Landscape Ecol
https://doi.org/10.1007/s10980-019-00831-w

RESEARCH ARTICLE

Contrasting use of habitat, landscape elements, and corridors by grey wolf and golden jackal in central Iran

Gilda Shahnaseri · Mahmoud-Reza Hemami · Rasoul Khosravi · Shima Malakoutikhah · Maryam Omidi · Samuel A. Cushman

Received: 26 February 2019 / Accepted: 29 April 2019

Abstract

Context Increasing carnivore–human conflict has threatened the survival of many carnivore species, thus evaluating habitat requirements, landscape connectivity and the protection of biological corridors is critical to guide conservation of carnivores.

Objectives We evaluated the suitability of study landscape for grey wolf and golden jackal, assessed how well populations of each species are connected by movement corridors, and examined the feasibility of optimal multi-species conservation strategies based on intersection of habitat and connectivity areas of multiple species.

Methods We modeled the distribution of the two canids in central Iran based on an ensemble approach. The distribution predictions were used to estimate landscape resistance. We then used species occurrence data and the resistance layers to identify core habitats and corridors using the resistant kernel and factorial least-cost path methods.

Results Our results indicated high potential for large parts of the landscape to support the occurrence of the two canid species. However, the predicted connectivity networks were not very strong and extended. The strongest connections for both species were between western and eastern populations. Only a small shared linkage was detected for the two species with the highest numbers of LCPs.

Conclusions Our results provided critical information for the conservation of grey wolf and golden

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-019-00831-w) contains supplementary material, which is available to authorized users.

G. Shahnaseri · M.-R. Hemami (✉) · S. Malakoutikhah
Department of Natural Resources, Isfahan University of Technology, Isfahan 8415683111, Iran
e-mail: mrhemami@cc.iut.ac.ir

G. Shahnaseri
e-mail: Shahnaseri.gilda@gmail.com

S. Malakoutikhah
e-mail: s.malakouti@na.iut.ac.ir

R. Khosravi
Department of Natural Resources and Environmental Engineering, College of Agriculture, Shiraz University, Shiraz 71441-65186, Iran
e-mail: r-khosravi@shirazu.ac.ir

M. Omidi
Isfahan Department of Environment, Isfahan, Iran
e-mail: omidi.doe@gmail.com

S. A. Cushman
Rocky Mountain Research Station, USDA Forest Service, Flagstaff, AZ, USA
e-mail: sam.cushman@gmail.com

Published online: 20 May 2019

jackal in Iran and identified the most critical core areas and corridors that link them. Carnivore conservation in Iran should focus on safeguarding these key strongholds and improving the permeability, habitat quality and reducing mortality risk in the corridor linking them.

Keywords Niche overlap · Core habitats · Golden jackal · Grey wolf · Connectivity · UNICOR

Introduction

Habitat fragmentation and degradation are recognized as the main threatening factors to survival of mammal species worldwide (Schipper et al. 2008). Large mammals are particularly vulnerable to habitat loss and fragmentation due to low population density, high habitat area requirements, low reproductive potential and direct persecution by human (Clark et al. 1996; Noss et al. 1996). Thus, conservation of large mammals typically requires both protection of extensive core areas and establishment of movement corridors among them (e.g., Cushman et al. 2018), particularly when core habitat patches are isolated in a matrix across anthropogenic landscapes (McClure et al. 2017).

Given that species conservation in human-dominated landscapes requires an understanding of the eco-geographical preferences and thus distribution of the target species (Rodríguez-Soto et al. 2011), species distribution modeling forms a foundation for conservation planning and assessment of species. Species distribution models (SDMs; also referred to as ecological niche models, ENMs) are the main tools used to predict suitable habitat (Guisan and Thuiller 2005; Franklin 2010; Peterson et al. 2011). By identification of statistical relationships between the distributional data and explanatory variables, SDMs estimate the response function of individual variables and their contribution in occurrence of the species as well (Peterson 2001).

Modelled suitable habitats within human-dominated landscapes are often characterized by isolated patches embedded in heavily fragmented landscapes (Cushman et al. 2016). As species with large habitat requirements, large mammals such as carnivores cover long distances seeking prey or mates. Thus, reaching destination habitats often requires moving through a hostile matrix where they have to contend with human disturbances and threats (Cushman et al. 2018).Thus, large scale conservation of these species often requires protecting or improving landscape permeability (Crooks et al. 2011; Riordan et al. 2016) by designating corridors or linkages between habitat areas (Cushman et al. 2009; Crooks et al. 2011; Cushman et al. 2018).

A frequent impediment in reliably predicting connectivity for large mammals is paucity of data on distribution, dispersal ability and effect of different landscape features on their movement (Epperson et al. 2010; Cushman et al. 2013a). To address it, connectivity modeling approaches adopting concepts from landscape ecology provide powerful analytical tools (Epperson et al. 2010). A range of connectivity modeling tools has been developed to identify and map movement corridors of wildlife species (Cushman et al. 2013c; Zeller et al. 2018). One of the most commonly used approaches for quantifying landscape connectivity the least-cost path (LCP) modeling which identifies the single route offering the lowest cumulative movement cost between two habitat patches. However, assuming that all individuals use a single least-cost path is unrealistic. To avoid this, an alternative approach, known as factorial least cost path analysis (Cushman et al. 2009), is to model connectivity based on a synoptic view in which LCP between all source locations and all target locations are simultaneously predicted (Cushman et al. 2014), which provides a measure of the full network of connectivity across the population. Conserving multiple least cost paths for large carnivores is an essential priority because their potentially interconnected populations are often scattered across large landscapes incorporating protected areas (Cushman et al. 2018).

All connectivity models require quantifying landscape resistance - the ability of a landscape feature in facilitating or impeding species movement through that feature (Spear et al. 2010). Species distribution models have been widely used to quantify landscape resistance (Keeley et al. 2017). Resistance values are usually derived from SDMs through applying a negative linear function (Singleton et al. 2002; Hunter et al. 2003; Larkin et al. 2004) that increase the resistance values at a constant rate, when suitability values decrease (Keeley et al. 2016). However, this correlation may not be applicable to obtain resistance

values in long movement stages because species may have more flexibility in selecting habitats during long-distance movements such that they move through moderately suitable habitats that have low suitability during home range movements (Gastón et al. 2016; Keeley et al. 2016). For this reason and to prevent resistance values to drop dramatically at very high suitability values (Keeley et al. 2016), it is suggested to use the negative exponential function instead of a linear one (Trainor et al. 2013).

Conservation of wildlife resources in Iran has mainly relied on establishing isolated Protected Area (PAs). Although for some species these relatively small and isolated PAs may be adequate, isolated PAs are not efficient for long-term conservation of most carnivores. Grey wolf (*Canis lupus*) and golden jackal (*Canis aureus*) are two of the most widely distributed carnivores in central Iran. High trophic level and flexibility in habitat requirements enabled these canids to occur across a wide range of habitats including human occupied landscapes. Over the last decades, following reductions in the density of prey species in Iranian PAs (Ziaie 1996), occurrence of these species across rural areas, where they can have access to anthropogenic food, including livestock, has increased. Consequently, they have become highly vulnerable to conflict with humans. For instance, human conflict with the grey wolf has resulted in the disappearance or large decline of the species' populations across most parts of its distribution range in Iran (Behdarvand et al. 2014). Maintaining connectivity among these residual populations could assist in conservation of these and other carnivore species.

In this study, we addressed four main objectives regarding populations of grey wolf and golden jackal in central Iran. First, we sought to predict distribution of these canids to identify areas where they have high probability of occurrence based on an ensemble modeling approach. Second, we modelled functional corridors for each canid by developing models of landscape connectivity and identifying movement corridors connecting populations of each species in central Iran. To accomplish this, a synoptic connectivity approach (Cushman et al. 2014), combining distribution models with the factorial least-cost path analysis (FLCP) was applied. We predicted the LCP among the core habitat areas which were identified based on a kernel resistance approach using species occurrence points, resistance surface and species dispersal ability. The identified core areas in this way represent the most densely populated habitat areas, which were used as a measure to model connectivity among populations. Third, we evaluated the degree of core habitat protection provided by the PAs network and their importance in maintaining landscape connectivity for the target species. By combining results of distribution and connectivity models, we sought to identify priority areas for conservation of these canids and thus reduce their conflicts with humans in central Iran. Fourth, we evaluated the amount of overlap in the ecological niche, extent of predicted core habitats and linkage corridors between the two species to determine if efficient and optimal multi-species conservation strategies could be developed to simultaneously protect both species.

Materials and methods

Central Iranian ecosystems as a case study

For this study, we focused on populations of grey wolf and golden jackal distributed across the landscape in central Iran (Fig. 1). The studied landscape covers an area of approximately 107,000 km^2 and spans an extended altitudinal range from 680 up to 4415 m above sea level. The eastern and northwestern parts of the landscape are mostly dominated by low relief areas where altitude reaches a maximum of 1000 m. In contrast, the western parts represent topographically more heterogeneous landscapes because of high mountains that stretch in a north–south direction. Due to the arid to semi-arid climate of the study area, the density of vegetation cover across much of the area is low, except for the western parts where a more mesic climate has resulted in development of high-density vegetation. The highest density of rural and urban areas is in the western and southwestern parts, where high density of agricultural lands, human settlements, and roads exist. The network of PAs in this study includes four management categories including national parks, wildlife refuges, protected areas, and no-hunting areas, which accounts for 20% of the landscape area (Table S1).

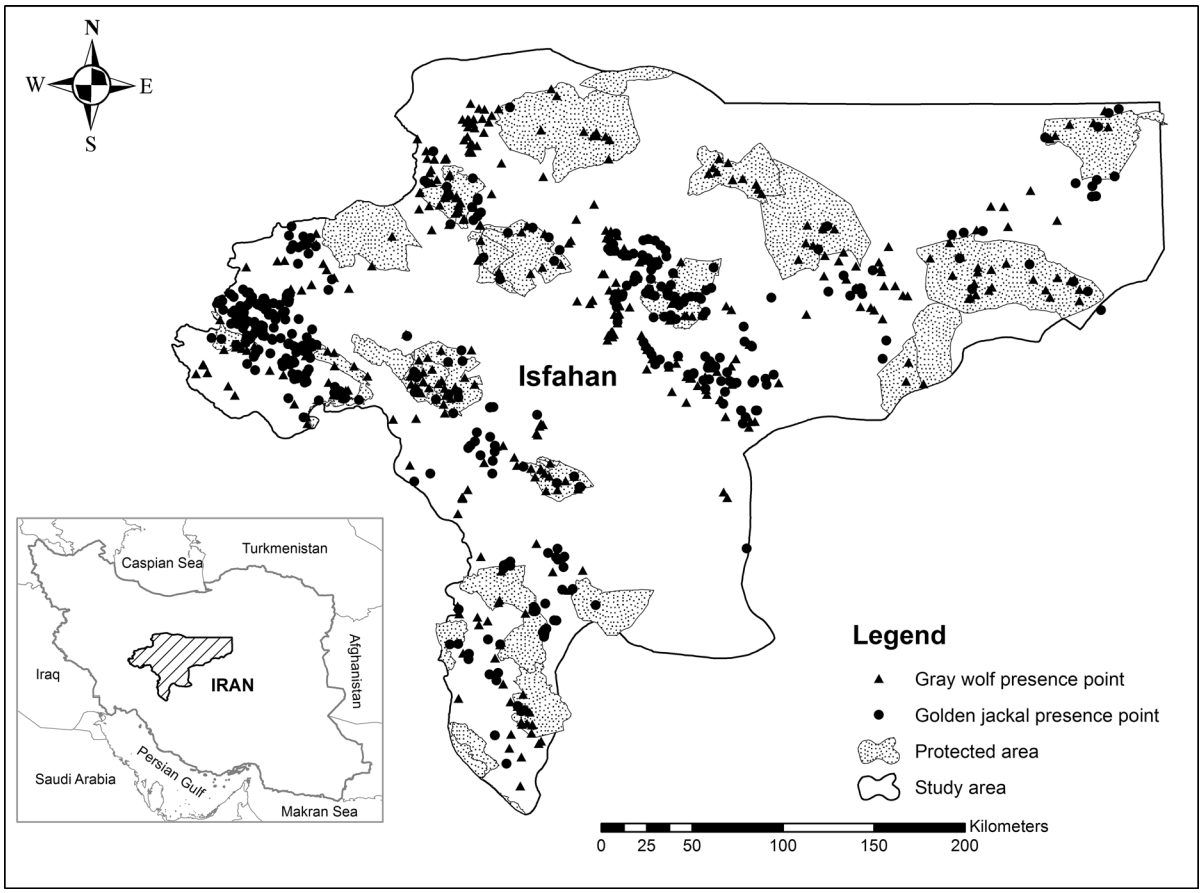

Fig. 1 Location of the study landscape in Iran, for modeling landscape connectivity and biological corridors of grey wolf and golden jackal

Species occurrence data

The occurrence data for grey wolf (454 records) and golden jackal (448 records) were collected during a 5-year period (2013–2017) based on direct observations, camera trapping and indirect signs (tracks and scats). Guards of the Isfahan Provincial Department of Environment (IPDoE) assisted us in collecting occurrence data. Before using the data, they were evaluated for likely errors such as spatial biases rising from uneven sampling efforts across the study area. Uneven sampling efforts may result in dataset with high clumping structure in some regions while other regions may suffer inadequate sampling efforts. This error can be identified by quantifying the degree of spatial autocorrelation in data. We applied a Global Moran's *I* test to check for any spatial autocorrelation in collected data. To reduce the spatial autocorrelation, we selected a 5 km distance threshold according to similar studies (Ahmadi et al. 2017; Khosravi et al. 2018) and kept only one presence point within each 5 km interval distance which resulted in 251 points for grey wolf and 258 points for golden jackal (Fig. 1).

Environmental variables

Considering the ecological requirements of grey wolf and golden jackal, we selected the most relevant environmental factors to predict distribution of grey wolf and golden jackal from four groups of climatic, topographic, habitat and human influence variables. Climate data were obtained from the WorldClim database at 1 km spatial resolution developed by Hijmans et al. (2005) (www.Worldclim.org). Landcover, prey availability and soil adjusted vegetation index (SAVI) were the three habitat variables used for

the species. For landcover classes, we used three categories of forest, rangelands and shrublands as the preferred landcover types for occurrence of both species. We used SAVI instead of the more common index of NDVI because, it includes a factor to correct the soil reflectance which makes it more applicable for dry and semi-dry regions like our study area. We produced 23 monthly SAVI index maps for the year 2017 using time series of MODIS at spatial resolution of 250 m in Erdas Imagine v.9.1. Software. To reduce the dimensionality of the data, a PCA analysis was performed on all the 23 series of SAVI layers and the first component with the highest variance in the data was selected. For prey availability, we focused on distribution of four main prey species including wild goat (*Capra aegagrus*), wild sheep (*Ovis orientalis*), Persian gazelle (*Gazella subgutturosa*), and Indian gazelle (*Gazella bennettii*). To produce maps of prey availability for each canid species across the study area, we took a three step approach. First, using survey data on species abundance (IPDoE, unpublished data, Table S5), the density of each prey species in each protected/unprotected area was determined. We gave similar prey density value to each 1 km^2 grid cell of a given area. In the second step, developed maps of prey population density and distribution probability (habitat suitability maps of the four prey species produced by Hemami and Esmaeili (2013) using maximum entropy approach at a spatial resolution of 500 m) were multiplied to provide a pixel-based measure of prey availability. Third, prey availability maps were weighted according to the relative abundance of each prey species in the diet of each canid species in the study area (Shahnaseri 2017).

Roughness index (Elevational differences between adjacent cells of a digital elevation grid) was calculated to reflect the relief characteristics of the study area. To evaluate the effect of humans on the distribution of the grey wolf and golden jackal we used the Human Footprint Index map downloaded from the Global Human Footprint Dataset (WCS and CIESIN 2005), and then clipped this to the extent of the study landscape, resulting in a HI index map ranging from 0 to 93. In addition, we also included agricultural lands obtained from the Iranian Forests, Ranges and Watershed Management Organization (IFRWO) as another important anthropogenic factor influencing distribution of the canids. Due to lack of data on the density of livestock, and given the high correlation between livestock presence and rural areas, density of villages was considered as a proxy of livestock density and was calculated within grids of 3 × 3 km using kernel density analysis. All of these data layers were prepared in raster format with grid size of 1 × 1 km. For those layers having finer grid size, resampling to the coarser resolution of 1 km was performed using bilinear resample function in Arcmap. After preparing all the explanatory variables, we computed the Pearson correlation between each Paris of variables and removed those with correlation coefficient higher than the selected threshold of 0.60 (Vergara et al. 2016; Table 1).

Distribution modeling

We used the BIOMOD2 package (Thuiller et al. 2009) in R v.4.1.0 (R Development Core Team, Pinheiro et al. 2015) to implement ensemble modeling of species distribution for both species. By fitting several SDMs and exploring a range of predictions across more than one set of uncertainty sources, ensemble modeling increases the accuracy of the model predictions (EM; Araújo and New 2007) and thus decreases the uncertainty associated with using a single SDM. Here, the ensemble models were developed using five species distribution models (SDMs), including generalized linear models (GLM), maximum entropy (MaxEnt), generalized additive model (GAM), generalized boosting model (GBM) and random forest (RF). In addition to occurrence points, a set of 5000 pseudo-absence points were randomly selected from background as pseudo-absence points across the study area. We partitioned the occurrence points and used 75% of the data for training and the remaining 25% for model evaluation. To combine the output of all distribution models and obtain the ensemble predictions, we employed a weighted-averaging approach whereby each statistical model is weighted according to its predictive accuracy on the independent evaluation data (Thuiller et al. 2009). The ensemble models were evaluated for their accuracy using two measures, including the area under the curve (AUC) of a receiver operating characteristic (ROC) and true skill statistic (TSS). The relative contribution of each environmental variable in the final ensemble map was assessed by variable randomizations (Thuiller et al. 2009). As sympatric species, we also quantified how well distribution of grey wolf and golden jackal overlaps

Table 1 List of environmental variables used to predict distribution of grey wolf and golden jackal in Central Iran

Variable	Description	Source
Roughness index	Elevational differences between adjacent cells of a digital elevation grid	Digital Elevation Model (DEM) USGS.org
SAVI	Soil-adjusted vegetation index	MODIS satellite images
Bio1	Annual mean temperature	www.Wordclim.org
Bio2	Mean diurnal range	www.Wordclim.org
Bio4	Temperature seasonality	www.Wordclim.org
Bio15	Precipitation seasonality	www.Wordclim.org
Bio19	Precipitation of coldest quarter	www.Wordclim.org
Human Influence Index (HI)	Representing cumulative impact of population density, roads, land use/cover, infrastructures and human access	http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic
Agriculture	Euclidean distance	(IFRWO)
Forest	Euclidean distance	(IFRWO)
Range lands		
Shrublands		
Prey availability	Potential distribution maps of preferred prey species weighted by their population densities in the study area and relative abundance in the canid species diet (see text)	Hemami and Esmaeili (2013)
Villages	Density of villages within grids of 3 × 3 km	(IFRWO)

using the niche identity test using Schoener's D index in ENMTools. (Warren et al. 2008, 2010).

Modeling connectivity corridors

We obtained landscape resistance maps for each species by converting suitability scores derived from ensemble models using a negative exponential function. Connectivity modeling was based on Factorial least-cost path (FLCPs) approach (Cushman et al. 2009) implemented in UNICOR software (Landguth et al. 2012). Factorial least-cost path analysis is technically similar to least-cost path (LCP) analysis, but is designed to overcome the limitation of this method associated with the number of source and target points and to produce a synoptic measure of total landscape connectivity (Cushman et al. 2014). Two data layers were used as input into the software: (1) the resistance surface, and (2) the point file containing the geographic coordinate of each recorded individual's location. To overcome drawbacks of the initially modelled LCPs and to represent the potential of the entire landscape in supporting species movement, the LCPs were smoothed as a function of cumulative cost (e.g., Cushman et al. 2013b). The relative cost of moving through the pixels surrounding each LCP was estimated using a kernel density and Gaussian function. The buffered LCPs were then summed to produce maps of corridor density for each species (Cushman et al. 2013a). The value of each pixel in this map indicates the frequency of the LCPs passing through that pixel across the landscape. We set no threshold for maximum dispersal distance of the target species when modeling the LCPs (e.g., Cushman et al. 2013b).

Core habitats are defined as areas with the highest density of dispersing individuals. To identify these landscape features, we used the resistant kernel approach (Compton et al. 2007) implemented in UNICOR software using occurrence points and resistance maps for each target species as inputs. The cumulative resistant kernel surface is proportional to the expected density of individuals of the study species moving through each cell (e.g. spatial incidence function; Kaszta et al. 2018), which makes it an ideal means to predict and map population core areas. To

calculate the density of grey wolf and golden jackal in each habitat pixel, all pixels containing occurrence points were initially set as source points and assigned maximum density value of 1. Using kernel density function, the density of each species in pixels around the source points was then computed based on the cumulative movement cost to reach a given pixel and species. The core habitats were extracted from the cumulative resistance kernel maps as contiguous units accounting for 10% of the highest resistance kernel values for each species (Cushman et al. 2013a).

Ranking landscape core habitats in the connectivity network

We evaluated the importance of core habitat patches in connectivity network of the canids using probability of connectivity index (PC; dPC; Saura and Pascual-Hortal 2007) in Conefor 2.6 (Saura and Torne 2009). This index uses patch characteristics (such as patch area, habitat quality, population size, etc.) and movement probability (P_{IJ}) from patch i to patch j to calculate three sub-indices related to different ways a patch contributes to connectivity (e.g., dPCintra, dPCflux and dPCconnector, see Saura and Rubio 2010) as follows:

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} ai \times aj \times Pij}{AL^2} \quad (1)$$

where a_i and a_j are selected attribute of patch i and j, and A_L corresponds to the maximum of the selected attribute for the study landscape (for example, if patch area is selected, this parameter refers to the landscape total area).

The P_{IJ} is a function of edge-to-edge inter patch distance in a way that more distinct patches have lower P_{IJ}. Here we used area, as a patch characteristic, and measured the Euclidean distance between pairs of patches as a measure for edge-to-edge intra-patch distance (Saura and Rubio 2010) to obtain the PC index for individual patches. The computation of PC requires setting a dispersal distance threshold above which a given source patch is not accessible to species. Since, no information about the maximum dispersal distance of the two species was available, we computed PC based on dispersal thresholds of 50, 100, 200, 300, 400) (Khosravi et al. 2018) to overcome the uncertainty. Since dPC is a probabilistic index, it was required to specify probability values corresponding to Euclidean distances. Assuming each selected dispersal threshold as the maximum distance, the probability distance of 0.05 was selected as suggested by Saura and Pascual-Hortal (2007). We also evaluated the importance of each core areas as a stepping stone within the connectivity network based on value of dPC connector fraction (Saura and Rubio 2010).

Results

Distribution of grey wolf and golden jackal

Prediction of the ensemble models for grey wolf and golden jackal revealed that large parts of the landscape had the potential to support the occurrence of these canids (Fig. 2). However, the predicted suitable areas for golden jackal were more concentrated and spatially demarcated. Among all the SDMs, RF and GLM represented the highest and lowest performance in predicting habitat suitability for both species, respectively (Table 2). For both species, all five employed models produced good discriminating power (AUC values above 0.8); however, the accuracy of the models was better for golden jackal compared to grey wolf. For grey wolf, distance to agricultural lands and prey availability and for golden jackal distance to agricultural lands, roughness index and human foot print were the most important variables predicting occurrence of the canids in our study area. We found very little contribution for human impact, availability of prey species and topographic variables in predicting distribution of the species (Table S2).

Overlaid binary maps of the distribution models revealed that approximately 40% of the highly suitable habitats were shared between grey wolf and golden jackal. The significance of this spatial overlap was further confirmed by niche identity test and value of 0.79 for the Schoener's D index.

Core habitats and biological corridors

From the initial set of identified core habitats for the canids, isolated patches (having no least LCP moving through or connecting them to other patches) smaller than 100 km^2 were removed, which respectively resulted in 16 and 21 core patches for grey wolf and golden jackal, respectively (Figs. 3, 4). Core habitats

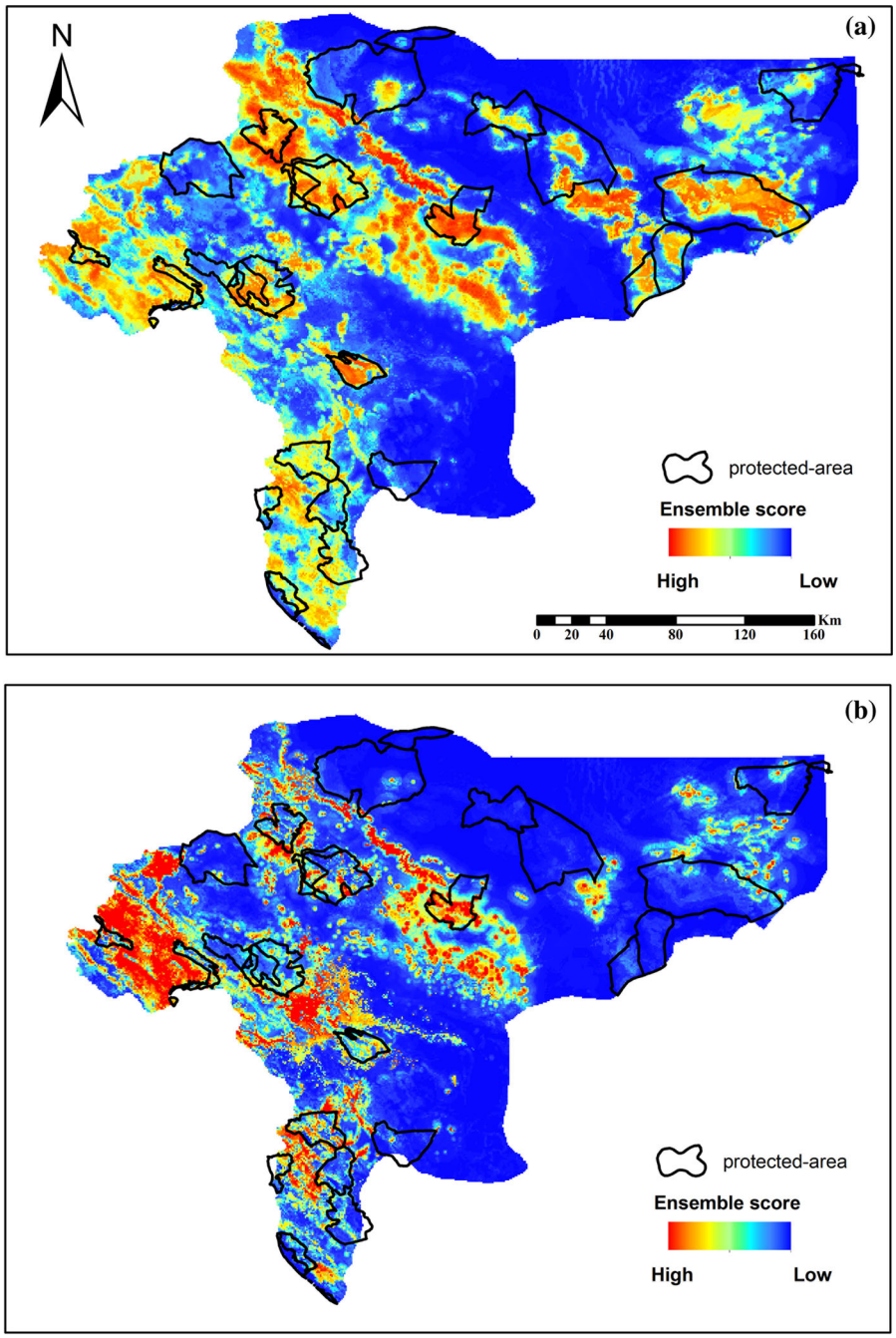

Fig. 2 Predicted suitability of the study area for **a** grey wolf and **b** golden jackal based on the combined result of five SDMs

for grey wolf were larger in size and more widely distributed than golden jackal. Core habitats of grey wolf were partly (54%) covered by the PAs among which P20 in east incorporated the largest proportion. For golden jackal, individual core habitats were comparatively smaller. There were only four large patches (larger than 1000 km^2) of golden jackal habitat, which were located in central, southern and western parts of the study landscape (patches 1, 2, 3 and 4). Although the entire extent of some PAs (e.g., P12 and P6) was qualified as core habitats for golden jackal, only 20% of the core habitats were covered by the network of PAs for this species. We found an overlap of approximately 35% between core habitats

Table 2 Accuracy evaluation of the statistical models (AUC, TSS) used to predict distribution of grey wolf and golden jackal in central Iran

Model	Species	
	Grey wolf	Golden jackal
GLM	0.76–0.41	0.94–0.70
MaxEnt	0.81–0.48	0.90–0.73
GAM	0.82–0.54	0.89–0.76
GBM	0.87–0.59	0.93–0.80
RF	0.99–0.99	0.99–0.99
EM	0.92–0.69	0.95–0.78

of the two species, the majority of which was associated with the central and western patches.

The raster maps produced from the factorial least cost path analysis showed a gradient of corridor density across the landscape (Figs. 3, 4). Approximately 33% and 38% of the entire study landscape were, respectively, estimated to support movement of grey wolf and golden jackal, with varying degrees of strength. For both species, sections containing a high density of LCPs occupied only a small proportion of the networks. However, these areas were of considerably larger extent for golden jackal (33% of the study area) compared to the grey wolf (8.9% of the study area).

The strongest connection for grey wolf was predicted between central and eastern populations and between core habitats of 1, 3 and 7 (connecting P6 and P20). With a weaker strength but still a high-density of LCPs, this corridor extended toward the west connecting patch 1 to patch 4. For this species, the lowest degree of connectivity was estimated for western, northern and southeastern populations, where only one LCP was predicted to connect the core

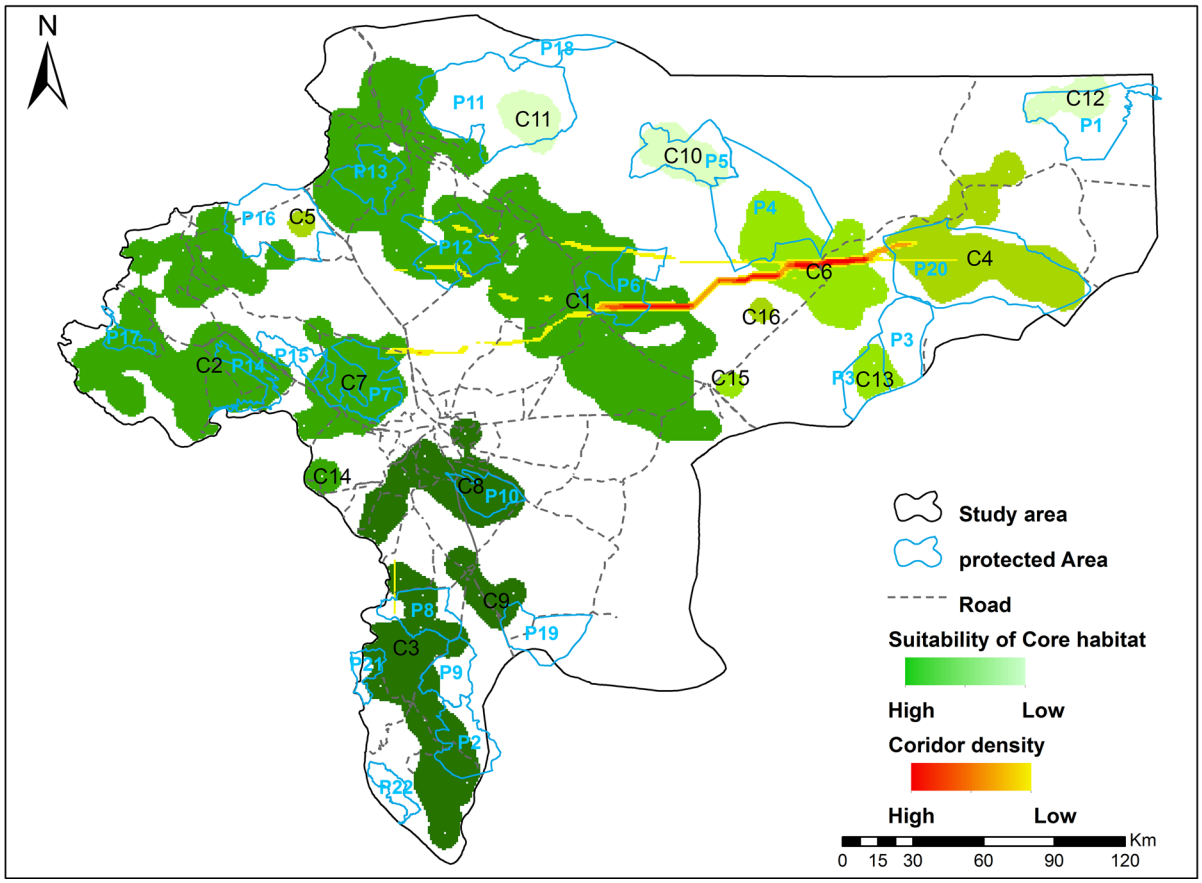

Fig. 3 The estimated suitability of core habitats for grey wolf in central Iran and the strength of corridors connecting them from weak (yellow) to strong (red) for grey wolf. (Color figure online)

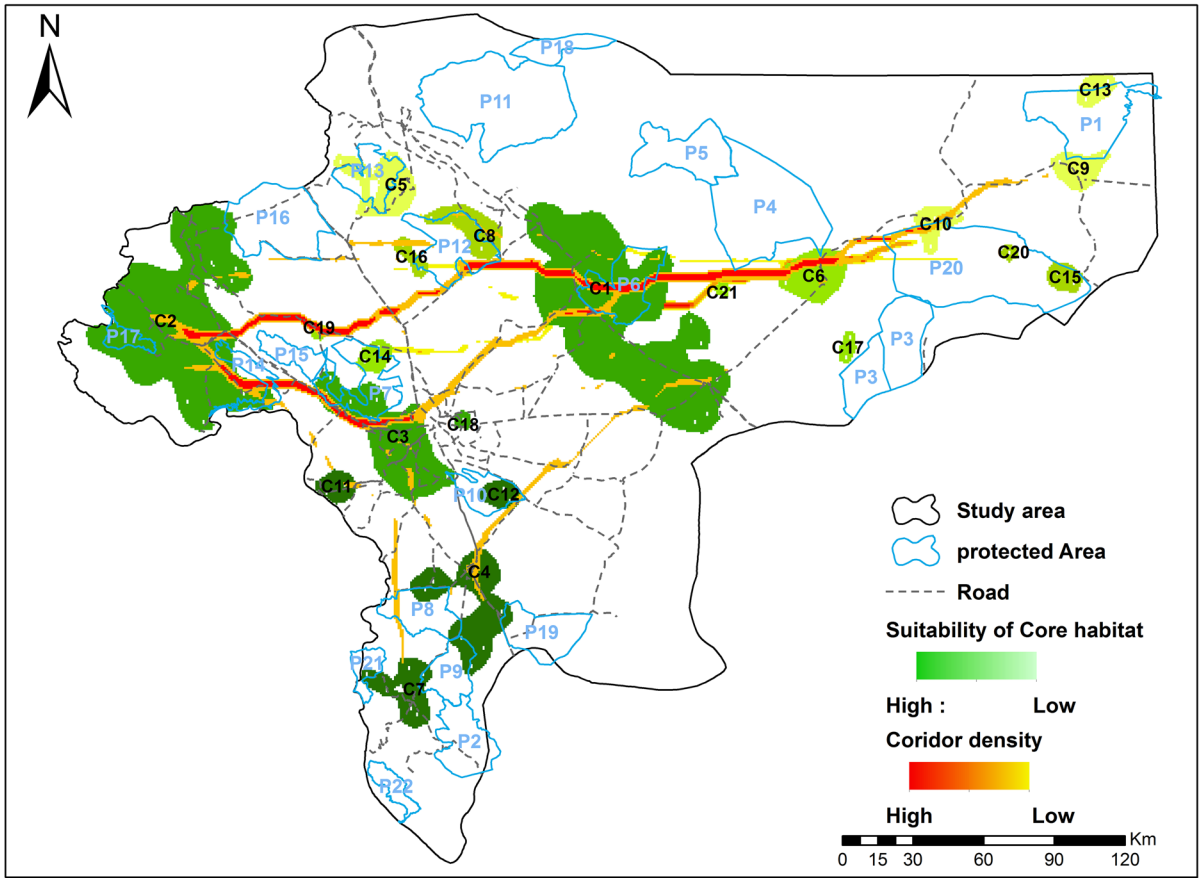

Fig. 4 The estimated suitability of core habitats for golden jackal in central Iran and the strength of corridors connecting them from weak (yellow) to strong (red) for golden jackal. (Color figure online)

habitats. Mapped corridors for the golden jackal, revealed a more robust connectivity network for movement of this species. We identified two major connectivity nodes in the center and eastern part of the landscape where the largest number of LCPs traversed. Through connecting several cores (7, 1, 19, 2, 3 and 2), these least cost path networks provided stronger connections between eastern and western populations of golden jackal as compared to grey wolf. Based on the density of LCPs, southern and northern populations of golden jackal were predicted to be more isolated than other populations. Intersecting corridor maps of both species, we identified only a small linkage node with the highest numbers of factorial LCPs for both canids, though the corridors of the two species are in close proximity (Fig. 5). The linkage passed through the unprotected landscape in the eastern part of the study area (south of the P4 No Hunting Area) and accounted for nearly 7.2% of the connectivity network. Another important linkage was also predicted in the western part of the province connecting P14 and P15 and associated core habitats though with a lesser strength. Both species also shared two large core habitats in west and central part of the province. With only one linking corridor, connection of the western shared patch is more limited than the central patch (Fig. 5).

The distribution of corridor density within the network of PAs demonstrated that the highest numbers of the factorial LCPs funneled through PAs of P12, P20 and P6 for grey wolf, and P12 and P6 for golden jackal. Five and six, out of 22 PAs, contained no LCPs for populations of these two canids, respectively, and thus were identified as isolated PAs. Nearly the entire least cost path network for both species was impacted by roads (Fig. 5). The most critical intersections were associated with major nodes where high densities of LCPs were concentrated (e.g., Cushman et al. 2013a).

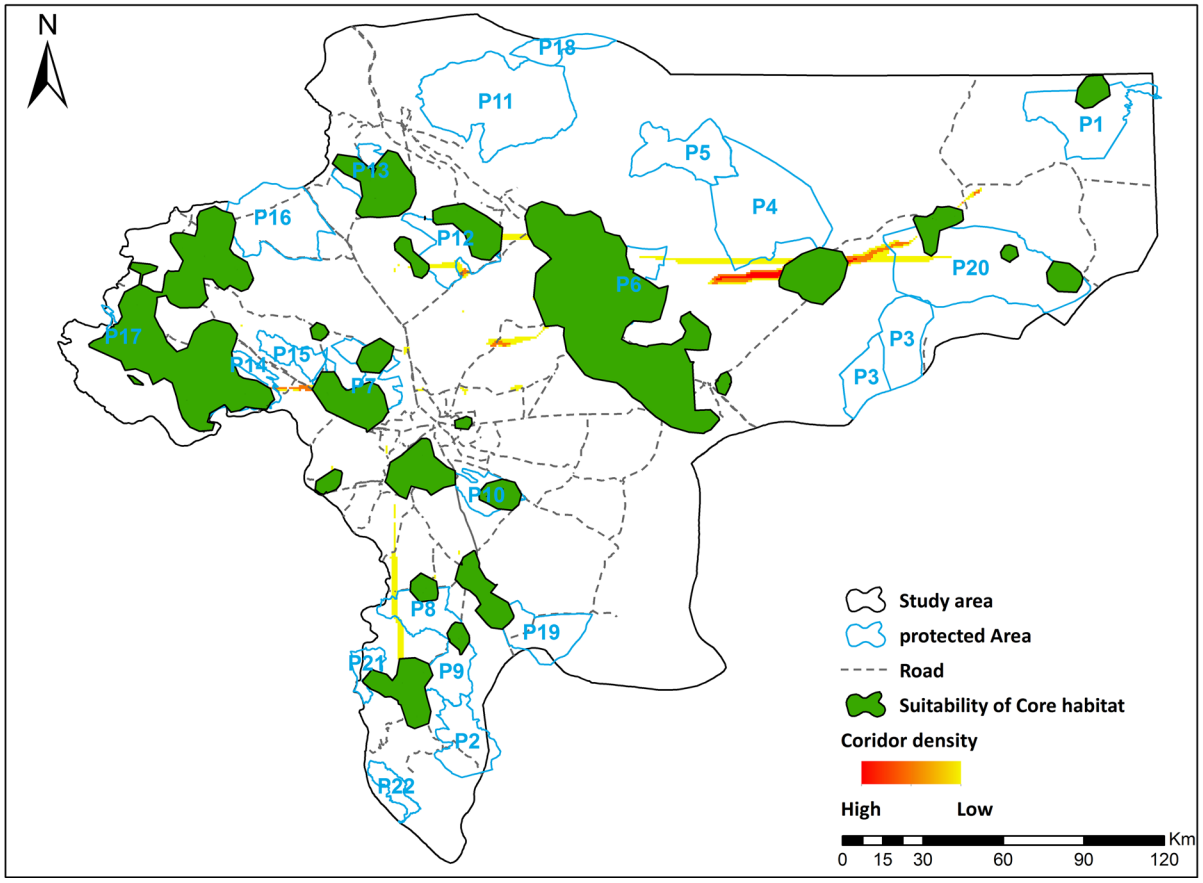

Fig. 5 Distribution and density of movement corridors and core habitats shared by both grey wolf and golden jackal in central Iran

Contribution of core habitats to landscape connectivity

Values of dPC were estimated to be positively correlated with patch area, such that the most important patches for both canids were those occupying the largest extents in the landscape (e.g., patches 1, 2 and 3; Figs. 3, 4 Table S3 and S4). For the majority of core habitats, we found variation in rank of a given core patch in connectivity importance when changing the dispersal distance thresholds. In this regard, only patches 1, 2 and 16 for wolf, and 1, 2, and 3 for jackal retained the same ranking regardless of dispersal ability. With increasing dispersal distance, there was an increase in connectivity importance of 62.5% of the core habitats of grey wolf and 75% of the core habitats of golden jackal. The importance of patch number 16 was estimated to be the lowest in the connectivity network of grey wolf with respect to different dispersal abilities of this carnivore. In contrast, for the golden jackal the least important habitat core differed as the species dispersal ability changed. For example, over dispersal distances of 50, 100 and 200 km, habitat core 20 had the least contribution in overall habitat connectivity for this species. While for distances greater than 200 km, this was replaced with core habitat number 19. Comparing values of dPC calculated for each core habitat, we identified at which dispersal distance the maximum contribution of a given patch to maintaining connectivity occurred. For grey wolf, half of the cores reached their highest importance at a dispersal distance of 400 km. A similar result was obtained for the golden jackal. For this species, there was no peak in importance of any of the core habitats at dispersal distances of 50 and 300 km.

Plotted values of sum of dPC-connectors against the range of selected dispersal distances (Fig. S1)

showed that at all distances the contribution of the dPC connector was higher for grey wolf, indicating a more important role of cores as stepping stones in facilitating movement of this species. Peaks on these graphs depict distances at which the importance of habitat patches as stepping stone among other patches is the highest. This point for golden jackal was obtained at the distance of 200 km, with nearly 15% contribution of dPC-connector. For grey wolf, this value was achieved at the shorter distance of 100 km, where contribution of dPC-connector was about 45%. Over distances of 100 and 200 km, there was a decreasing trend in importance of core patches as element of stepping stone in the connectivity network of the studied canids. Assuming 100 and 200 km as the maximum dispersal distances, respectively, patch number 6 (dPC-connector of 12.24%, located in P16 wildlife refuge) and 5 (dPC-connector of 4.89%, located in P12 protected area) were recognized as the best intermediate cores to facilitate movements of grey wolf and golden jackal.

Discussion

In this study we provided a quantitative assessment of population connectivity for two sympatric species of canids combining concepts of distribution and connectivity modeling techniques. Based on the ensemble distribution models, large parts of the study area were predicted as potential suitable habitats for both species; a considerable proportion of these areas were identified as key core habitats. However, as the results of connectivity modeling revealed, these extended networks of core habitat areas were not well connected by robust and strong movement corridors.

Distance to agricultural lands was the most important explanatory variable out of those tested in predicting occurrence of both canid species however with different responses. While, probability of golden jackal occurrence decreased with decreasing distance from agricultural lands, occurrence of grey wolf was positively correlated with this variable. Importance of this anthropogenic variable for golden jackal is justifiable considering species feeding behaviour. Golden jackal prefers small prey species which could be easily accessible in agricultural lands such as small birds. In addition, as a species with scavenger behaviour, dumping of wastes from livestock and poultry sectors in the vicinity of cultivated lands is another reason for the high desirability of such areas for golden jackal. The tendency of golden jackal to associate with areas managed by humans was the main reason for identifying large parts of suitable habitats outside the network of PAs. In contrast to golden jackal, distribution of the grey wolf was predominantly influenced by a non-human related factor e.g., density of natural prey species; a finding reported for other carnivore species in Iran too (e.g., Ahmadi et al. 2017; Khosravi et al. 2018). Presently, core populations of the ungulate species are almost confined to isolated protected areas (Khosravi et al. 2018) due to extensive human interventions. This is the reason explaining why unlike golden jackal, the entire or proportions of the core habitats for grey wolf were located within the borders of protected areas. Over the last decades, the density of ungulates has been decreasing in Iran due to overhunting (Ziaei 2009). This has resulted in attraction of grey wolf populations to areas around human settlements, where they can search for alternative food sources. As a result of this behaviour, grey wolf occurrence ranges have been expanded from protected areas to human dominated parts of the province resulting in high spatial overlap in suitable habitats of both species.

We integrated the identified core habitats and functional corridors with the network of PAs to determine how well critical paths and core habitats are represented by the protected network in the study landscape. For the golden jackal, we found low contribution of the PAs as core habitat, which was explained by the dependency of the species on human-altered areas. For this canid, the highest overlap between core habitats and protected sites was observed for P6, which incorporates a considerable number of villages. On the contrary, for the grey wolf, PAs played a more important role in protecting populations of the species, as over half of the core habitats (54%) intersected with the protected area network. However, the coverage of PAs is not sufficient particularly for those cores in the western, southern and central parts of the study area due to their small size. Dependency of grey wolf on PAs, which is also reported by Capitani et al. (2006), is directly associated with relatively high prey availability within the PAs and the safety they afford from anthropogenic mortality. Among the different protected areas, we found the highest coverage of grey wolf core habitats

by P20. This is the largest protected area in the study area and supports large numbers of natural prey species including wild goat, wild sheep and Indian gazelle. P20 has also been documented to have a high potential for supporting other carnivore species such as critically endangered Asiatic cheetah (*Acinonyx jibatus venaticus*) and Persian leopard (*Panthera pardus saxicolor*; Khosravi et al. 2018). Furthermore, we found a high overlap between the grey wolf core habitats and areas of high village density and agricultural lands in the landscape. This implies the importance of livestock as an anthropogenic prey for this species.

The most robust functional corridors for grey wolf were predicted between eastern and central populations (Fig. 3). The high permeability of the landscape across these areas is mainly the result of very low human populations and the abundance of prey species within the PAs. In this regard, P20, P6 and C1 and C3 and the corridor linkages between them were recognized as critical landscape elements in maintaining the landscape connectivity for grey wolf. Khosravi et al. (2018) reported the same result in a similar study on multiple carnivore species including grey wolf. Eastern and central populations, however, were predicted to be weakly connected to the populations in the north, south and west, as also found by Khosravi et al. (2018) and Moqanaki and Cushman (2017). Low connectivity among these populations is likely driven by the high concentration of roads and urban areas, resulting in increased landscape resistance, and low density of prey species in the PAs in the northern and southern parts of the study area.

The grey wolf has shown adaptability to anthropogenic landscapes (Weaver et al. 1996). Thus, the human disturbed areas may not be perceived as strong barriers to movements of the species. Therefore, the functional connectivity among populations, even those predicted to be isolated, could be stronger than what was predicted by the connectivity model. More extended and stronger functional corridors were predicted for movement of golden jackal, particularly between the eastern and western parts of the landscape. Human-associated food resources available around rural areas may be the main reason for the importance of villages as a linking habitat for the movement of this carnivore.

Vulnerable parts of the connectivity network were found at points where roads intersected densely movement corridors (e.g., Cushman et al. 2013b). Vulnerability of these locations is related to the high potential for collisions with vehicles and exposure to other human mortality agents in the proximity of roads. Risk of collision was expected to be higher for populations of golden jackal due to higher numbers of intersections along the main corridors. There is also a high density of different types of roads within the important core patches. However, these did not seem to have a significant negative impact on the distribution of the two species. In fact, roads in the cores, particularly secondary and unpaved roads, may assist the species to have access to suitable habitats elsewhere (Kabir et al. 2017). Furthermore, due to providing better visibility and mobility opportunities, these structures may help the studied species to more readily search for the prey (Mesler 2015).

The results of this study provide important information for the conservation of grey wolf and golden jackal in Iran. In our study area, there were low densities of corridors to support movements of each species and we identified only a small shared corridor for the two species. As in open habitats, corridors of different species may not be identical; a multi-species corridor designed through overlapping corridor maps of a set of species may not adequately accommodate their movements. Therefore, we suggest considering movement corridors of each species independently in conservation planning. Sustaining species movements also requires protecting key core habitats as any loss of these habitats may result in population reduction of the canids. Accordingly, carnivore conservation in Iran should focus on safeguarding these key strongholds and improving the permeability, habitat quality and reducing mortality risk at the corridors linking them.

Acknowledgements We are grateful to the Isfahan Department of Environment for providing occurrence data and to the gameguards for assisting us in collecting species occurrence records.

References

Ahmadi M, Nezami Balouchi B, Jowkar H, Hemami MR, 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(6):592–603

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22(1):42–47

Behdarvand N, Kaboli M, Ahmadi M, Nourani E, Mahini AS, Aghbolaghi MA (2014) Spatial risk model and mitigation implications for wolf–human conflict in a highly modified agroecosystem in western Iran. Biol Conserv 177:156–164

Capitani C, Mattioli L, Avanzinelli E, Gazzola A, Lamberti P, Mauri L, Scandura M, Viviani A, Apollonio M (2006) Selection of rendezvous sites and reuse of pup raising areas among wolves Canis lupus of north-eastern Apennines, Italy. Acta Theriol 51(4):395–404

Clark TW, Paquet PC, Curlee AP (1996) General lessons and positive trends in large carnivore conservation. Conserv Biol 10(4):1055–1058

Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conserv Biol 21(3):788–799

Crooks KR, Burdett CL, Theobald DM, Rondinini C, Boitani L (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos Trans R Soc B Biol Sci 366(1578):2642–2651

Cushman SA, Elliot NB, Bauer D, Kesch K, Bothwell H, Flyman M, Mtare G, Macdonald DW, Loveridge AJ (2018) Prioritizing core areas, corridors and conflict hotspots for lion conservation in southern Africa. PloS one 13(7):e0196213

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ (2016) A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. Landsc Ecol 31(6):1337–1353

Cushman SA, Landguth EL, Flather CH (2013a) Evaluating population connectivity for species of conservation concern in the American Great Plains. Biodivers Conserv 22(11):2583–2605

Cushman SA, Lewis JS, Landguth EL (2013b) Evaluating the intersection of a regional wildlife connectivity network with highways. Mov Ecol 1(1):12

Cushman SA, Lewis JS, Landguth EL (2014) Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. Diversity 6(4):844–854

Cushman SA, McKelvey KS, Schwartz MK (2009) Use of empirically derived source-destination models to map regional conservation corridors. Conserv Biol 23(2):368–376

Cushman SA, McRae B, Adriaensen F, Beier P, Shirley M, Zeller K (2013c) Biological corridors and connectivity. Key Top Conserv Biol 2:384–404

Epperson BK, McRae BH, Scribner KI, Cushman SA, Rosenberg MS, Fortin MJ, James PM, Murphy M, Manel S, Legendre P, Dale MR (2010) Utility of computer simulations in landscape genetics. Mol Ecol 19(17):3549–3564

Franklin J (2010) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge

Gastón A, Blázquez-Cabrera S, Garrote G, Mateo-Sánchez MC, Beier P, Simón MA, Saura S (2016) Response to agriculture by a woodland species depends on cover type and behavioural state: insights from resident and dispersing Iberian lynx. J Appl Ecol 53:814–824

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8(9):993–1009

Hemami M-R, Esmaeili S (2013) Biodiversity assessment and conservation prioritisation of Isfahan province. In: Soffianian, A (ed) Land use planning studies and strategic plan document for Isfahan province development. Research report submitted to the Isfahan Provincial Goverment. Department of Natural Resources, Isfahan University of Technology

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25(15):1965–1978

Hunter RD, Fisher RN, Crooks KR (2003) Landscape-level connectivity in coastal southern California, USA, as assessed through carnivore habitat suitability. Nat Areas J 23:302–314

Kabir M, Hameed S, Ali H, Bosso L, Din JU, Bischof R, Redpath S, Nawaz MA (2017) Habitat suitability and movement corridors of grey wolf (Canis lupus) in Northern Pakistan. PloS one 12(11):e0187027

Kaszta Ż, Cushman SA, Sillero-Zubiri C, Wolff E, Marino J (2018) Where buffalo and cattle meet: modelling interspecific contact risk using cumulative resistant kernels. Ecography 41(10):1616–1626

Keeley AT, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc Ecol 31(9):2151–2162

Keeley ATH, Beier P, Keeley BW, Fagan ME (2017) Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc Urban Plan 161:90–102

Khosravi R, Hemami MR, Cushman SA (2018) Multispecies assessment of core areas and connectivity of desert carnivores in central Iran. Divers Distrib 24(2):193–207

Landguth E, Hand B, Glassy J, Cushman S, Sawaya M (2012) UNICOR: a species connectivity and corridor network simulator. Ecography 35(1):9–14

Larkin JL, Maehr DS, Hoctor TS, Orlando MA, Whitney K (2004) Landscape linkages and conservation planning for the black bear in west-central Florida. In: Animal conservation forum. Cambridge University Press, Cambridge, pp 23–34

McClure ML, Dickson BG, Nicholson KL (2017) Modeling connectivity to identify current and future anthropogenic barriers to movement of large carnivores: a case study in the American Southwest. Ecology and evolution 7(11):3762–3772

Mesler JI (2015) Modeling habitat suitability and connectivity of grey wolf (*Canis lupus*) populations in the Pacific Northwest. M.Sc. Thesis, Humboldt State University

Moqanaki E, Cushman S (2017) All roads lead to Iran: predicting landscape connectivity of the last stronghold for the critically endangered Asiatic cheetah. Anim Conserv 20(1):29–41

Noss RF, Quigley HB, Hornocker MG, Merrill T, Paquet PC (1996) Conservation biology and carnivore conservation in the Rocky Mountains. Conserv Biol 10(4):949–963

Peterson AT (2001) Predicting SPECIES'Geographic Distributions Based on Ecological Niche Modeling. Condor 103:599–605

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological

niches and geographic distributions (MPB-49). Princeton University Press, Princeton

Pinheiro J, Bates D, DebRoy S, Sarkar D (2015) R Development Core Team. 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1-117

Riordan P, Cushman SA, Mallon D, Shi K, Hughes J (2016) Predicting global population connectivity and targeting conservation action for snow leopard across its range. Ecography 39(5):419–426

Rodríguez-Soto C, Monroy-Vilchis O, Maiorano L, Boitani L, Faller JC, Briones MÁ, Núñez R, Rosas-Rosas O, Ceballos G, Falcucci A (2011) Predicting potential distribution of the jaguar (Panthera onca) in Mexico: identification of priority areas for conservation. Divers Distrib 17(2):350–361

Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landsc Urban Plan 83(2–3):91–103

Saura S, Rubio L (2010) A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography 33(3):523–537

Saura S, Torne J (2009) Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environ Model Softw 24(1):135–139

Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V, Lamoreux J, Rodrigues AS, Stuart SN, Temple HJ, Baillie J (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 80(322):225–230

Shahnaseri G (2017) Landscape permeability and niche overlap of the grey wolf (*Canis lupus*) and golden jackal (*Canis aureus*) in Isfahan province. Dissertation, Isfahan University of Technology

Singleton PH, Gaines WL, Lehmkuhl JF (2002) Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. Res Pap PNW-RP-549. U.S. Department of Agriculture, Forest Service, Pacific Northwest Res Station 89, Portland, p 549

Spear SF, Balkenhol N, Fortin MJ, McRae BH, Scribner K (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD–a platform for ensemble forecasting of species distributions. Ecography 32(3):369–373

Trainor AM, Walters JR, Morris WF, Sexton J, Moody A (2013) Empirical estimation of dispersal resistance surfaces: a case study with red-cockaded woodpeckers. Landsc Ecol 28:755–767

Vergara M, Cushman SA, Urra F, Ruiz-González A (2016) Shaken but not stirred: multiscale habitat suitability modeling of sympatric marten species (*Martes martes* and *Martes foina*) in the northern Iberian Peninsula. Landsc Ecol 31(6):1241–1260

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62(11):2868–2883

Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33(3):607–611

WCS, CIESIN (2005) Last of the Wild Project, version 2, 2005 (LWP-2): global human footprint dataset (geographic). NASA Socioeconomic Data and Applications Center (SEDAC), Palisades

Weaver JL, Paquet PC, Ruggiero LF (1996) Resilience and conservation of large carnivores in the Rocky Mountains. Conserv Biol 10(4):964–976

Zeller KA, Jennings MK, Vickers TW, Ernest HB, Cushman SA, Boyce WM (2018) Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Divers Distrib 24:868–879

Ziaie H (1996) A field guide to the mammals of Iran: 100 distribution maps. Department of the Environment, Tehran

Ziaei H (2009) A field guide to the mammals of Iran. Iran Wildlife Center Press, Tehran