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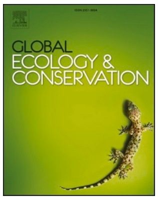

Evaluation of habitat suitability and migratory paths of an endangered raptor, Steppe Eagle (*Aquila nipalensis*) in Iran

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ABSTRACT

Understanding habitat suitability, the environmental variables limiting the distribution of species, and migratory paths are important issues for conservation of threatened bird species. Identifying areas important for birds and their overlap with conservation areas (CAs) can guide conservation managers in establishing new CAs. The Steppe Eagle (*Aquila nipalensis*) is a globally endangered winter visitor raptor in Iran. We used 164 occurrence records of Steppe Eagles and data on 12 environmental variables in Iran as input to ensemble modeling and electrical circuit theory models to identify, respectively, potential wintering areas and migratory paths between those wintering areas. Our results revealed that elevation, distance to rodents, mean diurnal range, distance to villages, and distance to cities were the most influential variables for habitat suitability in Iran. Potential wintering areas identified by our models were mainly located in the north and south of Iran and migratory paths connected these areas through the central plains. CAs covered about one-fifth of potential wintering areas. Conservation of the species within potential wintering areas and the migratory paths from northern to southern Iran is necessary for the survival of this endangered species in its entire distribution. Therefore, wildlife managers should pay increased attention to non-protected parts of potential wintering areas in order to establish new CAs and protect migration paths against threats. Our results pave the way for proper planning for the conservation of threatened raptors in Iran, particularly Steppe Eagle.

1. Introduction

Understanding habitat suitability and the environmental variables limiting the distribution of bird species is important for their conservation (Yousefi et al., 2017; Zhang et al., 2019). Species distribution models (SDMs) (Guisan and Zimmermann, 2000) use occurrence records and related environmental variables to identify suitable habitats and species distributions (Mohammadi et al., 2021; Almasieh et al., 2023; Almasieh and Mohammadi, 2023), including the distributions of bird species (Newton, 2007). Identifying suitable bird habitats and their overlap with conservation areas (CAs) can guide conservation managers to establish new CAs (Larson et al., 2004; López-López et al., 2007) and assess existing CAs in terms of their contribution to conservation. Moreover, SDMs can be used to predict migratory paths (i.e., connectivity or corridors) of birds in human-altered landscapes (Rödder et al., 2016). There are two main approaches to migratory path assessment: the least-cost path approach (Adriaensen et al., 2003) and the circuit theory

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approach (McRae et al., 2008). The circuit theory approach is considered to be superior as it identifies several probable paths between habitat patches rather than identifying a single possible path (Urban and Keitt, 2001; Urban et al., 2009).

Raptors (i.e., birds of prey) are among the most threatened bird species, with 30.6 % classified as threatened or near-threatened (IUCN, 2024). As top predators and scavengers, they play crucial roles in ecosystems, and their presence can serve as an indicator of biodiversity across the broader landscape (Burgas et al., 2014; Donazar et al., 2016; Khaleghizadeh and Anuar, 2019). Given their high mobility and wide distribution, effective protection of raptors requires careful planning (Engler et al., 2017; McClure et al., 2018). Furthermore, their sensitivity to anthropogenic disturbances prioritizes them in conservation plans (Rodríguez-Estrella et al., 1998; Zimmerling et al., 2013).

Steppe Eagles (*Aquila nipalensis*) are distributed in Asia, Africa, and small parts of Eastern Europe. The breeding range of the species mainly occurs in higher latitudes in Asia (Russia, Mongolia, and northeast of China) and its wintering range mainly occurs in Africa and southeast, south, and southwest of Asia (McGrady et al., 2021) (Fig. 1). The global population of the Steppe Eagle has experienced a significant decline, leading to its classification as endangered (EN) on a global scale by the IUCN (BirdLife International, 2021), placing it within the 3.7 % of bird species that are given this status. The main global threats to this species include conversion of steppes to agricultural lands, poaching, electrocution, and poisoning by veterinary diclofenac (Levin and Kurkin, 2013; Meyburg and Boesman, 2013; Sharma et al., 2014; Shobrak et al., 2022). In Iran, the Steppe Eagle is a rare winter visitor to in the regions south of the Caspian Sea and north of the Persian Gulf and the Oman Sea (Kaboli et al., 2016), and a passing migrant in many parts of the country (Kaboli et al., 2016). Therefore, the Department of Environment of Iran (DoE) has classified the species as a protected species due to its conservation value. According to Katzner et al. (2022), McGrady et al. (2021) and Meyburg et al. (2003, 2012), the major migratory path of the Steppe Eagle in Iran runs from the east of the Caspian Sea to the north of the Persian Gulf. Other migratory paths extend from the west of the Caspian Sea to the west and southwest of Iran, and from the northeast to the southeast of Iran, followed by the coastlines of the Oman Sea and the Persian Gulf (Katzner et al., 2022) (Fig. 1). In all migratory paths, some Steppe Eagles remain in Iran throughout the winter and the rest continue their way to the Arabian Peninsula and Africa (Katzner et al., 2022).

Iran is the main bridge between the breeding habitats of Steppe Eagles in higher latitudes and wintering habitats in lower latitudes (i.e., the Arabian Peninsula and Africa). Potential wintering areas and their coverage by CAs are unknown in Iran, making their identification crucial for maintaining and improving the conservation of this endangered species inside and outside the country. In addition, modelling of migratory paths between potential wintering areas could enable comparisons with previous studies. This study has three aims: (1) to model habitat suitability for the Steppe Eagle and identify the environmental factors that determine potential

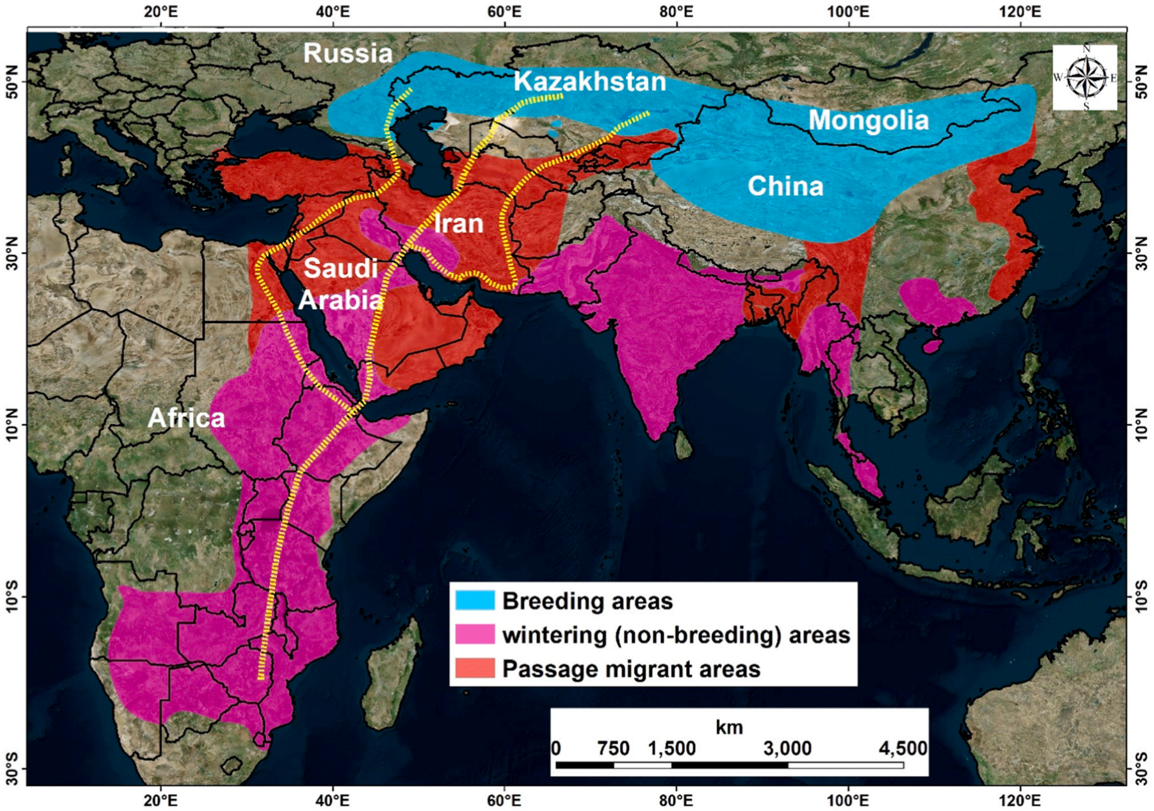

Fig. 1. Distribution of the Steppe Eagle in the world including breeding, passage migrant and wintering areas (according to BirdLife International, 2021). Dashed yellow lines represents the major migratory path of the Steppe Eagle in Iran (according to Katzner et al. 2022, McGrady et al. 2021 and Meyburg et al. 2003, 2012).

wintering areas, (2) to identify potential wintering areas and migratory paths, and (3) to evaluate the coverage of potential wintering areas by CAs in Iran.

2. Material and methods

2.1. Study area

Iran covers an area of 1,648,000 km^2 in southwest Asia and is characterized by its extensive grasslands and steppes (Noroozi et al., 2008). About one-fifth of the country consists of deserts, mainly Kavir and Lut deserts, which are bordered by the Alborz, Zagros and Kopet Dagh mountain ranges (Fig. 2). Nearly 16.5 % of Iran's area is protected by CAs, including national parks (NPs), wildlife refuges (WRs), protected areas (PAs), and no-hunting areas (NHAs), in descending order of conservation priority (Almasieh et al., 2022). NPs, WRs, PAs, and NHAs closely correspond to IUCN categories II, III, IV and IV-VI, respectively (Ahmadi et al., 2020). Natural pristine areas and areas with significant plant and animal communities are selected as CAs. Monitoring, protection, efficient projects and education of locals are carried out in these areas; largely, CAs have been effective in the conservation of the threatened species in Iran. Geographic and biogeographic factors have contributed to the high avian biodiversity in Iran (i.e., 551 species), approximately equal to that of Europe (Khaleghizadeh et al., 2017; Ashoori, 2018; Almasieh and Moazami, 2020). In addition, Iran has the highest number of passing migratory bird species in West Asia (Kirby et al., 2008; Nourani et al., 2014). Fifty-nine raptor species occur in Iran (35 Accipitriformes, 11 Falconiformes and 13 Strigiformes), of which 16 (27.1 %) are threatened or near threatened, including 1 critically endangered (CR), 4 EN, 6 vulnerable (VU) and 5 near threatened (NT) species (IUCN, 2024).

2.2. Habitat suitability modeling and environmental variables

To model habitat suitability for the Steppe Eagle and identify the environmental factors that determine potential wintering areas (our first aim), we obtained Steppe Eagle occurrence data from DoE rangers and experts. Occurrence data were collected during field surveys in CAs and non-conservations areas (hereafter non-CAs) across Iran, excluding the two large deserts of Kavir and Lut. Data collection encompassed 1216 survey days during 2015–2022 in 1200 random areas (using "generate random points" tool in Hawth's Analysis Tools version 3.27) determined by DoE. During September-March of each year (wintering time in Iran), field surveys were

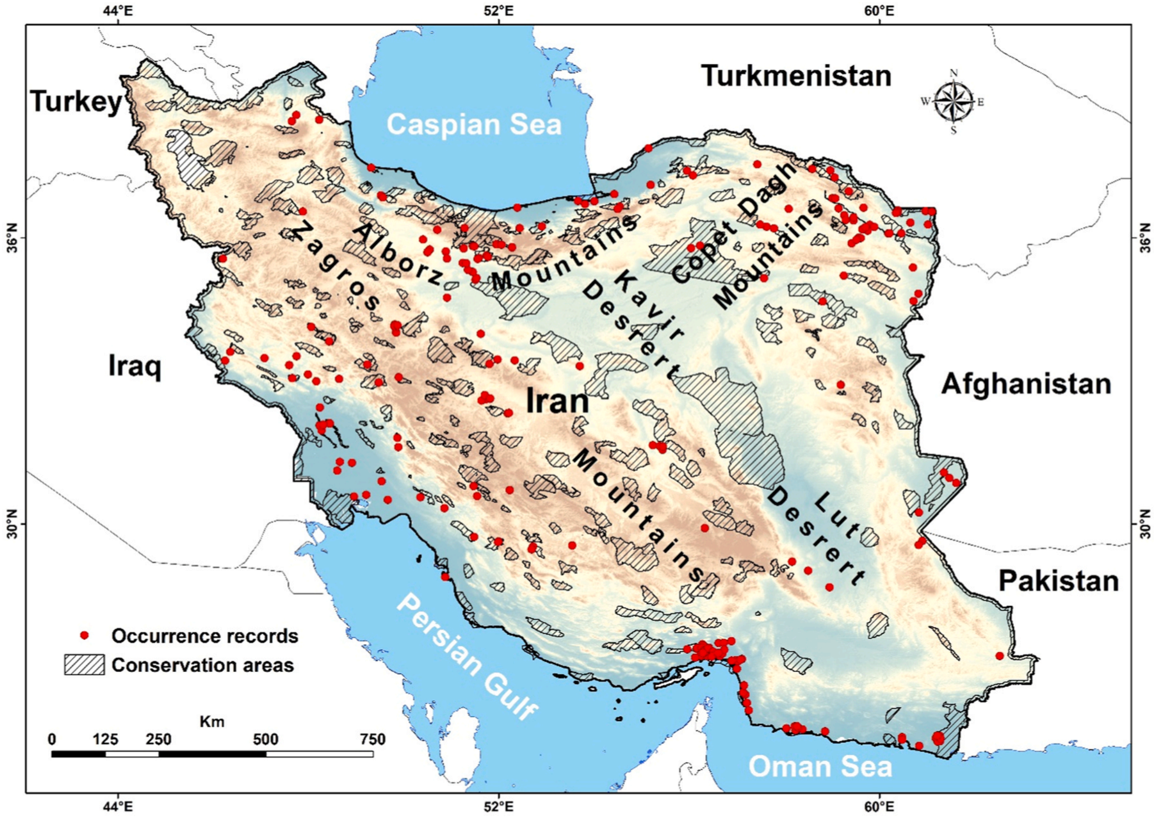

Fig. 2. Study area, including Iran, the main seas, mountains and deserts, conservation areas, and occurrence records of Steppe Eagle for habitat suitability modelling.

carried out by DoE experts and game wardens. Steppe Eagles were identified through daily direct observations from 7:00 AM to 7:00 PM using binoculars (Steiner, model Al-Saghar II 8×30, Germany) and digital cameras (mainly Canon SX60 with 65x magnification, Japan). Photos of eagles, confirmed by ornithologists to be Steppe Eagles, were recorded as occurrence records. In addition, consensus among experts (at least three ornithologists) regarding the presence of the species in an area was considered as confirmed occurrence.

Table 1

Environmental variables used for habitat suitability modelling of Steppe Eagle in Iran in six categories of topography, climate, land-cover, conservation, food and human-related before and after checking the correlation, variance inflation factor (VIF) filtering and primary MaxEnt modelling.

Variables category	Variables	Unit	Selected after checking the correlation	Selected after checking the VIF	Selected after primary MaxEnt modelling (final variables)
Topography	Elevation	Meters	Yes	Yes	Yes
	Slope	Degrees	Yes	Yes	Yes
	Aspect	-	Yes	Yes	No
	Topographic roughness	-	Yes	No	No
Climate	Annual mean temperature (BIO1)	Degrees Celsius	No	No	No
	Mean diurnal range (BIO2)	Degrees Celsius	Yes	Yes	Yes
	Isothermality (BIO3)	Percent	No	No	No
	Temperature seasonality (BIO4)	Percent	No	No	No
	Max temperature of warmest month (BIO5)	Degrees Celsius	No	No	No
	Min temperature of coldest month (BIO6)	Degrees Celsius	Yes	Yes	Yes
	Temperature Annual Range (BIO7)	Degrees Celsius	Yes	No	No
	Mean Temperature of Wettest Quarter (BIO8)	Degrees Celsius	No	No	No
	Mean Temperature of Driest Quarter (BIO9)	Degrees Celsius	No	No	No
	Mean Temperature of Warmest Quarter (BIO10)	Degrees Celsius	No	No	No
	Mean Temperature of Coldest Quarter (BIO11)	Degrees Celsius	No	No	No
	Annual Precipitation (BIO12)	Millimeters	Yes	No	No
	Precipitation of Wettest Month (BIO13)	Millimeters	Yes	No	No
	Precipitation of Driest Month (BIO14)	Millimeters	Yes	No	No
	Precipitation Seasonality (BIO15)	Percent	Yes	Yes	No
	Precipitation of Wettest Quarter (BIO16)	Millimeters	Yes	No	No
	Precipitation of Driest Quarter (BIO17)	Millimeters	Yes	No	No
	Precipitation of Warmest Quarter (BIO18)	Millimeters	Yes	No	No
	Precipitation of Coldest Quarter (BIO19)	Millimeters	Yes	No	Yes
Land-cover	Grassland density	Percent	Yes	Yes	No
	Agricultural land density	Percent	Yes	Yes	No
	NDVI	−1 to 1	Yes	Yes	Yes
Conservation	Distance to conservation areas (CAs)	Degrees	Yes	Yes	Yes
Food	Distance to rodents	Degrees	Yes	Yes	Yes
	Distance to artiodactyls	Degrees	Yes	Yes	No
	Cattle density	Number per km^2	Yes	Yes	Yes
	Sheep density	Number per km^2	Yes	Yes	No
	Goat density	Number per km^2	Yes	Yes	No
	Duck density	Number per km^2	Yes	Yes	No
	Chicken density	Number per km^2	Yes	Yes	No
Human	Human footprint	0–50	Yes	Yes	No
	Distance to roads	degrees	Yes	Yes	Yes
	Distance to cities	degrees	Yes	Yes	Yes
	Distance to villages	degrees	Yes	Yes	Yes

Location data were recorded using global positioning system devices (GPS). Moreover, field surveys and direct observations were randomly carried out by the third and fourth author in the northeast (84 survey days) and south (168 survey days) of Iran during 2018–2022 and the first two months of 2023 using the same method as DoE surveys. Following Ahmad et al. (2022), we considered a 5-km radius around each occurrence record to spatially filter records using the "spatially rarify occurrence data" tool in SDMtoolbox (Brown, 2014). We ran Moran's I test to check spatial autocorrelation. A 5-km filtering radius transformed the distribution of occurrence records to random.

Based on the ecology of the Steppe Eagle and previous research on raptors (e.g., Zhang et al., 2019; Ashrafzadeh et al., 2020; Ahmad et al., 2022), 38 environmental variables including topography, climate, land-cover, conservation, food sources, and anthropogenic variables were initially considered for habitat modelling (Table 1). Mentioned variables are widely used in habitat suitability modeling because they are the only relevant variables that are available as GIS layers (Beier et al., 2007). However, these variables are related to the behavior of the species. For example, topographic and land-cover variables affect thermal and orographic soaring of raptors such as Steppe eagles (Nourani and Yamaguchi, 2017; Nourani et al., 2018), which are limited to areas with enough atmospheric support to fly (Scacco et al., 2019; Brønnvik et al., 2022, 2024; Aikens et al., 2024).

We used a digital elevation model (DEM) with a resolution of 1 km based on 30-m Shuttle Radar Topography Mission images (SRTM, http://earthexplorer.usgs.gov) to create slope and aspect maps using the surface tool. Topographic roughness was calculated based on the standard deviation of DEM cells in a 5-km neighborhood (Farhadinia et al., 2015; Kaboodvandpour et al., 2021; Almasieh et al., 2022). We downloaded 19 climatic variables from http://worldclim.org (Fick and Hijmans, 2017) at a resolution of 1 km.

Land-cover maps for rangelands and agricultural lands were created from a land-cover map of Iran (FRWMO, 2010) using a circular-moving window with a 5-km radius. The map of Normalized Difference Vegetation Index (NDVI) was generated by averaging 16-day composite MODIS data for 2022 (MODIS MYD 13A1 V6 map at 500-m cell size; http://earthexplorer.usgs.gov). We considered Euclidean distance to CAs as a measure of relative security. In addition to feeding on anthropogenic waste, Steppe Eagles feed on rodents and the carcasses of herbivores; both wild and domestic species (Kaboli et al., 2016). We obtained distribution maps for 81 potential food species at a resolution of 25 km (Karami et al., 2016), including 71 rodents and 10 artiodactyls. The maps for rodents were overlaid to create a single distance to rodents map; similar process was performed for artiodactyls, yielding two maps representing food sources (Ahmadi et al., 2020). In addition, we obtained data on cattle density, sheep density, goat density, duck density and chicken density from http://www.livestock.geo-wiki.org (Robinson et al., 2014). We included human footprint as an indicator of human population pressure (population density), human access (roads and railroads), and infrastructure (built-up areas, nighttime lights, and land use) (Sanderson et al., 2002; Venter et al., 2016, Venter et al., 2018). Furthermore, we included distance to roads (DoE, 2018), distance to cities (FRWMO, 2010, Modified in Google Earth), and distance to villages (DoE, 2018) as other variables related to human activities. The description of environmental variables is presented in Supplementary Materials, Table S1. Variable maps were resampled to a resolution of 1 km and projected to the WGS 1984 coordinate system. All operations were performed in ArcGIS version 10.3.

In order to select the final variables, we checked multicollinearity by evaluating the correlation between variables and applying a variance inflation factor (VIF). First, from two variables with a correlation coefficient >0.7, one of them were excluded from the analyses. At this step, eight variables were excluded and 30 variables remained. Then, the usdm package (Naimi et al., 2014) in R 3.6.0 (R Core Team, 2019) was used to exclude variables with VIF > 3 (Zuur et al., 2010). From the 30 variables of the previous step, nine variables were excluded in this step and 21 variables remained. Finally, primary MaxEnt modelling was conducted to select the final variables based on variables contribution (Mohammadi et al., 2021). MaxEnt was run with 20 replicates and bootstrapping using 164 occurrence records, 21 environmental variables (remained from the previous two steps) and 1000 pseudo-absence records. Four values (0.5, 1, 2 and 5) were used as the regularization multiplier and the model with the highest area under the curve (AUC) of receiver operating characteristic (ROC) was selected as the final model (Fois et al., 2018). AUC ranges between 0.5 and 1, with 1 indicating perfect discrimination of occurrence records from pseudo-absence records. Eventually, twelve variables were retained for habitat modelling (Table 1).

We used the biomod2 package (Thuiller et al., 2019) in R to model habitat suitability in an ensemble approach, where predictions from multiple models are combined through average-weighting to increase accuracy (Araújo and New, 2007; Ashrafzadeh et al., 2018; Khosravi et al., 2018; Ahmadi et al., 2020; Ashrafzadeh et al., 2022; Almasieh and Cheraghi, 2022; Mohammadi et al., 2022). Biomod2 implements ten models, including four regression-based models (Generalized Linear Model [GLM], Generalized Additive Model [GAM], Multivariate Adaptive Regression Splines [MARS], and Flexible Discriminant Analysis [FDA]), five machine-learning models (Random Forest [RF], Maximum Entropy [MaxEnt], Generalized Boosting Model [GBM], Classification Tree Analysis [CTA], and Artificial Neural Network [ANN]) and one profile model (Surface Range Envelop [SRE]). We ran a primary analysis using ten prediction models. Ultimately, models with AUC >0.9 and true statistic skill >0.7 (TSS, equal to sensitivity plus specificity minus 1) were selected for final habitat modelling (Eskildsen et al., 2013). We used 75 % of the occurrence records as the training data set, and the other 25 % as test data (Ahmadi et al., 2020). We randomly generated 1000 pseudo-absence records across Iran outside a 5-km radius around each occurrence record. Modelling was conducted with 20 replicates for each model to achieve higher confidence (Barbet-Massin et al., 2012). Ensemble variable contributions and the most influential variables for habitat suitability were calculated using Biomod2. In addition, response curves of the occurrence records to the variables were created according to the model with the best performance.

2.3. Potential wintering areas and connectivity modelling

To identify potential wintering areas and migratory paths (our second aim), we converted the continuous map of ensemble habitat suitability into a binary map using a ROC curve threshold (Thuiller et al., 2012). We considered potential suitable areas that overlapped with occurrence records of Steppe Eagle as potential wintering areas.

Electrical-circuit theory can evaluate habitat connectivity in a landscape based on random walk (McRae and Beier, 2007; Almasieh et al., 2019). In this method, 'current' (i.e., Steppe Eagles) moves between 'focal nodes' (i.e., potential wintering areas) in relation to 'voltage' (i.e., probability of eagles' movement) and resistance (non-wintering areas) (McRae et al., 2008; Roever et al., 2013). To identify possible migratory paths between potential wintering areas in Iran, connectivity modelling was performed in Circuitscape version 4 (McRae and Shah, 2009) using the "all-to-one" method. This method creates a map with all possible migratory paths between potential wintering areas (McRae et al., 2008). We created the resistance map from the ensemble suitability map according to Wan et al. (2019), and used it to identify the migratory paths between potential wintering areas. Using linear "rescale by function" tool in ArcGIS, we rescaled the ensemble map to a map of values between 0 and 1. We then used a negative exponential function to create the resistance map using: $R = 1000^{(-1\times\text{Ensemble Suitability Map})}$, where R represents the cost resistance value assigned to each pixel (Mateo-Sánchez et al., 2015). Finally, we rescaled the resistance values using linear interpolation to yield values ranging from 1–10; where 1 represents minimum resistance (Wan et al., 2019). We used potential wintering areas of Steppe Eagle as focal nodes and determined connectivity to the eight neighboring cells for all cells. Areas with lower resistance have a higher likelihood of migration and vice versa (Almasieh and Kaboli, 2019).

2.4. The coverage of potential wintering areas by CAs

Coverage of potential wintering areas by CAs (our third aim) was calculated as the ratio of potential wintering areas within CAs to the total area of potential wintering areas in Iran.

3. Results

3.1. Habitat suitability and variable contributions

We recorded 48 occurrences in the northeast and 92 occurrences in the south of Iran during our field surveys. An additional set of 139 occurrences were obtained from DoE, bringing the total to 279 occurrence records. Most occurrences were recorded in grasslands (n=120), followed by agricultural lands (73), bare lands (30), forests (25), water bodies (15), rocky mountains (12) and urban areas (4). Only 49 occurrences were recorded in CAs. After filtering for spatial autocorrelation, 164 occurrence records were retained for habitat modelling (Fig. 2).

We selected five models for final analysis (GLM, MARS, GBM, MaxEnt, and RF) as they achieved AUC>0.9 and TSS>0.7 in the preliminary analysis. The RF model had the highest AUC and TSS (Table 2). Elevation, distance to rodents, mean diurnal range (BIO2), distance to villages, and distance to cities were the most influential variables for habitat suitability (Table S2).

Habitat suitability modeling indicated that Steppe Eagles prefer regions situated at elevations of 0–1500 m above sea level and gentle slopes with a gradient of 0–5 degrees (Fig. 3). Steppe eagles also prefer areas with mild average daily temperatures (i.e., 8–12 °C) and are less likely to occur in areas that experience temperatures of <-5 °C in the coldest month and <200 mm of rainfall in the coldest season of the year. NDVI initially increased habitat suitability by 0.2, but stabilized at about 0.4. The probability of occurrence decreased gradually as distance to CAs increased and then stabilized at about 30 km. As distance to rodents increased, the probability of occurrence decreased sharply and then stabilized at about 10 km. As cattle density increased, the probability of occurrence increased gradually before stabilizing at about 40 cattle per km^2. The distance from human-related features, such as roads, cities, and villages, negatively affected habitat suitability since the probability of occurrence decreased sharply with increasing distance and then stabilized at about 15 km (Fig. 3).

According to the ensemble suitability map, areas with the highest predicted suitability for the Steppe Eagle are found in the north, northeast, and south of Iran. In addition, we found suitable habitats in the central plains (Fig. 4). The habitat suitability maps generated by the GLM, MARS, GBM, MaxEnt, and RF models are shown in Supplementary Materials (Fig. S1).

Table 2
Model performance for Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS), Generalized Boosting Model (GBM), Maximum Entropy (MaxEnt) and Random Forest (RF) models, in the habitat suitability of Steppe Eagle in Iran by using the area under the curve (AUC) of receiver operating characteristic (ROC) and true statistic skill (TSS).

Models	AUC	TSS
GLM	0.91	0.77
MARS	0.92	0.82
GBM	0.93	0.86
MaxEnt	0.92	0.83
RF	0.95	0.87

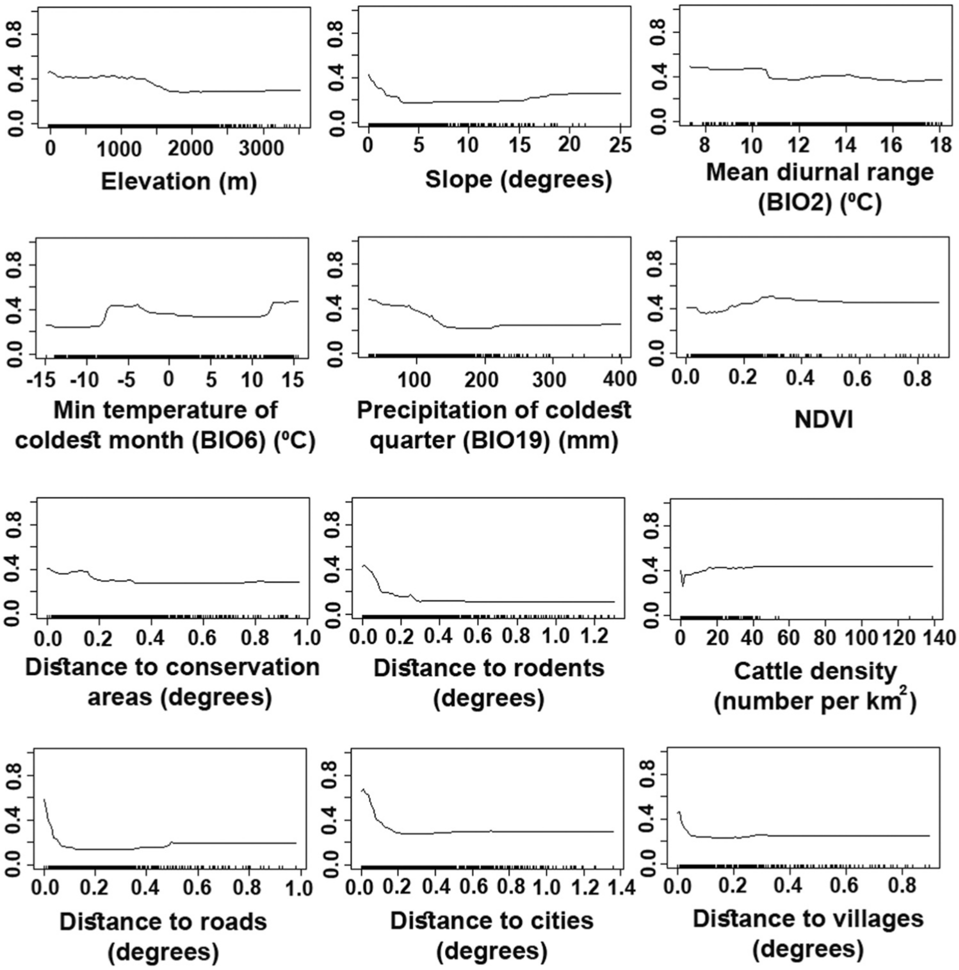

Fig. 3. Response curves of Steppe Eagle occurrence to the environmental variables in Iran in GBM model (the model with the best performance). The y-axis represents the probability of Steppe Eagle occurrence. Each 0.1° in the study area is equal to approximately 15 km.

3.2. Potential wintering areas and migratory paths

We identified 13 potential wintering areas for the Steppe Eagle in Iran, with a total area of about 210,300 km^2 (12.7 % of the study area) (Fig. 5 and Table 3). The largest potential wintering area was Wintering Area 1, located in the north of Iran (about 71,000 km^2), followed by Wintering Area 2, located in the south of Iran (about 36,000 km^2), and Wintering Area 3, located in the northeast of Iran (about 32,200 km^2). Additional information on potential wintering areas is presented in Table 3.

The main expected migratory path connected northeastern and northern Iran (the southeast of Caspian Sea) to southwestern Iran (north of the Persian Gulf), represented by the yellow line in Fig. 6. Alternative migratory paths ran from northeastern and northern Iran through the central plains to southern and southwestern Iran, represented by the dashed yellow lines. Other migratory paths extend from the northeast to the southeast (north of the Oman Sea), south and southwest (north of the Oman Sea and the Persian Gulf), represented by solid and dashed green lines; and from the northwest (southwest of the Caspian Sea) to the west, represented by the brown line.

High connectivity was predicted between Wintering Area 1, Wintering Area 3, Wintering Area 4, Wintering Area 7, and Wintering Area 10. Moderate connectivity was predicted between Wintering Area 2, Wintering Area 3, Wintering Area 8, and Wintering Area 13, as well as between Wintering Area 2, Wintering Area 4, Wintering Area 5, and Wintering Area 9, and between Wintering Area 10, Wintering Area 11, and Wintering Area 12. Low connectivity was predicted from Wintering Area 6 toward western Iran and Iraq (Fig. 6).

3.3. The coverage of wintering areas by CAs

About 20 % of predicted wintering areas overlapped with CAs. The three largest potential wintering areas, i.e., Wintering Area 1, Wintering Area 2, and Wintering Area 3, had 24.6, 15.7, and 18.7 % overlap with CAs, respectively. The largest area of overlap with

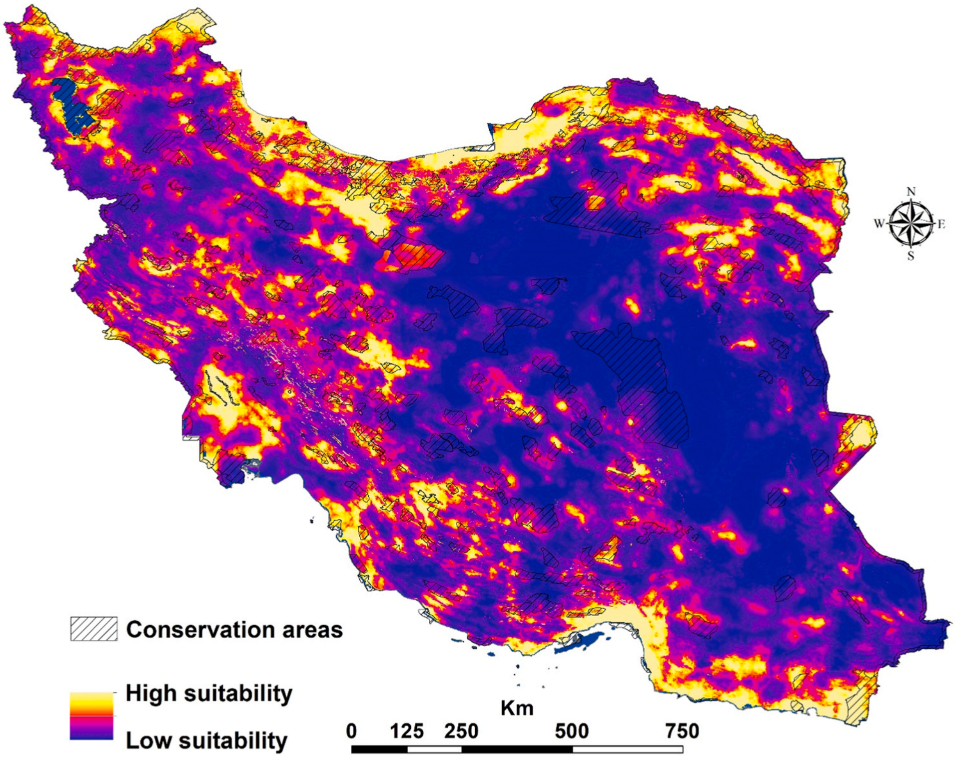

Fig. 4. Ensemble habitat suitability for steppe eagle in Iran based on Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS), Generalized Boosting Model (GBM), Maximum Entropy (MaxEnt) and Random Forest (RF) models using 164 occurrence records and 12 environmental variables.

CAs belonged to Wintering Area1 (about 17,500 km^2) and the smallest to Wintering Area 13 (54.8 km^2) (Table 3).

4. Discussion

Our study revealed potential suitable habitats and wintering areas of Steppe Eagle in Iran for the first time. In addition, potential migratory paths were identified to enable comparison with previous studies. Potential wintering areas were mainly located in the north and south of Iran and migratory paths connected these patches through the central plains. Our results revealed that elevation, distance to rodents, mean diurnal range (BIO2), distance to villages, and distance to cities were the most important variables for habitat suitability. CAs covered about one-fifth of potential wintering areas.

4.1. Variable contributions

Our modelling identified the environmental factors that drive Steppe Eagle potential wintering areas. For example, elevation was the most important variable as it has a close relationship with climate and vegetation cover. Furthermore, this variable affects the flight behavior of eagles to achieve higher energy expenditure during migration (Nourani and Yamaguchi, 2017; Ştefănescu and Balescu, 2019; Brønnvik et al., 2022). Elevation was also the most important variable for habitat suitability of three large raptors in China (Zhang et al., 2019), Golden Eagle (*Aquila chrysaetos*) in Romania (Ştefănescu and Balescu, 2019) and in different parts of the Iberian Peninsula (López-López et al., 2007; Tapia et al., 2007). The importance of elevation was also confirmed for another threatened raptor, Egyptian Vulture (*Neophron percnopterus*), in the west of Iran (Ashrafzadeh et al., 2020).

Climate (i.e., temperature and precipitation) affects the migratory paths and food availability for raptors (Ngila et al., 2023). This variable had a large effect on the distribution of three large raptors in China (Zhang et al., 2019), and of Steppe Eagle in Kenya (Ngila et al., 2023), Pakistan (Ahmad et al., 2022) and Iran (the present study). Similarly, mean diurnal range (BIO2) was the second most important variable for three large raptors in China (Zhang et al., 2019) and the third most important variable in the present study.

Rodents are important prey species for Steppe Eagles (Sundev et al., 2012; Ahmad et al., 2022); therefore, areas with a high diversity and density of rodents are expected to attract the species (Kaboli et al., 2016). This preference is more pronounced in northern and southern Iran, where winters are mild. However, Steppe Eagles mainly shift to scavenging and feeding on dumpsites and slaughterhouse waste in potential wintering areas such as Iran (Sharma and Sundar, 2009; Keijmel et al., 2020; McGrady et al., 2021). For instance, 84 and 79 Steppe Eagles were counted around a slaughterhouse and a dumpsite in Yasouj, Iran (located in Wintering Area

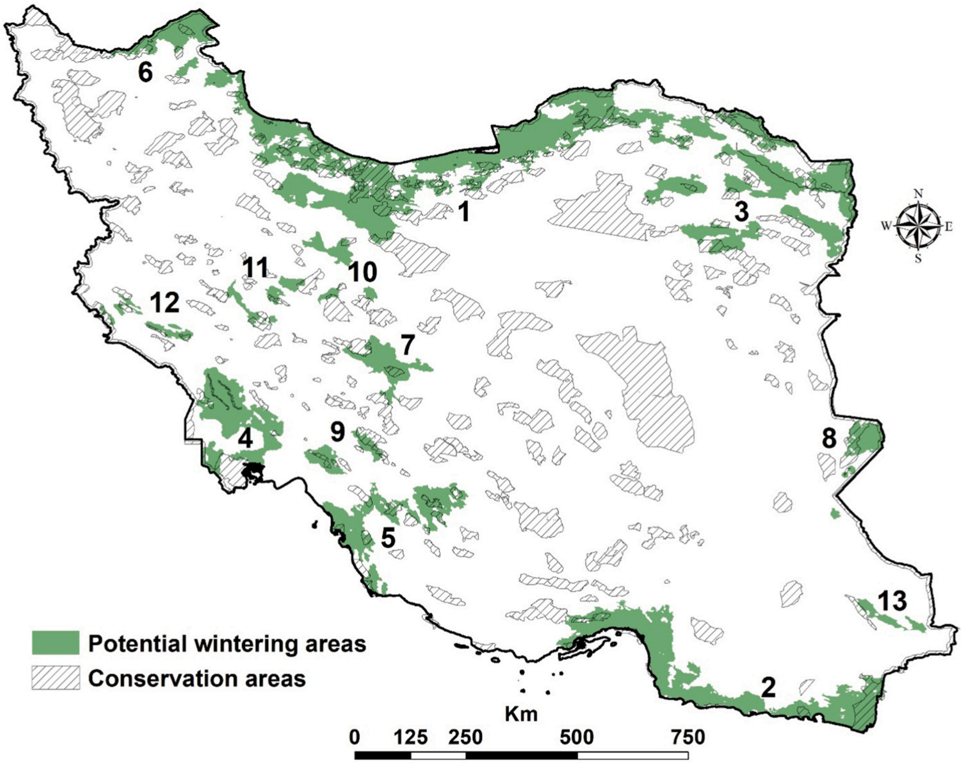

Fig. 5. Potential wintering areas and of Steppe Eagle in Iran based on binary map of habitat suitability modelling and suitable areas with occurrence records of this species (properties of the number of potential wintering areas are available in Table 3).

Table 3
Properties of potential wintering areas (i.e., area and CAs overlapped) created from binary map of habitat suitability modelling and suitable areas with occurrence records of Steppe Eagle in Iran.

	Area (km^2)	CAs overlapped	
		Area (km^2)	(%)
Wintering Area 1	70834.8	17424.1	24.6
Wintering Area 2	36019.2	5666.1	15.7
Wintering Area 3	32202.2	6023.6	18.7
Wintering Area 4	17198.9	1625.1	9.5
Wintering Area 5	16973.8	2668.6	15.7
Wintering Area 6	7964.9	3042.4	38.2
Wintering Area 7	7351.3	886.9	12.1
Wintering Area 8	4810.2	2096.6	43.6
Wintering Area 9	4351.1	1217.2	27.9
Wintering Area 10	3983.2	351.3	8.8
Wintering Area 11	3582.1	603.3	16.8
Wintering Area 12	2760.4	573.4	20.8
Wintering Area 13	2260.2	54.8	2.4
Total	210292.3	42233.4	20.1

9) in 2015 and 2016, respectively (Shafaeipour et al., 2018). Similarly, about 250 and 170 Steppe Eagles were counted in a dumpsite of Mashhad city (located in Wintering Area 3), in 2023 and 2024, respectively (unpublished data from the third author).

The tendency of Steppe Eagle to reside near human settlements (i.e., cities and villages) in order to feed on waste and livestock carcasses exposes them to the risk of death by humans (Keijmel et al., 2020; Ahmad et al., 2022). Therefore, public education is necessary to lessen this risk. In potential wintering areas and near human settlements, locals may encounter Steppe Eagles that are unable to fly due to low energy resulting from long migration. With higher awareness, locals can save these animals by delivering them to the DoE for rehabilitation. One such case was reported in Daregaz (Wintering Area 3) in 2023 (unpublished data from the third author).

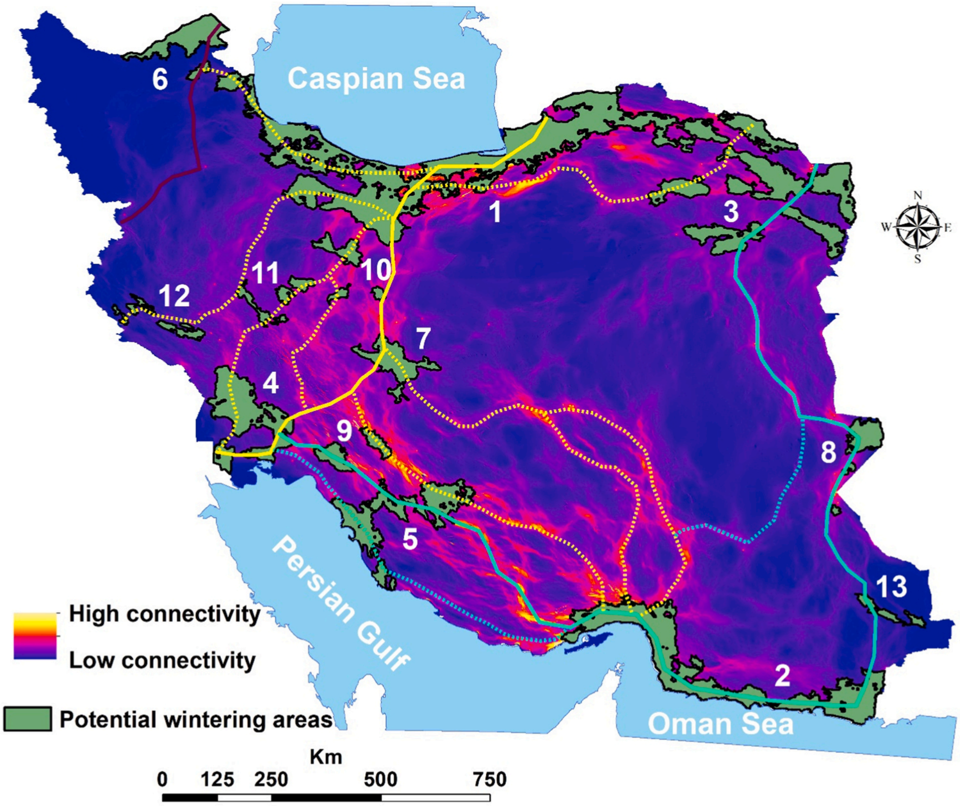

Fig. 6. Connectivity modelling and migratory paths between potential wintering areas for Steppe Eagle in Iran by using electrical-circuit theory. Solid and dashed lines represent the main and alternative migratory paths, respectively.

4.2. Potential wintering areas and migratory paths

Three prominent potential wintering areas (i.e., Wintering Area 1, Wintering Area 2, and Wintering Area 3) are located in the north and south of Iran, constituting two-thirds of the total area of potential wintering areas. In addition, four potential wintering areas were identified in the center and west of Iran (i.e., Wintering Area 7, Wintering Area 10, Wintering Area 11, and Wintering Area 13). Previous studies have identified these four potential wintering areas as areas for passing migrants (Kaboli et al., 2016; Mobasser, 2016). Information collected by rangers and experts at DoE show that Steppe Eagles also spends the winter in these areas.

The main predicted connectivity path in the present study (yellow line in Fig. 6), has been identified as the main migration path between Asia and Africa in previous studies using satellite tracking (Meyburg et al., 2003; Katzner et al., 2022). A large number of Steppe Eagles choose this migration path, as indicated by the observation of 350 individuals at the corridor's northern terminus in Iran, southeast of the Caspian Sea, within a 25-h period in October 2017 (Panuccio et al., 2018). Another connectivity path extends from northeastern to southeastern Iran and from southeastern to southwestern Iran (green line in Fig. 6). Some of these eagles join other Steppe Eagles on their migration to the Arabian Peninsula and Africa. This path has been addressed in previous studies (Katzner et al., 2022). Another migration path runs from northern Iran (west of the Caspian Sea) to western Iran (brown line in Fig. 6), continuing towards Iraq. Few Steppe Eagles use this migratory path, with the path acting as a bottleneck for migration throughout Iran (McGrady et al., 2021).

4.3. Future works

The identified potential wintering areas correspond with occurrence points. Although we achieved excellent modeling accuracy without using distance to dumpsites and slaughterhouses as an environmental variable, future works should include this variable to analyze habitat suitability more realistically. Since dumpsites and slaughterhouses are often located near settlements, the inclusion of distance to cities and villages has largely compensated for the absence of this variable in our analyses. Further, habitat suitability modelling predicted suitable habitats in the northwest of Iran despite the species not being reported from the area. These areas can be surveyed for potential wintering sites.

4.4. CAs and implications for conservation

Cold winters and changes in prey availability in high latitudes such as Russia and Kazakhstan force Steppe Eagles to migrate to low latitudes with milder winters such as Pakistan and Iran (Ahmad et al., 2022). Even in these countries, Steppe Eagles prefer areas in which the winter is relatively mild compared to other parts of the country, i.e. the Indus Delta in Pakistan (Ahmad et al., 2022) and the northern and southern regions of Iran (the present study), where live prey and livestock carcasses may be more plentiful. These are reasons why these countries are heavily used by Steppe Eagles in winter. Steppe Eagles use different migratory paths (McGrady et al., 2021), so identifying potential wintering areas and the main migratory paths in Iran is necessary for the conservation of this species. In addition, in the area preserves the landform. Currently, CAs protect up to one-fifth of the area of potential wintering areas. Establishing new CAs and expanding existing CAs to enhance coverage of potential wintering areas should be considered by wildlife managers. By doing so, the protection level of Steppe Eagle in Iran could increase from the current 20 % to as much as 40 %, similar to Golden Eagle in the east of the Iberian Peninsula (López-López et al., 2007).

CAs provide a favorable place for eagles by conserving biodiversity (species and their habitats), and the feeding on different existing taxa, especially rodents can limit eagles to CAs despite their high mobility (López-Peinado et al., 2023). In addition, due to the major change in the Steppe Eagles' diet to scavenging during wintering time, monitoring and control of dump sites and slaughterhouses near CAs can be done by DoE rangers and experts. One of these controls could be preventing the use of veterinary diclofenac in the industries of livestock and poultry husbandries due to the harmful effects of this drug on scavenger raptors like Steppe Eagle (Sharma et al., 2014). Another threat is electrocuted by power lines near the roads (McGrady et al., 2021). In this regard, necessary measures to reduce the loss of Steppe Eagles and other raptors (such as insulation of cables; Guil et al., 2011) should be monitored by DoE. Finally, conservation of vegetation cover and wetlands in CAs and limiting man-made constructions can preserve climate conditions and landform of the region (Lipka et al., 2023).

5. Conclusion

The present research aimed to identify suitable habitats, important potential wintering areas, and the potential migratory paths of Steppe Eagle throughout Iran. We found that only 20 % of Steppe Eagle potential wintering areas are protected, suggesting that the current protection level of lands steppe eagles use should be increased. Protection of these landscapes is likely to contribute to stabilizing and improving the conservation status of Steppe Eagle across its range. Our results pave the way for proper planning for the conservation of raptors in Iran, particularly Steppe Eagle.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03236.

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