an extensive area of high connectivity. Areas of high connectivity were concentrated in three regions, one in the northeast and the other two in central Iran (Fig. 3a). Core habitat of Asiatic cheetah was predicted to be a single large connected patch with high intensity of internal corridors. With low dispersal ability (i.e., 50-km; Fig. S5a), populations were predicted to be broken up into several smaller and isolated patches.

Under the 100-km dispersal ability scenario, which was the closest to the empirical dispersal distance (82-km) reported by Farhadinia et al. (2018c) for Persian leopard, northern Iran was predicted to provide important connectivity for the species (Fig. S6b). Also for Eurasian lynx (Fig. 3c) and Pallas's cat (Fig. 3e), northern Iran was predicted to provide important connectivity under the high dispersal scenarios. The predicted Eurasian lynx core habitat at 150-km dispersal ability was relatively widespread across northern, northwestern, and western Iran, with three large core habitat patches. However, the northwestern and western core habitat patches were predicted to have weak internal migration rates due to the low number of species occurrence location records from those areas. Connected populations of Pallas's cat were concentrated in northern and northeastern Iran. Most predicted core patches for this species in northern Iran were highly interconnected, with a few apparently isolated satellite subpopulations in northeastern Iran. There were also several small and isolated Pallas's cat core patches in west-central Iran.

For caracal, under the 100-km dispersal ability scenario, which was comparable to the empirical dispersal distance (95-km) reported by Hamidi et al. (2011), our model predicted highly concentrated connectivity in central Iran (Fig. 3d, Figs. S5–S10). This region was predicted to provide important connectivity for the species under higher dispersal movement scenarios. The predicted caracal core habitats at

dispersal abilities greater than100-km were predicted to be largely connected into a single large patch containing several core habitat patches with high migration rates among them. However, the connected area was predicted to be broken up into several isolated patches under the low dispersal scenarios. Connectivity in other parts of Iran was predicted to be weak for this species. Finally, there were several isolated wildcat core patches scattered throughout Iran (Fig. 3f).

3.5. Niche overlap

There was a relatively broad range of species-pair spatial niche similarity ranging from low to moderate niche overlap (Table S4). Asiatic cheetah and caracal showed the greatest (D = 0.56) and Eurasian lynx and caracal showed the least spatial niche overlap (D = 0.06). Asiatic cheetah and Persian leopard showed spatial niche overlap of 0.12.

3.6. Multi-species core habitat

There was nearly no core habitat that was shared by all six species. Specifically, < 0.002% of the total extent of predicted core habitats included all six species. Also, 0.44%, 1.87%, 5.43%, and 11.03% of the extent provided core habitats for five, four, three and two of the six species respectively (Fig. 4a). Predicted connectivity for multiple species was high in northern and central Iran, which confirms the importance of these two parts of the country in providing habitats and corridors for felids (Fig. 4b).

3.7. Effectiveness of CAs

The extent and percentage of protected core habitat and corridors differed among species (Fig. S11; Table 1). CAs were fairly effective in protecting core habitat patches but less effective in protecting corridors. Core habitats of Asiatic cheetah, caracal, and wildcat were the most protected (72–88%), whereas Persian leopard, Eurasian lynx, and Pallas's cat received less protection (56–58%). Protection of movement corridors was generally poor, ranging from 26 to 33% for 5 of 6 studied species. Only cheetah had > 50% protection on its corridors (Fig. 4b; Table 1).

4. Discussion

4.1. The effect of scale on spatial niche of felids

Consistent with previous multi-scale habitat selection studies of carnivores, we found that felids in Iran select different resources at multiple scales (e.g. Mateo-Sánchez et al., 2014; Hearn et al., 2018). Previous studies have shown that felids often correlate most strongly to human activities at relatively broad scales, whereas factors that affect resting and foraging typically are most important at finer scales (Mateo-Sánchez et al., 2014; Hearn et al., 2018). Although our results generally support these previous findings, we observed variation in optimal scales of each predictor variable across the study species (Fig. S1). For example, Eurasian lynx, Pallas's cat, and Persian leopard exhibited similar patterns of spatial scales in habitat selection for some variables (e.g. annual precipitation and degree of habitat protection), but most variables had different optimized spatial scales between the species.

The differentiation in spatial scale of habitat selection could be an important factor that facilitates coexistence of sympatric species (Larroque et al., 2017). Based on our findings, caracals exhibit broad-scale spatial overlap with Asiatic cheetahs, but variation in fine scale selection may allow them to avoid habitats that Asiatic cheetahs predominately select (Moqanaki et al., 2016; Moqanaki and Cushman, 2017). Both caracals and Asiatic cheetahs select relatively low elevation desert habitats, and also show negative correlations with highly disturbed habitats by anthropogenic activities (Moqanaki et al., 2016;
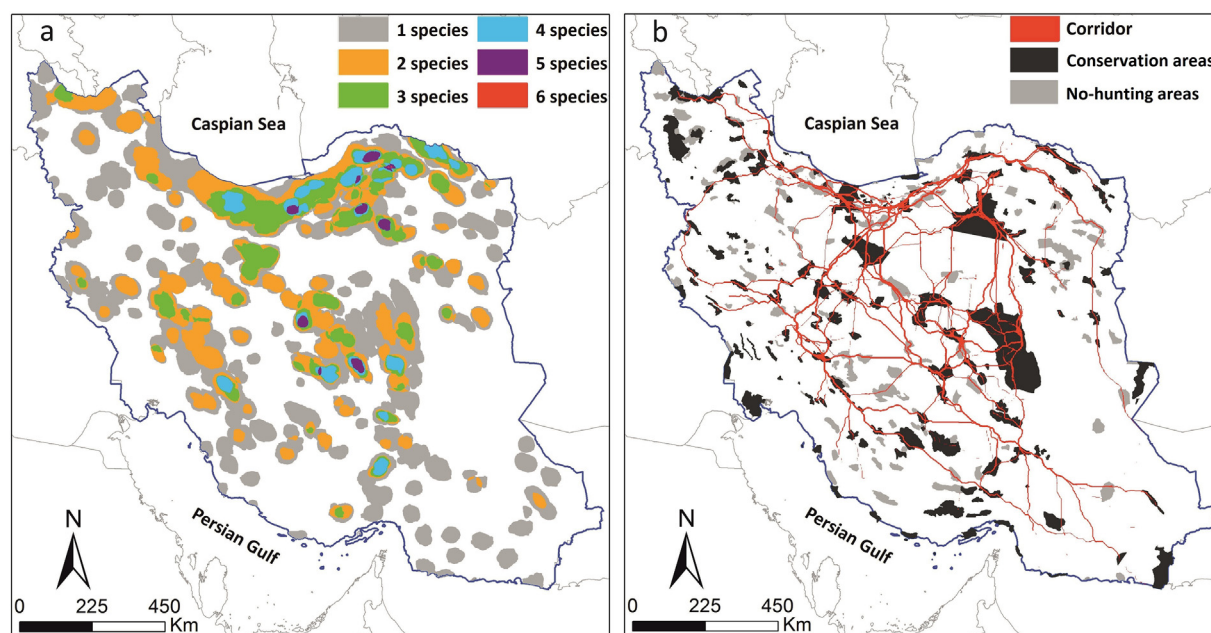
Fig. 4. Intersection map for (a) predicted core habitats and (b) corridors. The colors depict different species combinations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Ahmadi et al., 2017; Cheraghi et al., 2019) at broad scales. Asiatic cheetahs are mostly diurnal, inhabit mainly in lowlands covered by sparse vegetation and prey on small to medium-sized ungulates (Farhadinia and Hemami, 2010; Ahmadi et al., 2017), but caracals are predominantly nocturnal, occur in different habitats from flatland to mountains and feed on a variety of birds and small mammals (Moqanaki et al., 2016). In short, differences in prey selection allow them to coexist in the same habitat. Prey availability is often cited as an important determinant of felid space-use (Santos et al., 2019; Macdonald et al., 2019), but we do not have access to prey species data. Nevertheless, vegetation structure used in this study can be considered as a proxy for food availability and shelter (Hemami et al., 2018). Competition for similar prey species and interference competition are often primarily influenced by the relative body sizes of predators (Hearn et al., 2018). Given that prey preference varies with body sizes, these species could be able to partition trophic niches even when occupying similar habitat niches. The main prey of the Eurasian lynx consists mostly of small ungulates and lagomorphs (Moqanaki et al., 2010; Soyumert et al., 2019), whereas Pallas's cat and Persian leopard feed on smaller and larger animals respectively (e.g. Farhadinia et al., 2016b; Farhadinia et al., 2018b).

In accordance with our study, Khosravi et al. (2018) found low overlap between potential distribution of Asiatic cheetah and Persian leopard in the central Iranian plateau. In contrast, Hemami et al. (2018) and Cheraghi et al. (2019) found the relatively high levels of niche overlap between Asiatic cheetah and Persian leopard at the local scales

in the central Iranian plateau. Although the niche overlap between Asiatic cheetah, caracal, and Persian leopard has widely been recorded (Hemami et al., 2018), they vary in finer-scale preferences of habitat components (Khosravi et al., 2018) as well as temporal activity patterns.

4.2. Habitat connectivity and corridor network

Our landscape connectivity analysis showed that landscape connectivity for all species strictly depends on the dispersal distance used for the analysis. These differences in results have been seen in a number of other studies (e.g. Cushman et al., 2013). Indeed, Cushman and Landguth (2012a) argued that dispersal ability often has a substantially larger effect on connectivity predictions than variation in habitat pattern or resistance, and highlights the importance of improving knowledge of the functional dispersal ability and dispersal behavior of the species, given the large differences in predicted core areas and connectivity as a function of dispersal ability.

Our projected distribution models provide key information to assist wildlife managers in identifying highly suitable core habitats and essential connectivity corridors for dispersal and mating among core habitats for felid conservation. Consistent with Farhadinia et al. (2016a) who reported extensive movements (up to 217 km) of Asiatic cheetah, our predicted landscape connectivity for Asiatic cheetah at the 200-km dispersal distance suggests that central Iran has an extensive area of connectivity for the species (Fig. 3a). Such finding was also

Table 1

The extent and percent of core habitats and corridors covered by conservation areas (CAs) for six felids in Iran. The median value of habitat suitability for presence points was used as threshold to define the highly suitable habitats.

Species	Extent of core habitats (km²)	Extent of protected core habitats (km²)	% of protected core habitats	Extent of corridors (km²)	Extent of protected corridors (km²)	% of protected corridors
Asiatic cheetah	61,563	44,327	72%	38,984	22,353	57%
Persian leopard	104,028	60,873	58%	347,103	88,541	26%
Eurasian lynx	73,091	41,227	56%	76,433	25,234	33%
Caracal	59,246	48,410	81%	169,804	50,644	30%
Pallas's cat	58,940	33,635	57%	192,102	55,618	29%
Wildcat	46,734	41,410	88%	271,296	76,879	28%
Overall	246,331	136,022	55%	720,045	161,854	22%

consistent with Ahmadi et al. (2017), who reported high connectivity between northern and southern populations even when core habitats appeared to be separated by a large distance. Moreover, Moqanaki and Cushman (2017) suggested that the Iranian populations of Asiatic cheetah are divided into the three habitat patches that are fragmented even at large dispersal ability scenarios (200 to 300-km), which is generally supported by our findings. Our analyses at the low dispersal ability (e.g. 50-km) suggested that the central populations would be broken up into seven relatively isolated patches, whereas there will be a strong interconnection between the northern populations. Because cheetah may exhibit different dispersal distances and patterns to cope with unpredictable spatiotemporal dispersion of resources (Farhadinia et al., (2016a)), our dispersal scenarios provide a comprehensive picture of potential variations in habitat connectivity resulting from these differences. Also, our results suggest that habitat fragmentation could seriously threaten the populations of other meso-carnivores such as Pallas's cat (Farhadinia et al., 2016b) due to its extensive spatial requirements (Ross et al., 2012). Thus, it is likely that protection of very large areas is necessary to support viable populations of the species (Ross et al., 2012). Finally, our connectivity maps exhibit areas that may maintain infrequent, but critical, movements among populations of the felid species across Iran. These regions were predicted to provide important landscape connectivity for the felids (for a detailed description see Text S3 in Online Resource 1).

4.3. Effectiveness of CAs in multispecies spatial niche assessment

This study highlights the value of using a multi-species approach in species distribution and connectivity modeling (e.g. Cushman and Landguth, 2012b; Cushman et al., 2013). We were able to identify a number of habitat patches in central and northeastern Iran that provide support for ≥ 4 felid species (Fig. 4a). These areas are rare (< 2% of the total area of the country) and have high ecological importance and conservation value. Similarly, Cushman et al. (2013) evaluated core area and corridor intersection for three species of conservation concern across the American Great Plains, and found limited overlap of corridors or core areas, while Cushman and Landguth (2012b), in an evaluation of connectivity intersection among 144 species found that overlap was highly dependent on the interaction of dispersal ability and habitat niche.

This study emphasizes that CAs are essential to provide extensive and contiguous habitat that is required for conserving Iranian felids (e.g. Farhadinia et al., 2018a). Prey species such as ungulates are more abundant in CAs and rarely seen in unprotected areas. CAs are also important because carnivores are sensitive to human disturbance and require large home ranges (Cheraghi et al., 2019; Baker and Leberg, 2018). Consistent with previous findings, unprotected areas in Iran exhibit high resistance to movement and result in isolated habitat patches for most felids (Moqanaki and Cushman, 2017). Recent studies (Farhadinia et al., 2018c; Cheraghi et al., 2019) suggest that Iranian felids such as Asiatic cheetah and Persian leopard have larger home range requirements than their counterparts in other countries. The high habitat area requirements of these species in Iran suggests that protection of core habitats, and the linkages among them, should be the main conservation strategy for Iranian felids (e.g. Cushman et al., 2018).

Unfortunately, poaching within CAs is posing an immediate threat (Ghoddousi et al., 2019). Thus, we encourage increased law enforcement and international cooperation to protect the CAs from poaching and other illegal human activities. Additionally, our findings show that movement corridors receive relatively poor protection under the current design of CAs (Table 1). This problem has been discussed for Asiatic cheetahs (Ahmadi et al., 2017, Moqanaki and Cushman, 2017) and Persian leopards (Farhadinia et al., 2015; Ashrafzadeh et al., 2019; Hosseini et al., 2019) in Iran. We have also identified small and isolated habitat patches outside current CAs (Fig. S11) that may play a critical role as stepping stones for supporting connectivity between CAs (Ahmadi et al., 2017; Khosravi et al., 2019). There is an urgent need to prioritize conservation efforts in protecting these corridors and isolated habitat patches as parts of a composite strategy built on protecting and potentially expanding core populations and linking them with stepping stones and linkage corridors.

4.4. Implications for conservation

This study provides important implications for conservation. First, it can serve as a baseline assessment of core habitats and landscape connectivity for Iranian felids (e.g. Cushman et al., 2018). Protecting viable populations of felid species requires conserving large and interconnected core habitats, and our analysis provides quantitative assessment and mapping of species-specific core areas and corridors, as well as multi-species intersection and union of core and corridor habitats across the full extent of Iran. This information can serve as a foundation for prioritization to increase CAs extent and/or improve management outside of CAs to conserve core or movement habitat (e.g. Cushman et al., 2018). In addition, this baseline assessment provides a foundation for evaluating alternative development and conservation scenarios, which is critical to identify the most effective and efficient ways to conserve habitat quality and connectivity of carnivores (e.g. Cushman et al., 2016; Kaszta et al., 2019).

Because of their large habitat requirements, conserving the felids can potentially provide an umbrella for protecting other co-existing species. Furthermore, charismatic species, in particular felids, can be effective ambassadors for conserving broader biodiversity (Macdonald et al., 2017). Our study also highlights the importance of considering multiple spatial scales in management and conservation of Iranian carnivores. Our analysis shows that habitat selection and connectivity predictions are both very sensitive to scale, and incorrect scale of analysis can very readily result in incorrect inferences that may lead to dramatically inefficient or ineffective conservation actions.

Importantly, we found that CAs play a major role in providing core habitat and connectivity for felids in Iran, confirming the importance of setting aside lands exclusively for wildlife, and suggesting the future conservation evaluations formally explore increasing the number, extent and protection status of CAs, particularly in areas we identify as important core and connectivity habitat for multiple species or the union of core and connectivity habitat for a collection of focal species, such as the felid guild. Our analysis also identified habitat patches outside the CAs and a large majority of predicted corridors were outside areas receiving any formal protection. In addition to expanding conservation networks to increase coverage of these areas, conservation efforts should also work to improve habitat and population protection in the lands that are not formally protected, particularly those that are in strategic locations between key core areas or along key corridor routes (e.g. Cushman et al., 2018).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108523.

CRediT authorship contribution statement

Mohammad Reza Ashrafzadeh: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Rasoul Khosravi:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Mohammad Ali Adibi:** Investigation, Writing - review & editing. **Atie Tak Tehrani:** Investigation, Writing - review & editing. **Ho Yi Wan:** Conceptualization, Methodology, Writing - review & editing. **Samuel A. Cushman:** Conceptualization, Methodology, Writing - review & editing.

Declaration of competing interest

Acknowledgements

References

Ahmadi, M., Nezami Balouchi, B., Jowkar, H., Hemami, M.R., Fadakar, D., Malakouti-Khah, S., Ostrowski, S., 2017. Combining landscape suitability and habitat connectivity to conserve the last surviving population of cheetah in Asia. Divers. Distrib. 23, 592–603.

Araújo, M.B., Peterson, A.T., 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93, 1527–1539.

Ashrafzadeh, M.R., Khosravi, R., Ahmadi, M., Kaboli, M., 2018. Landscape heterogeneity and ecological niche isolation shape the distribution of spatial genetic variation in Iranian brown bears, Ursus arctos (Carnivora: Ursidae). Mamm. Biol. 93, 64–75.

Ashrafzadeh, M.R., Naghipour, A.A., Haidarian, M., Khorozyan, I., 2019. Modeling the response of an endangered flagship predator to climate change in Iran. Mammal Res 64, 39–51.

Baker, A.D., Leberg, P.L., 2018. Impacts of human recreation on carnivores in protected areas. PLoS One 13, e0195436.

Bellamy, C., Scott, C., Altringham, J., 2013. Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. J. Appl. Ecol. 50, 892–901.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob. Ecol. Biogeogr. 21, 481–497.

Brown, J.L., 2014. SDM toolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol. Evol. 5, 694–700.

Cheraghi, F., Delavar, M.R., Amiraslani, F., Alavipanah, K., Gurarie, E., Jowkar, H., Hunter, L., Ostrowski, S., Fagan, W.F., 2019. Inter-dependent movements of Asiatic Cheetahs Acinonyx jubatus venaticus and a Persian Leopard Panthera pardus saxicolor in a desert environment in Iran (Mammalia: Felidae). Zool. Middle East 65, 283–292.

Coetzee, B.W., 2017. Evaluating the ecological performance of protected areas. Biodivers. Conserv. 26, 231–236.

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.

Crookston, N.L., Finley, A.O., 2008. YaImpute: an R package for kNN imputation. J. Stat. Softw. 23, 1–16.

Cushman, S.A., Elliot, N.B., Macdonald, D.W., Loveridge, A.J., 2016. A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. Landsc. Ecol. 31, 1337–1353.

Cushman, S.A., Landguth, E.L., 2012a. Ecological Associations, Dispersal Ability, and Landscape Connectivity in the Northern Rocky Mountains. Res. Pap. RMRS-RP-90. 90 US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO (21 pp.).

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

Cushman, S.A., Wasserman, T.N., 2018. Landscape applications of machine learning: comparing random forests and logistic regression in multi-scale optimized predictive modeling of American marten occurrence in northern Idaho, USA. In: Humphries, G.R., Magness, D.R., Huettmann, F. (Eds.), Machine Learning for Ecology and Sustainable Natural Resource Management. Springer, Cham, Switzerland, pp. 185–203.

Cushman, S.A., McKelvey, K.S., Schwartz, M.K., 2009. Use of empirically derived source-destination models to map regional conservation corridors. Conserv. Biol. 23, 368–376.

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

Cushman, S.A., Elliot, N.B., Bauer, D., Kesch, K., Bahaa-el-din, L., Bothwell, H., Flyman, M., Mtare, G., Macdonald, D.W., Loveridge, A.J., 2018. Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. PLoS One 13, e0196213.

Davis, C.L., Rich, L.N., Farris, Z.J., Kelly, M.J., Di Bitetti, M.S., Blanco, Y.D., Albanesi, S., Farhadinia, M.S., Gholikhani, N., Hamel, S., Harmsen, B.J., 2018. Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. Ecol. Lett. 21, 1401–1412.

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F.T., D'Amen, M., Randin, C.,

Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40, 774–787.

Evans, J.S., Oakleaf, J., Cushman, S.A., Theobald, D., 2014. An ArcGIS toolbox for surface gradient and geomorphometric modeling, version 2.0-0. The Nature Conservancy and University of Wyoming, Laramie, Wyoming, USA [online] URL. http://evansmurphy.wix. com/evansspatial.

Farashi, A., Shariati, M., Hosseini, M., 2017. Identifying biodiversity hotspots for threatened mammal species in Iran. Mamm. Biol. 87, 71–88.

Farhadinia, M.S., Hemami, M.R., 2010. Prey selection by the critically endangered Asiatic cheetah in central Iran. J. Nat. Hist. 44, 1239–1249.

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. Biol. Conserv. 191, 770–778.

Farhadinia, M.S., Gholikhani, N., Behnoud, P., Hobeali, K., Taktehrani, A., Hosseini-Zavarei, F., Eslami, M., Hunter, L.T., 2016a. Wandering the barren deserts of Iran: illuminating high mobility of the Asiatic cheetah with sparse data. J. Arid Environ. 134, 145–149.

Farhadinia, M.S., Moqanaki, E., Adibi, M.A., 2016b. Baseline information and status assessment of the Pallas's cat in Iran. Cat News Spec. Issue 10, 38–42.

Farhadinia, M.S., Hunter, L.T., Jowkar, H., Schaller, G.B., Ostrowski, S., 2018a. Asiatic cheetahs in Iran: decline, current status and threats. In: Nyhus, P.J., Marker, L., Boast, L.K., Schmidt-Küntzel, A. (Eds.), Biodiversity of World: Conservation From Genes to Landscapes, Cheetahs: Biology and Conservation. Academic Press, San Diego, United States, pp. 55–69.

Farhadinia, M.S., Johnson, P.J., Hunter, L.T., Macdonald, D.W., 2018b. Persian leopard predation patterns and kill rates in the Iran–Turkmenistan borderland. J. Mammal. 99, 713–723.

Farhadinia, M.S., Johnson, P.J., Macdonald, D.W., Hunter, L.T., 2018c. Anchoring and adjusting amidst humans: ranging behavior of Persian leopards along the Iran-Turkmenistan borderland. PLoS One 13, e0196602.

Fournier, A., Barbet-Massin, M., Rome, Q., Courchamp, F., 2017. Predicting species distribution combining multi-scale drivers. Glob. Ecol. Conserv. 12, 215–226.

Ghoddousi, A., Soofi, M., Hamidi, A.K., Ashayeri, S., Egli, L., Ghoddousi, S., Speicher, J., Khorozyan, I., Kiabi, B.H., Waltert, M., 2019. The decline of ungulate populations in Iranian protected areas calls for urgent action against poaching. Oryx 53, 151–158.

Grassel, S.M., Rachlow, J.L., Williams, C.J., 2015. Spatial interactions between sympatric carnivores: asymmetric avoidance of an intraguild predator. Ecol. Evol. 5, 2762–2773.

Habibzadeh, N., Ashrafzadeh, M.R., 2018. Habitat suitability and connectivity for an endangered brown bear population in the Iranian Caucasus. Wildl. Res. 45, 602–610.

Hamidi, A.Kh., Ghadirian, T., Memarian, I., Hooman, F., Mousavi, M., 2011. Re-wilding an illegally captured Caracal (Caracal caracal) in Iran. In: 25 International Congress for Conservation Biology, Auckland, New Zealand, 5–9 December 2011.

Hearn, A.J., Cushman, S.A., Ross, J., Goossens, B., Hunter, L.T., Macdonald, D.W., 2018. Spatio-temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? PLoS One 13, e0200828.

Hemami, M.R., Esmaeili, S., Brito, J.C., Ahmadi, M., Omidi, M., Martínez-Freiría, F., 2018. Using ecological models to explore niche partitioning within a guild of desert felids. Hystrix 29, 216–222.

Holland, J.D., Bert, D.G., Fahrig, L., 2004. Determining the spatial scale of species' response to habitat. Bioscience 54, 227–233.

Hosseini, M., Farashi, A., Khani, A., Farhadinia, M.S., 2019. Landscape connectivity for mammalian megafauna along the Iran-Turkmenistan-Afghanistan borderland. J. Nat. Conserv. 52, 125735.

Kabir, M., Hameed, S., Ali, H., Bosso, L., Din, J.U., Bischof, R., Redpath, S., Nawaz, M.A., 2017. Habitat suitability and movement corridors of grey wolf (Canis lupus) in Northern Pakistan. PLoS One 12, e0187027.

Karami, M., Ghadirian, T., Faizolahi, K., 2016. The Atlas of Mammals of Iran. Jahad Daneshgahi, kharazmi Branch, Iran.

Kaszta, Ż., Cushman, S.A., Hearn, A.J., Burnham, D., Macdonald, E.A., Goossens, B., Nathan, S.K., Macdonald, D.W., 2019. Integrating Sunda clouded leopard (Neofelis diardi) conservation into planning and restoration planning in Sabah (Borneo). Biol. Conserv. 235, 63–76.

Keeley, A., Beier, P., Gagnon, J., 2016. Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc. Ecol. 31, 2151–2162.

Khosravi, R., Hemami, M.R., Cushman, S.A., 2018. Multispecies assessment of core areas and connectivity of desert carnivores in central Iran. Divers. Distrib. 24, 193–207.

Khosravi, R., Hemami, M.R., Cushman, S.A., 2019. Multi-scale niche modeling of three sympatric felids of conservation importance in central Iran. Landsc. Ecol. 34, 2451–2467.

Klaassen, B., Broekhuis, F., 2018. Living on the edge: multiscale habitat selection by cheetahs in a human-wildlife landscape. Ecol. Evol. 8, 7611–7623.

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.

Larroque, J., Ruette, S., Vandel, J.M., Devillard, S., 2017. Level-and scale-dependent habitat selection for resting sites by 2 syntopic Martes species. J. Mammal. 98, 1709–1720.

Lewis, J.S., Bailey, L.L., VandeWoude, S., Crooks, K.R., 2015. Interspecific interactions between wild felids vary across scales and levels of urbanization. Ecol. Evol. 5, 5946–5961.

Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. In: R news. 2. pp. 18–22.

Macdonald, D.W., Bothwell, H.M., Kaszta, Ż., Ash, E., Bolongon, G., Burnham, D., Can, Ö.E., Campos-Arceiz, A., Channa, P., Clements, G.R., Hearn, A.J., 2019. Multi-scale

M.R. Ashrafzadeh, et al.

Biological Conservation 245 (2020) 108523

habitat modelling identifies spatial conservation priorities for mainland clouded leopards (Neofelis nebulosa). Divers. Distrib. 25, 1639–1654.

Macdonald, E.A., Hinks, A., Weiss, D.J., Dickman, A., Burnham, D., Sandom, C.J., Malhi, Y., Macdonald, D.W., 2017. Identifying ambassador species for conservation marketing. Glob. Ecol. Conserv. 12, 204–214.

Mateo-Sánchez, M.C., Cushman, S.A., Saura, S., 2014. Scale dependence in habitat selection: the case of the endangered brown bear (Ursus arctos) in the Cantabrian Range (NW Spain). Int. J. Geogr. Inf. Sci. 28, 1531–1546.

Mateo-Sánchez, M.C., Balkenhol, N., Cushman, S.A., Pérezm, T., Domínguez, A., Saura, S., 2015. A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? Landsc. Ecol. 30, 1405–1420.

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. Landsc. Ecol. 31, 1161–1175.

Moqanaki, E.M., Cushman, S.A., 2017. All roads lead to Iran: predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. Anim. Conserv. 20, 29–41.

Moqanaki, E.M., Farhadinia, M.S., Mousavi, M., Breitenmoser, U., 2010. Distribution and conservation status of the Eurasian lynx in Iran. Cat News 53, 32–35.

Moqanaki, E.M., Farhadinia, M.S., Tourani, M., Akbari, H., 2016. The caracal in Iran: current state of knowledge and priorities for conservation. In: Cat News Spec. Issue. 10. pp. 33–37.

Murphy, M.A., Evans, J.S., Storfer, A., 2010. Quantifying Bufo boreas connectivity in Yellowstone National Park with landscape genetics. Ecology 91, 252–261.

Pontius Jr., R.G., Walker, R., Yao-Kumah, R., Arima, E., Aldrich, S., Caldas, M., Vergara, D., 2007. Accuracy assessment for a simulation model of Amazonian deforestation. Ann. Assoc. Am. Geogr. 97, 677–695.

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., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Roemer, G.W., Gompper, M.E., Van Valkenburgh, B., 2009. The ecological role of the mammalian mesocarnivore. BioScience 59, 165–173.

Ross, S., Munkhtsog, B., Harris, S., 2012. Determinants of mesocarnivore range use: relative effects of prey and habitat properties on Pallas's cat home-range size. J. Mammal. 93, 1292–1300.

Samelius, G., Andrén, H., Liberg, O., Linnell, J.D.C., Odden, J., Ahlqvist, P., Segerström, P., Sköld, K., 2012. Spatial and temporal variation in natal dispersal by Eurasian lynx in Scandinavia. J. Zool. 286, 120–130.

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.

Santos, F., Carbone, C., Wearn, O.R., Rowcliffe, J.M., Espinosa, S., Lima, M.G.M., Ahumada, J.A., Gonçalves, A.L.S., Trevelin, L.C., Alvarez-Loayza, P., Spironello, W.R., 2019. Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. PLoS One 14, e0213671.

Soyumert, A., Ertürk, A., Tavşanoğlu, Ç., 2019. The importance of lagomorphs for the Eurasian lynx in Western Asia: results from a large scale camera-trapping survey in Turkey. Mamm. Biol. 95, 18–25.

Wan, H.Y., Cushman, S.A., Ganey, J.L., 2019. Improving habitat and connectivity model predictions with multi-scale resource selection functions from two geographic areas. Landsc. Ecol. 34, 503–519.

Wereszczuk, A., Zalewski, A., 2015. Spatial niche segregation of sympatric stone marten and pine marten–avoidance of competition or selection of optimal habitat? PLoS One 10, e0139852.

Wiens, J.A., 2001. The landscape concept of dispersal. In: Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (Eds.), Dispersal. Oxford University Press, New York, pp. 96–109.

Yusefi, G.H., Faizolahi, K., Darvish, J., Safi, K., Brito, J.C., 2019. The species diversity, distribution, and conservation status of the terrestrial mammals of Iran. J. Mammal. 100, 55–71.