A predictive spatial model for gray wolf (Canis lupus) denning sites in a human-dominated landscape in western Iran

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ORIGINAL ARTICLE

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Abstract Predictive models of species denning habitat are useful for understanding distribution of core use areas and identifying areas with potential conflicts. Wolf den site selection in unmanaged areas with dominance of agriculture-lands and human disturbance is not completely understood. We used a GIS multivariate model based on the Mahalanobis distance statistic and 11 digital habitat layers to evaluate gray wolf denning site suitability in Hamedan province (HP), western Iran. Results showed that >74 % of dens occurred in potential denning sites that occupied 14 % (2,785 km^2) of the study area. Based on sensitivity analysis with ROC, we found that the distance to rangelands, elevation, and distance to roads, human settlements and streams were the most predictive variables. Our potential distribution model of wolf den sites showed a very good overall performance according to classification accuracy and discrimination capacity. Denning in elevated rugged terrains adjacent to rangelands and away from roads and villages revealed that wolf den distribution in HP is highly influenced primarily by factors associated with human disturbance. The derived predicted distribution map can be used to prioritize areas for conservation, identify areas with potential conflicts, and to implement adaptive management in regions beyond wilderness and protected areas.

Keywords Gray wolf · Den site selection · Mahalanobis distance model · Hamedan province · Iran

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Introduction

The grey wolf, a habitat generalist species, is the most widely distributed of all land mammals and inhabits all vegetation types in the Northern hemisphere (Mech and Boitani 2003). Wolves are not dependent on wilderness areas (Mech 1995; Treves et al. 2011) and, if they are not in conflict with human activities and have adequate ungulate prey, can disperse in a mixture of managed, human dominated, and semi-wild areas (Mech 1995; Mladenoff et al. 1999). Because of its high adaptability and resilience to diverse habitats, the gray wolf has viable populations with relatively fair conditions in most regions of Iran (Ziaei 2008) and, just as in Europe, in Iran wolves usually live in multiple-use landscapes that are surrounded by human settlements (Salvatori and Linnell 2005; Ziaei 2008).

Today a great proportion of the Earth is dominated by a mosaic of agriculture, urbanization, logged forests and degraded lands (Ehrlich 1995; Vitousek et al. 1997; Tinoco Torres et al. 2011), which leads to an overlap of human and wildlife requirements, resulting in human–wildlife conflicts (IUCN 2003). Consequently, wolves, as habitat generalists, are encountering human-induced mortality and are decreasing due to persecution, hybridization, and more limited prey abundance (Mech and Boitani 2003; Fernández and de Azua 2010; Rich et al. 2012).

Hamedan Province (HP) is one of the most suitable habitats for wolves in western Iran due to its favorable environmental conditions. This province contains a variety of land uses and habitat types, including agricultural lands and rural areas, as well as national forests,

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rangelands and protected areas managed by different governmental organizations. Though this mixture is a favorable condition for recolonization by wolves (Treves et al. 2011), it could lead to complications in conflict management. Because of the lack of a clear boundary between wolf habitat and human activities, wolf–human conflicts such as livestock depredations and attacks on humans has increased in HP. Consequently, execution of wolves and their pups and destruction of active dens is commonly carried out by local people [Hamedan Department of Environment (DoE), unpublished reports].

Dens tend to be located in the central zone of wolf territories (Ciucci and Mech 1992; Trapp et al. 2008) and show higher intensity of use throughout the year compared to other parts of the territory (Trapp et al. 2008; Unger et al. 2009). Wolves select den sites based on habitat characteristics at high spatial scales (Norris et al. 2002; Person and Russell 2009) and make use of them year-round. Therefore, den locations may be useful for prioritizing areas for management and conservation objectives at a macro-spatial scale. Overlap of wolf habitats with human activities has led to various conflicts that make decision making difficult for wildlife managers. The first step for conflict management would be to determine wolf habitat suitability (Corsi et al. 1998; Cayuela 2004; Treves et al. 2011). In fact, quantitative assessment of den sites would allow managers to identify the most effective variables that influence reproductive success and determine areas of potential human–wolf conflict. Numerous studies have focused on wolf reproduction and denning (Ballard and Dau 1983; Ciucci and Mech 1992; Theuerkauf et al. 2003a; Unger et al. 2009). Results indicate that habitat composition and human disturbance such as coniferous forest patches away from roads and development (Norris et al. 2002; Theuerkauf et al. 522003b), or topographic features such as elevation, slope, and proximity to freshwater (Unger 1999; Person and Russell 2009), are the most effective variables that affect den site selection by wolves. The majority of publications on this subject are conducted in forested ecosystems, national parks or protected areas, and wolf den site selection in unmanaged areas with agriculture-dominated lands and human disturbance, as seen in HP, has not been comprehensively investigated. We performed a potential suitability model to assess wolf den site selection using Mahalanobis Distance method as a presence-only dependent model.

Unlike what is commonly believed, presence-only suitability modelling methods are very few, the most common being a rectilinear envelope (e.g., BIOCLIM, Busby 1991) or distance-based envelope (e.g., Mahalanobis distance, Clark et al. 1993). Methods such as Maxent or GARP require background data or pseudo-absence data to perform suitability models (Phillips et al. 2006), but are often mistakenly used as presence-only methods (Barbet-Massin et al. 2012). Nevertheless, confirmation of absence of a species is very difficult to obtain, especially for highly mobile and generalist species. To overcome this problem, we used a Mahalanobis distance model to cope with the uncertainty of absence locations. We evaluated den site selection by wolves in HP with respect to topography, landcover, livestock and human densities, and roads. Our objectives were to (1) investigate factors influencing wolf den site selection, and (2) develop a predictive model of suitable den site habitats throughout HP as a human-dominated area.

Materials and methods

Study area

The study area lies between 47°34′–49°36′E and 35°25′–3$\mathring{5}$15′N and covers an area of 19,546 km^2 (Fig. 1). The region has a cold semi-arid climate with an average annual precipitation of 325 mm and mean annual temperature of 11 °C. Croplands and orchards are the dominant land cover, accounting for 6,157 km^2 (32 % of the area) and comprising mostly irrigated and dry farming. Rangelands, as another dominant land cover, include rugged terrain covered with grass-shrub lands, with the dominance of *Astragalus* spp., *Bromus* spp. and *Festuca ovina* covering 6,563 km^2 (33 %) of the study area. Another 425 km^2 (2 %) of the area consists of fragmented stands of mixed-deciduous and planted forest of Persian oak (*Quercus brantii*), Hawthorn (*Crataegus* spp.), *Cornus australis* and Cherry plum (*Prunus divaricata*) in valleys and mid-slopes (Safikhani et al. 2007). The rest of the province is covered with rocky, barren areas and residential areas. In HP there are six protected areas covering 600 km^2 (3 %) of the province. Three main wild ungulate species of the region are the wild goat (*Capra aegagrus*), wild sheep (*Ovis orientalis*), and the wild boar (*Sus scrofa*). Their population is fragmented and restricted to protected areas and no accurate estimation of their population size is available.

HP is one of the most compact provinces of the country from a demographic point of view (88 people/km^2). This density is twice as much as the average population density in other provinces in Iran. About 48 % of people live in townships and 52 % in villages. Economic activity in the region consists mainly of livestock rearing and agriculture (Reyahi Khoram and Fotros 2011).

Data collection

In this study, due to political and financial constraints, tracking tools [such as global positioning system (GPS)-collars] were not used. However, interviews and surveys of the hunting managers and rural inhabitants can be cost effective and can provide reliable data on biological aspects of wildlife habitat use (White 2005). Therefore, to locate a sufficient number of active wolf

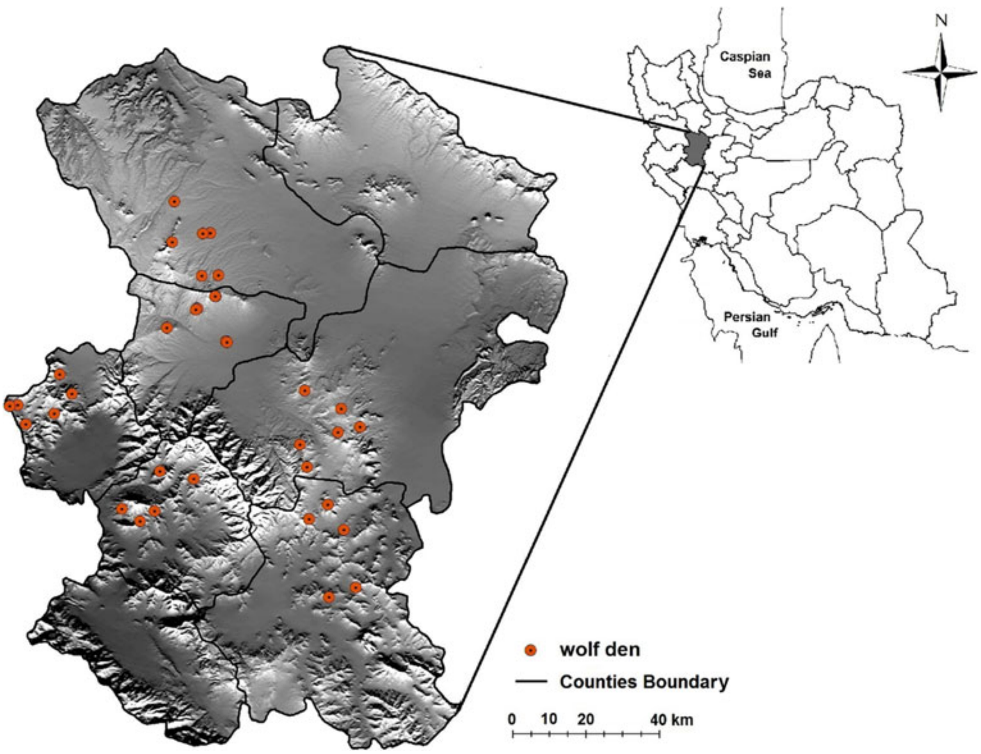

Fig. 1 Location of Hamedan province (HP) as the study area in western Iran in a topographic view. *Dots* Sites where wolf dens have been found

Table 1 Variables and value range used in the Mahalanobis distance model to perform habitat suitability for denning wolves in Hamedan province (HP)

Variable	Mean	SD	Value range	Source
Elevation	2,006	249	1,546–3,651	Based on DEM generated by SRTM with 100 m pixel size
Slope	4.4	5.4	0–41.2	Calculated from DEM with ArcGIS 9.3
Aspect	1.07	0.7	0–2	Beers transformation of aspect
Solar radiation	735,042	32,104	438,900–936,869	Calculated from DEM with ArcGIS 9.3
VRM	0.003	0.006	0–0.14	Calculated based on Sappington et al. (2007)
Distance to stream	557	435	0–3,716	Calculated with ArcGIS 9.3, Euclidean distance on maps
Distanc to range	2,431	2,587	0–14,741	(derived from the Iranian Department of Forestry and Rangelands)
Distanc to road	4,718	4,272	0–29,064	
Distance to human settlements	2,078	1,355	0–9,546	
Human density	88	10	35–110	Interpolated from the data derived from the Statistical Center of Iran
Livestock density	112	18	81–169	

VRM Vector ruggedness measure, DEM digital elevation model, SRTM shuttle radar topography mission

dens, we conducted an extensive field study and used informed locals, especially herders, information from Hamedan DoE game wardens, and direct field survey. We patrolled the study area by motorcycle and tried to navigate areas where we expected to find wolf dens. Our field survey did not involve chasing the wolves to locate their dens. Also, since the most critical period during the life cycle of wolves is the pup development, data collection began after confirming that wolf packs had left their dens, between May and June. After finding dens and ensuring the absence of wolves and pups, we recorded longitude and latitude of dens using a GPS.

Model attributes

We used a geographic information system (GIS) to generate data layers for 11 habitat variables. We chose variables most likely to represent unique aspects of den site selection (Norris et al. 2002; Trapp et al. 2008; Person and Russell 2009; Unger et al. 2009; Table 1). A digital elevation model (DEM) with a resolution of 100 m was used to calculate five topographic variables: elevation, slope, aspect, solar radiation index, and vector ruggedness measure (VRM) (Table 1). Because circular measures cannot be used to calculate the Mahalanobis distance statistic (Clark et al. 1993), we performed cosine-transformed aspect, based on Beers transformation of aspect (Beers et al. 1966). Using Spatial Analyst in ArcGIS 9.3, solar radiation was calculated as the total amount of incoming solar insulation (WH/m^2 year) that reaches a certain position on the Earth's surface. The VRM developed by Sappington et al. (2007), calculated as a measure of terrain ruggedness, incorporates heterogeneity in both aspect and slope and quantifies local variations in terrain (Sappington et al. 2007). Human activities within the study area include mostly roads, agricultural and residential areas. Thus, we calculated human density, livestock density, proximity to human settlements, and proximity to roads as anthropogenic variables. We calculated proximity to rangelands (including meadows and grasslands) as the only remaining natural habitats for the wolf in HP with low human activity. To calculate proximity to streams, using ArcGIS 9.3 hydrology tools, we first determined stream courses. Then we used existing maps of rivers and streams to verify correct delineation of streams. We set the resolution of all GIS data layers based on the pixel size of the DEM layer (100 m).

Data analysis

To predict suitable den sites, we calculated Mahalanobis distance (D^2) value for each pixel. Mahalanobis distance, as a measure of habitat similarity, can be used to predict species occurrence based on location data and raster-based GIS layers. In this method, every map cell is assigned a score based on how similar it is to the multivariate mean of the habitat characteristics within the occupied map cells (Clark et al. 1993; Farber and Kadmon 2003; Jenness et al. 2011). This technique is well-suited for modelling wide-ranging animals such as wolves, because it requires only presence data for input and reduces the complexities of locating absence points (Corsi et al. 1998; Podruzny et al. 2002). In addition, D^2-based models do not require multivariate normality in the habitat data and they account specifically for covariance among habitat variables (Knick and Dyer 1997). Mahalanobis distance was calculated using the following equation:

$$D^2 = (x - \mu)^{\mathrm{T}} \Sigma^{-1} (x - \mu)$$

where x is a vector of habitat characteristics for each pixel in the GIS grid, μ is the mean vector of habitat characteristics of the sample locations, T is the vector to be transposed and Σ^{-1} is the inverse of the variance–covariance matrix calculated from the sample locations. We calculated the D^2 statistic in ArcGIS 9.3 for each pixel in the study area using Land Facet Corridor Designer (Jenness et al. 2011). The D^2 scores can range from 0 to infinity, so it can be difficult to interpret and evaluate results especially in management decision making. We recoded D^2 scores to P values based on the Chi-square distribution to create habitat suitability measure that ranges from 0 to 1 (Clark et al. 1993; Jenness et al. 2011).

Habitat suitability threshold

The continuous output of the Mahalanobis Distance model allows fine distinctions to be made between the modelled suitability of different areas. But it is necessary to convert quantitative measures of habitat suitability to qualitative maps for decision making in land management and conservation (Boyce et al. 2002; Phillips et al. 2006). According to the calculated suitability values, a threshold can be developed to indicate favorable predicted areas from unfavorable ones. These binary transformed probabilities could also be used in assessing the validation of models by threshold-dependent methods (Fielding and Bell 1997; Phillips et al. 2006). To determine the probability threshold, we performed a null model by generating 1,000 random locations within the whole study area using Hawth's Tools (Beyer 2004). We then developed cumulative frequency distribution based on P values associated with wolf den locations and those associated with null model locations. We identified the greatest difference between the two cumulative frequency graphs as the threshold value to classify wolf den habitat to suitable and unsuitable (Griffin et al. 2010; Hollenbeck et al. 2011). Pixels with D^2 values above the threshold value represent more favorable habitat, whereas pixels with values below the threshold are less favorable (Hollenbeck et al. 2011).

Sensitivity and important factors

To determine the importance of environmental variables in den site selection, after running the model with all the variables, variables were temporarily removed from the operation in turn, the model was refitted and receiver operating characteristic (ROC) of the new model was calculated (Mahiny and Turner 2003). The advantage of this method is that variable sensitivity (the effect of each variable in the performance of the model) is determined based on differences in ROC of refitted model and full model (Pontius and Schneider 2001; Mahiny and Turner 2003). To determine model sensitivity, we used the ROC command in Idrisi 15 Andes edition.

Assessment of model validation

As the wolf den records were limited, we did not split up the data set to use one part for model calibration and another for validation. Instead, we assessed the reliability of the potential distribution model by classification accuracy and discrimination capacity validation criteria based on presence locations and pseudo-absence locations. Appropriate selection of pseudo-absence locations for presence-only species distribution modelling can influence the appropriateness and accuracy of the model prediction (Chefaoui and Lobo, 2008; Barbet-Massin et al. 2012). It is highly recommended to select pseudo-absence data outside a pre-defined region based on a simple preliminary model or based on a minimum distance to the presence location (Engler et al. 2004; Lobo et al. 2010), or random selection of geographically and/or environmentally stratified pseudo-absences (Barbet-Massin et al. 2012).

To provide appropriate accuracy we selected pseudo-absence locations in equal numbers to the presence locations, considering geographic and biologic restrictions. We generated random points within a range of 1,700–2,700 m a.s.l., which is the known altitude range where the wolf dens occurred. Also the distance between pseudo-absence points and observed presence points was controlled not to fall below 7 km, which is considered to be the radius of average wolf territory size in southern latitudes (Jędrzejewski et al. 2007).

We calculated the area under the curve (AUC) derived from the ROC plots, as a threshold-independent measure to compare the predicted values of habitat suitability assigned to presence and pseudo-absence locations. An AUC value can be interpreted as the probability of differentiation between presence and absence locations. A model with no predictive power would have an AUC of 0.5, while a perfect model would correspond to an AUC of 1.0. (Hosmer and Lemeshow 2000; Boyce et al. 2002). Since the area under the ROC curve, as a discrimination measure, is not a reliable measure of validation of the model by itself (Lobo et al. 2008), we considered classification accuracy to imply greater precision in describing the distribution of wolf dens in the performed model (Fielding and Bell 1997; Romero et al. 2012). Thus, we used a set of well known evaluates of classification accuracy based on the favorability thresholds including: correct classification rate (CCR), misclassifications of presences and absences (omission and commission errors), the probability of correctly predicted presence location (sensitivity), the probability of correctly predicted absence location (specificity), and Cohen's Kappa (Lobo et al. 2008; Romero et al. 2012).

Results

We documented 35 wolf den locations based on local peoples' information (17), Hamedan DoE wardens' knowledge (14) and direct field survey (4). Mahalanobis distance values calculated for the study area ranged from 1.07 to 2,658.3. The greatest D^2 values indicated landscape conditions that were most dissimilar to current wolf den sites, depicting highly urbanized or human activity areas, such as townships or villages, and areas occupied by road networks. Since the D^2 values exhibited an extremely large range, we rescaled the D^2 values to P values to facilitate model interpretation and assessment. P values that corresponded to wolf den locations ranged from 0.03 to 0.96 ($\bar{x}$ = 0.53, SD = 0.23) whereas random locations, as a measure to represent the entire area, had P values that ranged from 0 to 0.8 ($\bar{x}$ = 0.08, SD = 0.16).

Based on cumulative frequency distributions of P values for wolf den locations and null model locations, our habitat model effectively discriminated between areas typically used by wolves and those considered unsuitable (Fig. 2). The P values threshold

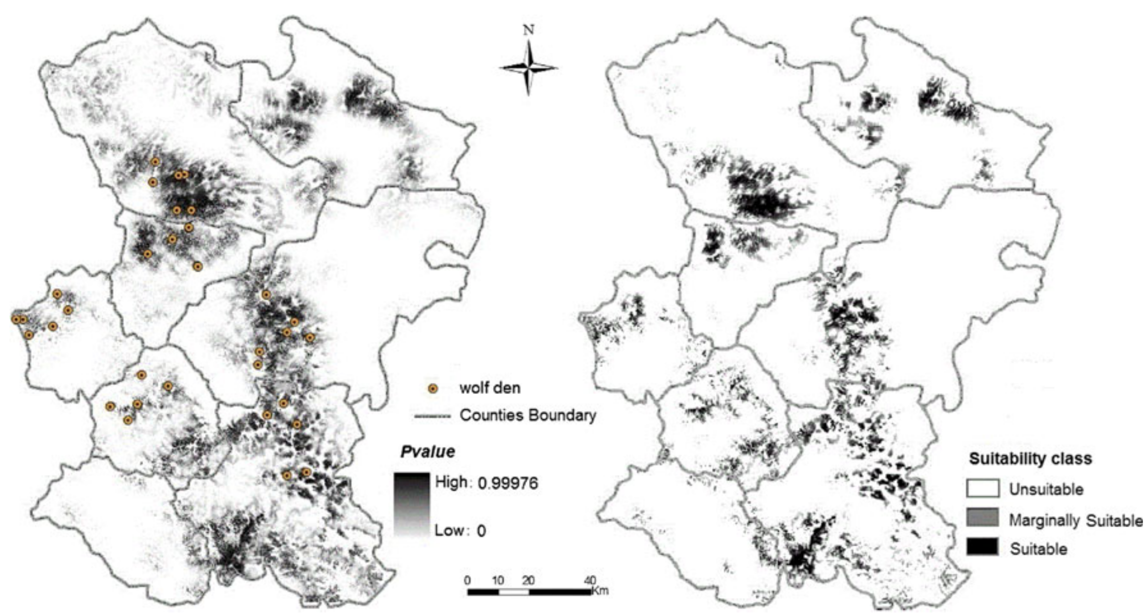

Fig. 2 Map depicting probability values of suitable habitat for denning wolves based on the Mahalanobis distance (*left*) and categorized by suitability based on threshold (*right*). *Darker colours* Areas where suitability is higher

for wolf den sites was 0.32 (Fig. 3). Using pixels with P values above the threshold of 0.32, we estimated 2,785 km^2 (14.75 %) of HP as suitable wolf den sites (Table 2).

The model sensitivity result also indicated that the effect of variables on wolf den site selection was different (Fig. 4). Based on difference in ROCs of refitted models and full model, variables including distance to rangelands, distance to streams, elevation and distance to roads had higher importance, because removing them had the most effect on model predictability.

According to all the parameters considered to assess classification accuracy and discrimination capacity, our favorability model indicates a high performance for predicting wolf denning sites (Table 3). Cohen's Kappa, which ranges from 0 to 1, was 0.65, so was considered acceptable according to Landis and Koch (1977). Specificity and sensitivity values (also ranging from 0 to 1) were higher than 0.8, the Correct Classification rate was 0.83, and the omission and commission errors were 0.20 and 0.14, respectively. Discrimination capacity (AUC, ranging from 0.5 to 1) was also equal to 0.894 (P < 0.001), and indicates excellent discrimination, according to Hosmer and Lemeshow (2000).

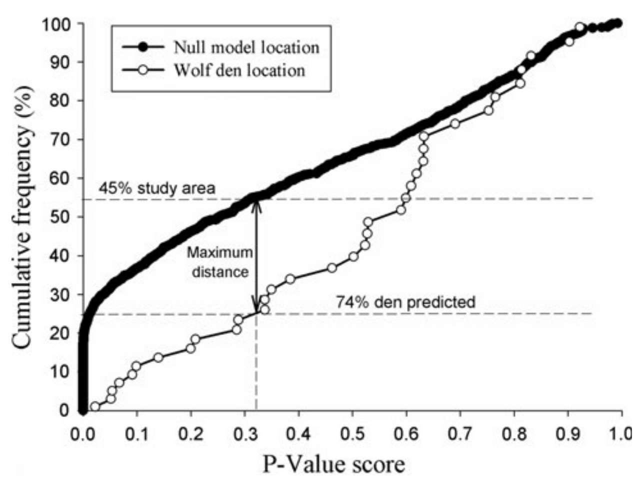

Fig. 3 Cumulative frequency of P-value used to identify suitable habitat for Gray Wolf dens in HP. The greatest difference between P-value of wolf den locations and the null model indicates the threshold at which the continuous suitability map was categorized

Table 2 Area and percentage of wolf denning habitat within three classes of Mahalanobis distance P-values

Category[a]	P-value class	Area (km^2)	% of area
Unsuitable	0–0.31	16,006.76	85.17
Marginally suitable	0.32–0.66	1,302.94	9.33
Suitable	0.66–0.9997	564.76	5.42

[a]Classes corresponded to suitability threshold

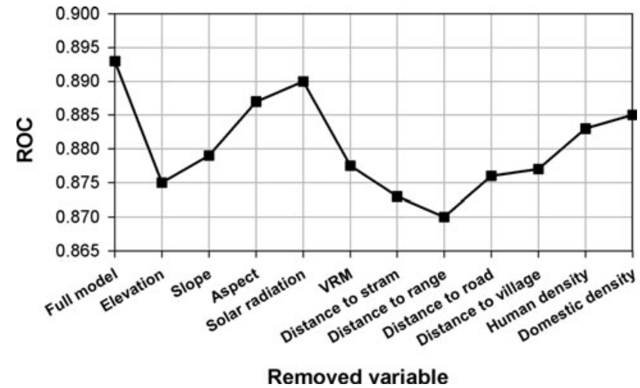

Fig. 4 The results of analysis of model sensitivity using receiver operating characteristic (ROC) used to identify most influential variables. Removing variables in turn and calculating ROC of refitted models and the full model allowed the effects of variables in the performance of the model to be determined

Table 3 Assessment of performance of the Mahalanobis distance model for wolf den site suitability according to classification accuracy and discrimination capacity of the model

		Predicted		Percentage correct
		Presence	Absence	
State	1	28	7	
	0	5	30	
Omission error				20
Commission error				14
Sensitivity				80
Specificity				86
Correct classification rate				83
Cohen's Kappa				65

Classification criteria were based on P-value of 0.32 as the suitability threshold

Discussion

We provide the first large-scale assessment of potential wolf den habitat in western Iran based on the collection and analysis of ecological data for model building and validation. Regarding environmental variables, we applied a Mahalanobis Predictive model, as a quantitative index to predict areas with potential suitability for denning wolves. Dens were considered as the ideal areas in the Mahalanobis distance method. Mahalanobis distances were calculated for each point using the standard difference between the mean, variance and covariance of variables in ideal areas and any other point in the region (Clark et al. 1993; Podruzny et al. 2002; Jenness et al. 2011). We used a cumulative frequency distribution graph to help determine the optimal P-value cut-off (Griffin et al. 2010). This process allowed us to generate a qualitative suitability map and seek a balance between specificity and sensitivity of the model. The resulting P-value of 0.32 maximized the difference between specificity and sensitivity and, at this P-value cut-off, the model with 83 % CCR, noticeably distinguished between habitat typical of denning wolf and areas not used by wolves. It must be noted that, with a *P*-value of 0.5, a commonly used favorability threshold (Woolf et al. 2002; Kuemmerle et al. 2011), we would not have attained a balanced habitat classification despite a constant AUC and many of the presence locations would have been classified as unfavorable and omission errors would have been high.

Because of the high mobility, high reproductive rate and low dependency to particular habitats, wolves have higher ecological resilience compared to other large carnivores (Mech and Boitani 2003). However, at present, human intervention through resource exploitation, habitat destruction and execution is the most important threat to the long-term survival of wolves, especially where they come into conflict with humans (Smith et al. 2010; Rich et al. 2012). Hence wolf habitat selection should be considered not only with regard to biological factors, but also with respect to human-associated disturbance factors (Mech and Boitani 2003; Cayuela 2004). Wolf denning in our study area appears to be influenced by both human presence and natural landscape attributes. Based on sensitivity resulting from ROC, the most influential habitat conditions associated with wolf den locations was distance to ranges ($\bar{x}$ = 1291, SD = 1687), distance to streams ($\bar{x}$ = 424, SD = 392), elevation ($\bar{x}$ = 2,119, SD = 128) and distance to roads ($\bar{x}$ = 6,106, SD = 2,739). Wolves selected particular land-cover features for denning depending on the landscape they occupied. We found that land cover through remnant rangelands, remote from human activities is the most effective variable to determine potential denning habitats across the area. In fact, in HP, rangelands are the only region in which, due to the specific soil features and topographic conditions, human interventions rarely occur. European and North American researchers have indicated that suitable habitats for wolves are located in areas where forest cover is widespread, human impact is low and wild prey abundance is high (Mladenoff et al. 1999; Norris et al. 2002; Theuerkauf et al. 522003b; Karlsson et al. 2007; Jędrzejewski et al. 2008). However Jędrzejewski et al. (2008) mentioned that wherever their primary habitat (forests) is rare (as in HP), wolves trend to be dispersed in meadows and rangelands, or in less-natural landscapes such as mixed-use agroecosystems (Treves et al. 2011). Based on available landcover features used by wolves in HP, it seems that our findings are consistent with these patterns.

We used VRM as a measure of ruggedness (Sappington et al. 2007). We found that wolves selected den sites that were in relatively elevated areas ($\bar{x}$ = 2,119, SD = 128) and rugged terrains. This was also observed by Salvatori et al. (2002). In a study on wolf habitat selection, Jędrzejewski et al. (2005) mentioned that areas most suitable for wolves are located in mountainous regions, due to avoidance of human disturbance. This is in contrast with Matteson (1992) in Montana, Norris et al. (2002) in southeastern Ontario, and Person and Russell (2009); their results showed that wolves selected denning sites in expansive areas with gentle slopes at low elevations rather than elevated benches in rugged terrain. The reason may be because their study area was in protected forests with low human disturbance and appropriate canopy cover, whereas in HP with its agriculture-dominated landscape, there is insufficient vegetation cover and wolves are restricted to denning in elevated rugged terrains that provide the maximum concealment for wolves and have the least human activity due to limited accessibility. Based on our findings that wolves selected den sites in rangelands and elevated rugged terrains with the least human disturbance, it is suggested that wolves in HP prefer to keep their distance from humans. Human activity intolerance by denning wolf is also mentioned by Norris et al. (2002), who indicated that wolves avoided clear land and humans. However, Thiel et al. (1998) reported that wolf populations in Minnesota are expanding, with closer contact with human active areas, which indicates a tolerance to human activities close to their den or rendezvous sites.

Also, based on ROC sensitivity, we found that distance to roads and villages were important predictive variables in mapping wolf denning sites. We revealed that wolves in our study area select denning sites in natural habitats away from such human interventions. Considering the high anthropogenic pressure on the studied wolf habitat (average 88 people/km^2) in comparison with wolf habitats in Europe, with an average human density between 20 and 30 in Croatia, Spain and Italy (Theuerkauf et al. 2007), importance of these factors would be expected. Similar to our findings, Unger et al. (2009) also mentioned that, with the expansion of wolf populations in human-dominated areas, anthropogenic disturbance is likely to become a more important factor in wolf den site selection. Human activities may have caused an alteration in habitat composition and security, and there is general agreement that factors associated with human disturbance seem to be the most important factors affecting wolf distribution (Corsi et al. 1998; Cayuela 2004; Mech and Boitani 2003). This avoidance of humans has also been reported in a study conducted in the Dalmatian part of Dinarids, Croatia (Kusak et al. 2005) and Bialowieza forest in eastern Poland, where wolves tended to locate dens further away from forest edges, villages and intensively used roads (Theuerkauf et al. 2003a). We found that proximity to stream courses was an important variable and dens were often found near water, which, as mentioned by Norris et al. (2002), Trapp et al. (2008) and Unger et al. (2009), is probably due to the increased need for hydration by lactating females.

Understanding the patterns of disturbance and conflicts between humans and wildlife is essential for habitat and species management (Smith et al. 2010; Treves et al. 2011; Rich et al. 2012). Therefore, habitat suitability models and regional planning based on such patterns are considered very useful management tools (Corsi et al.

1998; Cayuela 2004; Jędrzejewski et al. 2008). In fact, map-based conservation planning can help to facilitate human-wolf coexistence by identifying areas where there is high probability of conflict (Treves et al. 2009; Edge et al. 2011). Also because of their tendency to use marginal habitats and human-induced resources, most of the world's carnivores are recovering and are dispersing in less-natural landscapes such as mixed-use agroecosystems rather than in wildernesses (Treves et al. 2011). This was also apparent in HP, where protected areas contain a small portion of the region (only 3 %) and are not the only den habitats selected by wolves. Our study suggests that mapping the wolves' suitable den sites and considering them as core use zones in wolf territories along with an identification of areas with high conflict potential can lead to effective adaptive management beyond wilderness and protected areas.

Our model can be regarded as the first wolf habitat suitability study in Iran. One must always take into account that predictive models must be applied cautiously in decision making. This is because many factors may be involved that have not been considered or may have been disregarded. For this purpose, it is strongly recommended that all predictive models be verified, calibrated, and validated prior to application. Further studies on wolf home range and distribution area are needed in Iran. It would be particularly useful to apply wolf telemetry techniques or similar proficiencies. Unfortunately this was not done in this study due to the lack of relevant and sufficient equipment.

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