Ornis Fennica 96: 77–89. 2019

Ensemble of small models for estimating potential abundance of Caucasian grouse (*Lyrurus mlokosiewiczi*) in Iran

Nader Habibzadeh* & Tobias Ludwig

*N. Habibzadeh, Department of Environmental Science, Tabriz Branch, Islamic Azad University, Tabriz, Iran. * Corresponding author's e-mail: habibzadeh@iaut.ac.ir*
T. Ludwig, Bavarian Regional Authority of Environment / Ornithological Station Garmisch-Partenkirchen, Germany

Received 22 June 2018, accepted 22 December 2018

The need to obtain information on population size to inform management actions for conservation is imperative. Despite this, reliable data on Caucasian grouse abundance is scarce in Iran. The goal of this study was to explore the potential distribution of Caucasian grouse using an ensemble of small models with outstanding performance for modelling rare species' distributions to estimate the potential population size in Iran. We fitted an ensemble of small models with generalized boosted model (GBM) and maximum entropy (MaxEnt), and then built a final ensemble prediction by averaging across these two ensembles of small models. We considered ten environmental descriptors (land-cover, anthropogenic and topographic features) which were extracted over a 70 hectare spatial extent surrounding 22 Caucasian grouse lek occurrences. The best model's prediction map was used to estimate the potential population size of Caucasian grouse in Iran. The ensemble of small models with generalized boosted model showed higher transferability performances than the two other models on both 10-fold cross-validation and a geographically independent dataset. Based on the published species' densities and our prediction map, the potential population size of Caucasian grouse for Iran was estimated to be 98–196 individuals, which is considerably less than 350 reported by previous assessments. The predicted distribution map can be used to select priority areas for conservation, and to identify survey locations for the species in areas which so far have been poorly sampled.

1. Introduction

One of the pivotal criteria used by biodiversity conservation institutions for providing insight into species conservation status is population size (Butchart *et al.* 2004). In practice, however, data on species abundance are often not available or too expensive to collect. Use of expert opinions to make decisions on species conservation categories when there is a lack of reliable knowledge of species abundance and distribution is common (Putland 2005). Moreover, there is recently an increased practice of using species distribution models (hereafter SDMs; Guisan & Zimmermann 2000, Guisan & Thuiller 2005) to characterize patterns of species' occurrence and abundance (Pacifici *et al.* 2017). The outputs of SDMs are related not only to the probability of occurrence, but also to other key parameters of populations such as abundance (Weber *et al.* 2016, Fois *et al.* 2018). Although the suitability is not able to predict the actual abundance as there is a commonly triangular relationship between predicted suitability for species occurrence and abundance (Acevedo *et al.* 2017), it is possible to determine maximum abundance that a population can attain without completely explaining abundance in all localities (Vaz *et al.* 2008). This relationship offers the use of SDMs to estimate species abundance, thus providing more useful information for management and conservation goals (Yin & He 2014).

SDMs are statistical techniques used to predict the distribution of a species, based upon relating the observed distribution to several environmental variables (Austin 2007, Elith & Leathwick 2009). Their applications in the broad context of conservation biology are widely demonstrated (Guisan & Thuiller 2005, Visconti *et al.* 2016). Such applications are especially important for rare and threatened species with high conservation priority (Guisan *et al.* 2013). However, many studies indicate that using a high number of environmental predicators in relation to few occurrence records can lead to reduced model accuracy which makes producing accurate models of rare species' occurrence difficult (Stockwell & Peterson 2002, Wisz *et al.* 2008).

Poor applicability of standard SDMs to new data due to over-fitting restrictions (Vaughan & Ormerod 2005) combined with the importance of being able to predict rare species' occurrence over new areas for conservation planning, encourages conservationists to use cutting-edge SDM techniques. Ensembles of Small Models (hereafter ESMs) are a novel strategy proposed to circumvent this issue when predicting the distribution of rare species (Lomba *et al.* 2010). ESMs are applicable with various standard SDM techniques, and are built by fitting a large number of small bivariate models and then averaging them into an ensemble model where the small models are weighted by their cross-validated scores of predictive performance (Breiner *et al.* 2015).

The outstanding performance of ESMs to model rare species distribution (Breiner *et al.* 2015) encouraged the use of this approach on Caucasian grouse *Lyrurus mlokosiewiczi*, which have a restricted geographic range and only a small dataset (22 occurrences; Habibzadeh & Rafieyan 2016) in Iran. The Iranian population is the southernmost point of the species' range and is confined in the northwest of Iran (Gavashelishvili & Javakhishvili 2010). Caucasian grouse is found on steep slopes of subalpine and alpine meadows covered by widely scattered dwarf shrubs (e.g., rhododendron thickets) but in proximity to deciduous broad-leaf forest (Klaus *et al.* 1990, Gavashelishvili & Javakhishvili 2010, Habibzadeh & Rafieyan 2016).

Caucasian grouse is endemic to the Greater and Lesser Caucasus Mountains and categorized as Near Threatened on the IUCN Red List (BirdLife International 2018). It is the only representative of the family Tetraonidae in this region (Potapov 2008). Caucasian grouse has the smallest range of any grouse species (Baskaya 2003, Gavashelishvili & Javakhishvili 2010) and this range is highly fragmented (Gavashelishvili & Javakhishvili 2010).

Consequently, Caucasian grouse is one of the least studied grouse species (Baskaya 2003). A few studies have investigated the lek habitat of the Caucasian grouse (Gottschalk *et al.* 2007, Gavashelishvili & Javakhishvili 2010, Habibzadeh *et al.* 2010, 2013, Habibzadeh & Rafieyan 2016). Habitat loss and transformation are thought to be the major threats to the species, with many of the subalpine meadows within its range being used for intensive grazing (Storch 2007). In the Lesser Caucasus, gentler terrain, road construction and changes in land use provide relatively easy access for developers and hunters, contributing to increased disturbance and habitat degradation (Gavashelishvili & Javakhishvili 2010).

In Iran, a scarce and very local resident population of Caucasian grouse, which was first confirmed for Iran in 1971 (Scott 1976), is distributed within the Arasbaran region in East Azerbaijan province (Habibzadeh *et al.* 2010, Habibzadeh & Rafieyan 2016). Based on some reported counts, Khaleghizadeh et al. (2011) stated that the Iranian Caucasian grouse population had increased from 215 to 350 individuals between 2001 and 2009. Based on our knowledge about this peculiar species, the documented studies of population size estimation have not pointed out any details on their estimating approaches and so it is difficult to assess reliably Caucasian grouse population size and claim an increasing trend in Iran. According to Habibzadeh & Rafieyan (2016), the number of 27 breeding display sites (Habibzadeh *et al.* 2010) decreased to 22 lek sites within four years (2010–

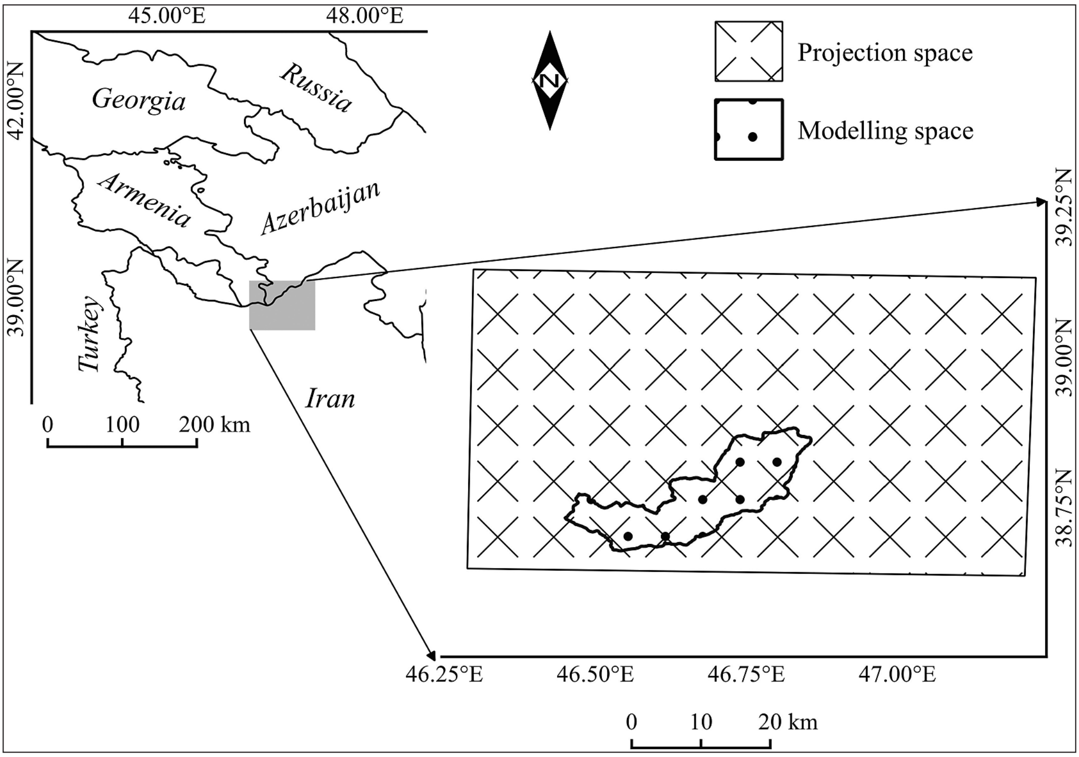

Fig. 1. The location of modelling (dotted area) and projection (crossed area) spaces used to estimate Caucasian grouse population size in Iran (shaded area).

2014) due to habitat destruction arising from increased development and overgrazing.

As Caucasian grouse population estimation by formal field techniques is difficult due to vast, rugged and climatically inclement areas (Gavashelishvili & Javakhishvili 2010), in this paper we merged the important environmental variables of previous studies (Gottschalk *et al.* 2007, Gavashelishvili & Javakhishvili 2010, Habibzadeh & Rafieyan 2016) into ensembles of small bivariate models to predict Caucasian grouse distribution across Iran. We then used these models to estimate the abundance of grouse in Iran using a low cost preliminary assessment with the few available occurrence records.

2. Materials and methods

2.1. Study area

We used the Caucasian grouse range (Habibzadeh & Rafieyan 2016) in the north-western Iranian uplands, covering the Lesser Caucasus, for conducting our study (Fig. 1). The grouse's range falls within one major region, Arasbaran, which constitutes the southern stretches of the Caucasus (Transcaucasia) (Asef & Muradov 2012). It is in a highly mountainous region rising from 256 to 2896 m above sea level (Parsa *et al.* 2016) which is located in the mixed mountainous systems biome (Shokri *et al.* 2004). The Arasbaran region consists of two distinct herder groups using the same summer rangelands: local villagers and nomads. Villagers occupy the rangelands where they subsist on livestock husbandry and farming, while the herding nomads move between the high rangelands and the foothills (Tashakori 2008). More information on regional characteristics can be found in Habibzadeh & Rafieyan (2016).

2.2. Sampling points

For this study, data on species occurrences (presence-only) included Caucasian grouse lek occurrences (Masoud 2004, Habibzadeh *et al.* 2013) verified by Habibzadeh & Rafieyan (2016) using morning (0.5 h before sunrise until 2.5 h after sunrise) and evening (2 h before sunset until sunset) foot and roadside surveys in spring 2013 and 2014, from mid–April to late May.

Since all SDMs require data on locations from which the subject is absent, and false absences can decrease the reliability of prediction models (Chefaoui & Lobo 2008), we used the "pseudo-absence" approach. Following the recommendations of Elith *et al.* (2006), one third of the available background modelling cells were randomly sampled across the study landscape at a minimum distance of 472 meters (see below) from each other, and also 1.1 km from presence locations to reduce the probability of false absences. We chose 1.1 km because there was a median autocorrelation of 1.05 km among environmental variables computed using R package blockCV (Valavi *et al.* 2018). For modelling, our dataset consisted of 22 Caucasian grouse lek occurrence records plus 1,000 pseudo-absence points.

2.3. Natural environmental variables

Since the reliability of species distribution modelling is based on selecting ecologically relevant environmental predictors (Elith & Leathwick 2009), we calculated land-cover, topographic and anthropogenic variables according to their acknowledged relevance to Caucasian grouse lekking behaviour (Gottschalk *et al.* 2007, Gavashelishvili & Javakhishvili 2010, Habibzadeh *et al.* 2010, 2013, Habibzadeh & Rafieyan 2016). We computed predictor variables within a 472-m radius or 70-ha circle, which corresponds to the maximum size of a Caucasian grouse lek on subalpine meadows along the treeline of the Little Chatipara, North Caucasus (Klaus *et al.* 1990). This scale also matches the minimum yearly home-range size of male Eurasian black grouse (*Lyrurus tetrix*) (mean 155 ha, range 70–236 ha; Starling 1992), a better-studied congener.

We used the Climate Change Initiative-Land Cover (CCI–LC) data version 1.6, provided by the European Space Agency (ESA) at almost 300-m spatial resolution for the 2010 epoch, which contains 22 primary and 14 sub-level land cover classes (ESA 2014). Our study area includes 16 primary classes (rain-fed croplands; irrigated or post-flooding croplands; mosaic cropland (> 50%) and natural vegetation (< 50%); mosaic natural vegetation (> 50%) and cropland (< 50%); tree cover, broadleaved, deciduous, closed to open (> 15%); tree cover, needleleaved, evergreen, closed to open (> 15%); tree cover, mixed leaf type (broadleaved and needleleaved); shrubland; grassland; mosaic tree, shrub (> 50%) and herbaceous cover (< 50%); mosaic herbaceous cover (> 50%), tree and shrub (< 50%); sparse vegetation (< 15%); shrub or herbaceous cover, flooded, fresh or saline or brakish water; urban areas; bare areas; water bodies) and one sub-level land cover class (tree cover, broadleaved, deciduous, closed (> 40%)).

We imported this land cover layer to FRAGSTATS 4.2 (McGarigal *et al.* 2012) and used a moving window of the chosen scale (472-m radius circle) to compute three land-cover variables: 1) the proportion of mosaic tree and shrub (> 50%) and herbaceous cover (< 50%), 2) the proportion of sparse vegetation (tree, shrub, herbaceous cover) (< 15%), and 3) patch richness (number of different patch types of 17 land cover classes).

Using the Advanced Space borne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) (ASTER GLOBAL DEM with a 3 arc-second (~ 90-m) pixel size, available on: https://lpdaac.usgs.gov), the most important factors describing topographic context were compiled: slope, sine and cosine of aspect, elevation, roughness and topographic exposure index (TOPEX). The roughness (as an index of irregularity of the surface) was calculated by the largest inter-cell difference of a central pixel and its surrounding cell (Wilson *et al.* 2007). The topographic exposure raster layer was generated using a model developed and provided by the Windthrow Research Group, University of British Columbia, Vancouver, Canada. The script calculates an index of exposure that is the summation of the maximum and minimum angles to the skyline within a user-specified distance in the eight cardinal directions (Perry & Wilson 2010). An exposure grid was produced for this study, simulating unweighted exposure at a 472-m limiting distance.

Following Gottschalk *et al.* (2007), the distance to settlements and roads was used for modelling to account for anthropogenic disturbance, such as poaching, predation by shepherd dogs and nest destruction by livestock. We used high resolution image tiles in Google Earth version 5.1 to extract road and settlement layers.

To provide congruence between the scales at which we measured environmental variables, we resampled topographic and anthropogenic variables to the pixel size of land-cover grids using average aggregation method and each layer was converted to the study's geographic projection.

Finally, variable redundancy within environmental variables was checked by Spearman's rank correlation (Supplementary information, Fig. S1). If two variables were highly correlated ($r \geq |0.7|$), the one which ranked lower in univariate models with the response variable was excluded to avoid collinearity. In this step, we also removed remaining predictor variables with Variance Inflation Factor (VIF) values larger than three (Zuur *et al.* 2007). The VIF is used to measure the degree of multi-collinearity of the *ith* independent variable with the other independent variables in a regression model (O'brien 2007).

We used the usdm-package (Naimi 2015) for the R environment (R Development Core Team 2014) to test the VIF. The package deploys a stepwise backward selection procedure to obtain a parsimonious model. This was accomplished by removing one variable at a time (the one with the highest VIF > 3) and recalculating VIF after each iteration until a set of non-collinear variables was obtained. Since roughness and slope showed high collinearity (Supplementary information, Fig. S1), we maintained slope because this variable has been shown earlier to have an influence on Caucasian grouse presence (Gavashelishvili & Javakhishvili 2010). The remaining ten environmental variables were used as the predictor variables (Table 1) both for modelling and projection. All GIS data were prepared and analyzed in QGIS (QGIS Development Team 2014).

2.4. Modelling techniques and ensemble forecasting

We fitted ESMs with generalized boosted models (GBMs; Friedman *et al.* 2000, Friedman 2001) and maximum entropy (Maxent; Phillips *et al.* 2006) to produce models with a high predictive performance and transferability (Breiner *et al.* 2018). In our study, a set of 10 uncorrelated predictors resulted in 45 bivariate predictor combinations. We evaluated each of the bivariate models using 10-fold cross-validated Area Under the receiver operating characteristic Curve (AUC; Fielding & Bell 1997, Lobo *et al.* 2008) value, which was then used to build a Somers' D weighted average of the 45 bivariate models as the ESM prediction (Breiner *et al.* 2015). Somers' D is $D = 2 \times (AUC–0.5)$ and gives more weight to models that perform well and less to those that perform poorly. Bivariate models with a Somers' D lower than 0 (i.e., AUC < 0.5) were set to zero and not used to build the ESMs (Breiner *et al.* 2015).

An indication of the contribution of each environmental variable in the ESMs calculated based on the difference in bivariate model weights where the variable was used compared to all bivariate model weights (Broennimann *et al.* 2018). One ESM was built for each modelling technique (i.e., ESM based on bivariate GBM (ESM_{GBM}) and bivariate MaxEnt models (ESM_{MaxEnt})). We then built a final ensemble prediction (ESM_{EP}) by averaging across these two ESMs, again using Somers' D weights (Breiner *et al.* 2015).

The distribution models were evaluated using two different sets of data. First, we separated our modelling dataset (22 presences and 1,000 pseudo-absences) into ten folds for cross-validation. We randomly allocated spatially segregated blocks to calibration and evaluation bins (folds) using R package blockCV (Valavi *et al.* 2018). To do so, we used the package blockCV to look at the existing autocorrelation in the environmental predictors based on 1,000 sampling points taken from each input environmental raster layer. This package uses an isotropic variogram to show the spatial autocorrelation ranges of input raster covariates and then the optimal block size is selected based on median spatial autocorrelation range across all input data (Valavi *et al.* 2018). We chose the size of spatial blocks equivalent to 2,200 meters which was substantially bigger than the range of spatial autocorrelation (1,050 meters) to obtain a good estimation of error (Roberts *et al.* 2017).

As the species' occurrence localities had a clumped pattern in the study area (Fig. 2), we also checked that block-to-fold allocations achieved the most even spread of species data across folds. Second, we used four independent species pres-

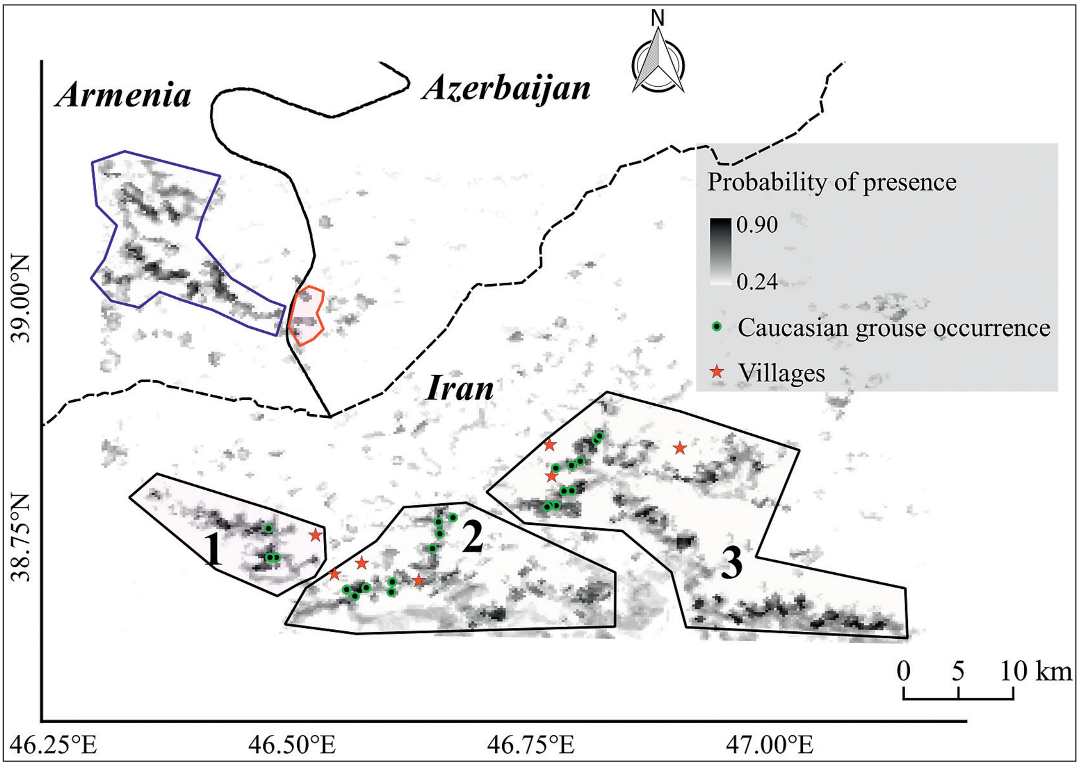

Fig. 2. Probability of Caucasian grouse occurrence in Iran and the southern parts of Armenia and Azerbaijan according to the Ensemble of Small Models fitted using the generalized boosted model (ESM_{GBM}). Darker shades show areas with a high probability of occurrence, lighter shades indicate low probability of occurrence. The green dots show the locations of lekking sites used to fit the model. The numbers inside the black polygons indicate three main landscapes including Kringan village (1), Molk-e-Talesh, Vanestan and Khoinaroad villages (2), and Kharil, Mazgar, and Makidi villages (3) which cover the predicted distribution of Caucasian grouse in Iran. The polygons marked by blue and red lines highlight the core predicted grouse distribution in southern Armenia and Azerbaijan, respectively.

ence records (Gavashelishvili & Javakhishvili 2010) and 400 generated pseudo-absences from the southernmost part of Armenia for evaluating the models independently (i.e., a transferability assessment).

2.5. Model evaluation

We used two indices to evaluate model performance: 1) the AUC and 2) the Boyce index as a presence-only index (Hirzel *et al.* 2006). The Boyce index varies from –1 to 1, where positive values indicate a model whose predictions are consistent with the presences distribution in the evaluation dataset, values close to zero mean that the model is not different from a chance model, and negative values indicate an incorrect model, which predicts poor quality areas where presences are more frequent (Hirzel *et al.* 2006). We used the R packages “biomod2” (Thuiller *et al.* 2009), “dismo” (Hijmans *et al.* 2017) and “ecospat” (Broennimann *et al.* 2018) to build and evaluate ESMs.

2.6. Estimation of population size

For population size estimation, we projected the best ESMs according to their transferability performance to a larger area that includes meadows in proximity to the forest line as a potential suitable habitat (Gottschalk *et al.* 2007, Gavashelishvili & Javakhishvili 2010, Habibzadeh *et al.* 2013, Habibzadeh & Rafieyan 2016) to generate prediction maps. This larger area which stretched from

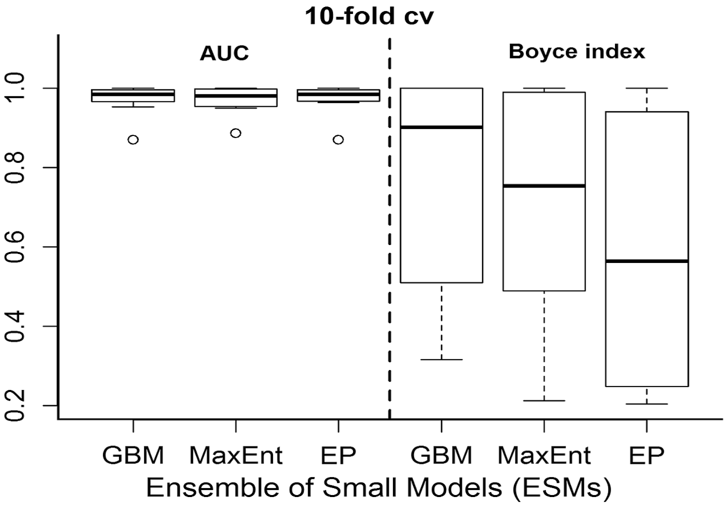

Fig. 3. performance of three Ensemble of Small Models (generalized boosted model (GBM), maximum entropy (MaxEnt), and ensemble prediction (EP) according to AUC and the Boyce index evaluated with the testing data from the 10-fold spatially segregated dataset. Higher values indicate better performing models.

46.28° N and 38.64° E to 47.23° N and 39.13° E (Fig. 1) is only potential suitable habitat within the southernmost part of Caucasian grouse's known range (Gavashelishvili & Javakhishvili 2010). The best model's prediction map was used to estimate Caucasian grouse population size by applying two alternative published average densities of 2.3 birds km^2 (Drovetski & Rohwer 2000) and 4.8 birds km^2 (Potapov 1985) on ensemble map occurrence probabilities weighted as follows (Gottschalk *et al.* 2007, Gavashelishvili & Javakhishvili 2010):

$$N = da \sum_{i=1}^{n} p_i \qquad (1)$$

where *N* is the total population size, *d* is the grouse density (birds km^2), *a* is the cell area (km^2), *pi* is the probability of occurrence value from the ensemble map in the *ith* cell of the study area, and *n* is the number of cells in the study area. Cells of the prediction map were excluded from our analysis if they had a probability of occurrence value lower than the average value for Caucasian grouse presence points. Since our goal was to assess whether Caucasian grouse in Iran is threatened, we adopted this threshold to avoid inflating the population estimate by allowing for low densities of birds to occur in cells which are likely to be truly unoccupied (Freeman & Moisen 2008). We also excluded the parts of the prediction map that were outside of Iran (i.e., in Armenia and Azerbaijan) from the analysis estimating Caucasian grouse population size for Iran (Fig. 1). Based on the same threshold used to exclude cells with a probability of occurrence value lower than the average value for Caucasian grouse presence points, we also identified how much of the Caucasian grouse range in Iran includes favorable habitat.

3. Results

The variables CA_100 (proportion of mosaic tree and shrub (> 50%) and herbaceous cover (< 50%)) and ELV (elevation) had the highest importance values, whereas the remaining variables were of low importance in the ensemble of small models. ELV contributed 99% and 100% to ESM_{GBM} and $\text{ESM}_{\text{MaxEnt}}$ models followed by CA_100 (76% and 58%), respectively (Supplementary information, Fig. S2).

The models' performance based on the mean AUC (± standard error) between ESMs on 10-fold cross validation all showed good overall prediction accuracy (Swets 1988; Fig. 3; $\text{ESM}_{\text{GBM}} = 0.97 \pm 0.04$, $\text{ESM}_{\text{EP}} = 0.97 \pm 0.04$, $\text{ESM}_{\text{MaxEnt}} = 0.97 \pm 0.04$). However, their performances based on AUC on the geographically independent dataset differed, with ESM_{GBM} (0.97) and ESM_{EP} (0.90) performing better than $\text{ESM}_{\text{MaxEnt}}$ (0.85).

ESM_{GBM} showed the highest transferability (the Boyce index) both given by the 10-fold cross validation (0.78 ± 0.30; Fig. 3) and the geographically independent dataset (0.96) than $\text{ESM}_{\text{MaxEnt}}$ (0.71 ± 0.30; 0.93) and ESM_{EP} (0.59 ± 0.35; 0.94).

If no true absences are available, the Boyce index provides a better evaluation criterion than AUC when modelling rare species (Breiner *et al.*

2015). Transferability performance is of importance if projections and inferences extend beyond the conditions represented by the data used to fit the model (Wenger & Olden 2012). Because $\mathrm{ESM}_{\mathrm{GBM}}$ showed higher transferability performances than $\mathrm{ESM}_{\mathrm{MaxEnt}}$ and $\mathrm{ESM}_{\mathrm{EP}}$ given the Boyce index and AUC criteria, we chose $\mathrm{ESM}_{\mathrm{GBM}}$ prediction map to estimate Caucasian grouse population size. Based on the estimated species' densities (Drovetski & Rohwer 2000, Potapov 1985) and the probability scores of the $\mathrm{ESM}_{\mathrm{GBM}}$ map which ranged from 0.24 to 0.90 (Fig. 2), Caucasian grouse population size for Iran, the southern parts of Armenia and Azerbaijan was estimated to be about 98–196, 24–48 and 6–12 birds, respectively. The center point of the Iranian Caucasian grouse population has approximately a distance 54 and 35 km from the centers of the Armenian and Azerbaijan populations.

We set the average threshold for suitability of habitat for Caucasian grouse at a probability of occurrence equal to 0.56, based on the average probability value for Caucasian grouse presence points. On this basis, a total area of 63.5 km^2 out of 3,358.1 km^2 was identified as suitable landscape for Caucasian grouse in Iran.

4. Discussion

Our results indicated that elevation and percent cover of mosaic tree and shrub (> 50%) and herbaceous cover (< 50%) are key determinants underlying the spatial configuration of Caucasian grouse leks in 70-ha landscapes. For Caucasian grouse as a subalpine obligated species during lekking (Storch 2000), mosaic tree and shrub (> 50%) and herbaceous cover (< 50%) appears to be one of the main determinant factors of spatial distribution. The previous reports (Gottschalk *et al.* 2007, Gavashelishvili & Javakhishvili 2010) clearly confirmed that elevation and the vicinity of forest edges are of great importance for determining Caucasian grouse distribution.

In our study area, landscapes around lek sites are covered by widely scattered dwarf shrubs e.g., *Rhododendron caucasicum* thickets. The structural and physiological characteristics of subalpine shrubs provide both main feeding resources, particularly in winter, and excellent cover from avian predators. During the breeding and display season, tree species such as birch (*Betula litwinowii*), oak (*Quercus macranthera*), and beech (*Fagus orientalis*) allow Caucasian grouse to roost on the branches of trees close to meadows (Habibzadeh *et al.* 2013) during the night or to avoid rainy conditions. This is in agreement with knowledge of Caucasian grouse landscape requirements at the 472-m radii scale from Habibzadeh & Rafieyan (2016).

The habitat suitability maps produced by $\mathrm{ESM}_{\mathrm{GBM}}$ (Fig. 2) showed that the predicted Caucasian grouse distribution covers three main landscapes. These are the mountain ecosystems of 1) Kringan village, 2) Molk-e-Talesh, Vanestan and Khoinaroad villages, and 3) Kharil, Mazgar, and Makidi villages (Fig. 2) which support 13–26, 24–48, and 61–122 birds, respectively. This result shows that the Caucasian grouse population is probably distributed in a meta-population pattern, or living as isolated subpopulations given the species' sedentary habits (Isfendiyaroğlu *et al.* 2007) and its inability for long-distance movements (M. Masoud, Personal communication).

Population isolation, accompanied by a small population (98–196 birds), limited suitable habitat (63.5 km^2 out of 3,358.1 km^2), and population-specific climate conditions in the south-eastern Lesser Caucasus (Habibzadeh *et al.* in press) could result in a high influence of stochastic variation on the Caucasian grouse populations in Iran. However, future population genetic research may assess the validity of this assumption. Clearly, our estimate of 98–196 individuals provides good evidence to consider with caution the number of Caucasian grouse (350 individuals) reported by Khaleghizadeh *et al.* (2011) that was based on some unpublished data compiled by M. Masoud.

Based on the good prediction performance of our $\mathrm{ESM}_{\mathrm{GBM}}$, it could be used as a tool by the Iranian Department of Environment (DOE) for identification of potential habitats and population monitoring of Caucasian grouse over its entire range in Iran. Additionally, the model can contribute to important habitat management questions, such as which locations might be most suitable for habitat restoration efforts. The prediction map also indicated that the southern parts of Azerbaijan and Armenia provide a small suitable habitat for Caucasian grouse (16 km^2 out of 921.3 km^2; Fig. 2). Although the southern part of Azerbaijan supports a very small number of the species (6–12), the bird probably survives by trans-boundary migration which is facilitated with naturally well connected trans-boundary habitats.

Species distribution modelling methods which predict species distributions are an important tool for supporting conservation decisions, facilitating the link between modellers and decision makers (Guisan *et al.* 2013). In addition, the IUCN has begun to explicitly incorporate SDMs to estimate extent of occurrence as an extinction risk parameter and to explore the potential impacts of climate change on species' distributions (Cassini 2011). Here we used a powerful strategy for modelling rare species distributions, namely ESMs based on bivariate models (Breiner *et al.* 2015), to describe the potential distribution of Caucasian grouse in Iran and, in turn, its potential population size.

The vertebrates' studies benefit from SDMs as a useful proxy of abundance, although the general relationship between abundance and suitability is moderate (Weber *et al.* 2016). The study of large-scale abundance patterns using species distribution modelling can be done with low survey costs and less information (Weber *et al.* 2016). Most previous studies have found a positive relationship between modelled habitat suitability for a species and species' abundance on a local scale (Weber *et al.* 2016). Nevertheless, the validity of treating probability of occurrence as a surrogate for abundance is still questionable, as the relationship between the two has been found to vary with time, species, and spatial scale (Johnston *et al.* 2015). Since the relationship between habitat suitability and species abundance is triangular (VanDerWal *et al.* 2009), the outputs of our ESMs as surrogates of species abundance should be considered as the upper limit of abundance that Caucasian grouse can reach in a locality given its environmental characteristics, not the actual abundance (Muñoz *et al.* 2015, Acevedo *et al.* 2017).

Also, if the small number of lek locations used as presence points poorly represent the species' true occurrence over the study area due to biased sampling, the essential assumption of presence-only SDMs may not be met (Phillips *et al.* 2006). Because the lek survey was made from the ground, more accessible leks (due to such factors as road conditions and the distance travelled to reach the lek) might be more likely to be included in the sample. This outcome could represent convenience sampling (Anderson 2001) and may generate inaccuracies in SDMs (Gomes *et al.* 2018).

Although, the sampling method was biased to be closer to roads, the distance to road was not a significant variable in any of the models. So, our results were robust to this bias. There may also be a potential concern over the dataset used in our study which was mainly collected using field surveys in spring and autumn when Caucasian grouse concentrate near leks. However, the lek sites can be interpreted as the core area of Caucasian grouse distribution, because grouse use the additional areas close to lek sites in summer (Etzold 2005) and winter (Klaus & Vitovich 2006).

Our study did not assess disturbance by domestic animals at lek sites, thus it may be that many sites that appear suitable according to these models may have high levels of disturbance making them unattractive locations for breeding Caucasian grouse. Moreover, including all spatially referenced occurrence locations for a species in geographic space in its occupied niche is of limited value in conservation planning without estimates of population demography (e.g., survival probability) (Kahler & Cavalieri 2014). Therefore, if ecological niche modelling with species presence/absence data is applied without accounting for source/sink dynamics, results will include predictions of areas likely to serve as either population sources or sinks (Kahler & Cavalieri 2014).

Although our use of fine resolution data could have good predictive discrimination compared with Gavashelishvili & Javakhishvili (2010), we also must take into account the limits of the species distribution modelling approach for estimating species abundance. Related findings indicated that low habitat suitability may occur in areas of high abundance, probably due to environmental factors, correlated with forest structure, productivity, the degree of fragmentation, and climate that are not considered in modelling which may increase the actual environmental suitability of the area (Basile *et al.* 2016). Conversely, some unmeasured environmental factors, such as stochastic weather events, or biological constraints such as biotic interactions or limited dispersal capabilities, may hinder higher abundance in otherwise highly suitable areas (VanDerWal *et al.* 2009).

Therefore the distribution map generated by our final ESMs should be used with caution. Future work should focus on compiling additional field data on population distribution and abundance to carry out an assessment of the model's predictive performance and, once more presence data are available, consider incorporating additional variables into a similar analysis. For example, biologists familiar with Caucasian grouse habitat requirements should visit sites where the model predicts a high probability of occurrence, to evaluate the model's accuracy. However, the species' absence at such sites may also be caused by the triangular relationship between habitat suitability and species abundance (VanDerWal *et al.* 2009).

Gavashelishvili & Javakhishvili (2010) predicted suitable habitat for Armenia, although their map provided no suitable patch across the southern part of Azerbaijan. These differences might be due to the existence of cross-correlation and redundancy issues among habitat variables that entered the models, different spatial resolutions of the environmental layers or modelling techniques. Gavashelishvili & Javakhishvili (2010) used several modelling techniques including logistic regression, classification and regression tree, Mahalanobis distance, and maximum entropy to model the species' habitat suitability by relating the presence and absence locations of the species to environmental variables with 1 km spatial resolution.

Our study indicates that the Caucasian grouse population size in Iran is much less than required to maintain the evolutionary potential or viable population of a species (500 individuals; Jamieson & Allendorf 2012) and to prevent the loss of quantitative genetic variation (5,000 individuals; Frankham 1995). Therefore, if the species lives in isolation from its northern populations (in Azerbaijan and Armenia) the further hesitation of species conservationists to build connectivity between these populations will move Caucasian grouse further towards local extinction in Iran.

Acknowledgements. The authors would like to thank Tabriz branch, Islamic Azad University for the financial support to N.H., which is based on a research project contract with grant number 5–32801. The authors are grateful to the reviewer, Andrew Bladon whose comments greatly improved the manuscript.

Kaukasianteeren populaatiokoon mallintaminen Iranissa

Populaatiokokoon määrittäminen on äärimmäisen tärkeää tehokkaiden suojelutoimien kannalta. Kaukasianteeren populaatiokoosta on hyvin vähän tietoa. Tutkimuksemme tarkoituksena oli selvittää kaukasianteeren levinneisyyttä ja populaatiokokoa käyttämällä mallinnusmenetelmää (ESM), joilla tiedetään olevan erinomainen kyky mallintaa harvinaisten lajien levinneisyyttä.

Käytimme GBM ja MaxEnt mallinnusta, ja rakensimme lopulliset malliennusteet näiden keskiarvon perusteella. Analysoimme 10 eri ympäristömuuttujaa (maankäyttö-, kaupunki- ja topografisia muuttujia), jotka selvitettin 70 hehtaarin alata 22 kaukasianteeren soidinpaikoilta. Käytimme parhaan mallin ennustekarttaa kaukasianteeren populaatiokoon ennustamiseen Iranissa. GBM mallit suoriutuivat paremmin kuin muut useimmissa testeissä. Omien malliemme, ja aiemman kirjallisuuden perusteella kaukasianteeren populaatiokoko Iranissa on 98–196 yksilöä, mikä on huomattavasti vähemmän kuin aiempien arviointien 350 yksilöä. Tuottamaamme lajin esiintymisen ennustekarttaa voidaan käyttää hyväksi valittaessa ensisijaisia suojelualueita ja selvitettäessä vähän tutkittuja alueita.

References

Acevedo, P., Ferreres J., Escudero, M.A., Jimenez, J., Boadella, M. & Macro, J. 2017: Population dynamics affect the capacity of species distribution models to predict species abundance on a local scale. — Diversity and Distribution 23: 1008–1017.

Anderson, D.R. 2001: The need to get the basics right in wildlife field studies. —Wildlife Society Bulletin 29: 1294–1297.

Asef, M.R. & Muradov, P. 2012: Lepiotaceous fungi (Agaricaceae) in the Iranian part of Caucasia. — Turkish Journal of Botany 36: 289–294.

Austin, M. 2007: Species distribution models and ecological theory: a critical assessment and some possible new approaches. — Ecological Modelling 200: 1–19.

Basile, M., Valerio, F., Balestrieri, R., Posillico, M., Bucci, R., Altea, T., De Cinti, B. & Matteucci, G. 2016: Patchiness of forest landscape can predict species distribution better than abundance: the case of a forest-dwelling passerine, the short-toed treecreeper, in central Italy. — PeerJ 4: e2398.

Baskaya, S. 2003: Distribution and principal threats to

Caucasian black grouse *Tetrao mlokosiewiczi* in the Eastern Karadeniz Mountains in Turkey. — Wildlife Biology 9: 377–383.

BirdLife International 2018: Species factsheet: *Lyrurus mlokosiewiczi*. Available at http://www.birdlife.org (Accessed 02 July 2018).

Broennimann, O., Di Cola, V., Petitpierre, B., Breiner, F., Scherrer, D., D`Amen, M., Randin, C., Engler, R., Hordijk, W., Mod, H., Pottier, J., Di Febbraro, M., Pellissier, L., Pio, D., Mateo, R.G., Dubuis, A., Maiorano, L., Psomas, A., Ndiribe, C., Salamin, N., Zimmermann, N. & Guisan, A. 2018: Ecospat: Spatial Ecology Miscellaneous Methods. R package version 3.0. Available at http://cran.r-project.org/package=ecospat (Accessed 03 August 2018).

Breiner, F.T., Guisan, A., Bergamini, A. & Nobis, M.P. 2015: Overcoming limitations of modelling rare species by using ensembles of small models. — Methods in Ecology and Evolution 6: 1210–1218.

Breiner, F.T., Nobis, M.P., Bergamini, A. & Guisan, A. 2018: Optimizing ensembles of small models for predicting the distribution of species with few occurrences. — Methods in Ecology and Evolution 9: 802–808.

Butchart, S.H., Stattersfield, A.J., Bennun, L.A., Shutes, S.M., Akçakaya, H.R., Stuart, S.N., Hilton–Taylor, C. & Mace, G.M. 2004: Measuring global trends in the status of biodiversity: Red List Indices for birds. — PLoS Biology 2: e383.

Cassini, M.H. 2011: Ranking threats using species distribution models in the IUCN red list assessment process. — Biodiversity and Conservation 20: 3689–3692.

Chefaoui, R.M. & Lobo, J.M. 2008: Assessing the effects of pseudo-absences on predictive distribution model performance. — Ecological Modelling 210: 478–486.

Drovetski, S.V. & Rohwer, S. 2000: Habitat use, chick survival and density of Caucasian black grouse *Tetrao mlokosiewiczi*. — Wildlife Biology 6: 233–240.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti–Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. & Zimmermann, N.E., 2006: Novel methods improve prediction of species' distributions from occurrence data. — Ecography 29: 129–151.

Elith, J. & Leathwick, J.R. 2009: Species distribution models: Ecological explanation and prediction across space and time. — Annual Review of Ecology and Evolution Systematics 40: 677–697.

Etzold, J. 2005: Analyses of vegetation and human impacts in the habitat of the Caucasian black grouse *Tetrao mlokosiewiczi* in the Greater Caucasus/Azerbaijan. — Archiv für Naturschutzund Landschaftsforschung 44: 7–36.

European Space Agency (ESA) 2014: CCI Land Cover Product User Guide version 2.4, ESA CCI LC project. — Available at https://www.esa-landcover-cci.org (Accessed 23 July 2017).

Fielding, A.H. & Bell, J.F. 1997: A review of methods for the assessment of prediction errors in conservation presence/absence models. — Environmental Conservation 24: 38–49.

Fois, M., Cuena-Lombraña, A., Fenu, G., Cogoni, D., Bacchetta, G. 2018: Does a correlation exist between environmental suitability models and plant population parameters? An experimental approach to measure the influence of disturbances and environmental changes. — Ecological Indicators 86:1–8.

Frankham, R. 1995: Effective population size/adult population size ratios in wildlife: a review. — Genetics Research 66: 95–107.

Freeman, E.A., & Moisen, G.G. 2008: A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. — Ecological Modelling 217: 48–58.

Friedman, J.H. 2001: Greedy function approximation: a slope boosting machine. — The Annual of Statistics 29: 1189–1232.

Friedman, J., Hastie, T. & Tibshirani, R. 2000: Additive logistic regression: a statistical view of boosting. — The Annual of Statistics 28: 337–407.

Gavashelishvili, A. & Javakhishvili Z. 2010: Combining radio-telemetry and random observations to model the habitat of Near Threatened Caucasian grouse *Tetrao mlokosiewiczi*. — Oryx 44 (4): 491–500.

Gomes, V.H.F, Ij, S.D., Raes, N., Amaral, I.L., Salomâo, R.P., de Souza Coelho, L., Almeida Matos, F.D., Castilho, C.V., de Andrade, D., Cárdenas López, D. et al. 2018: Species distribution modelling: contrasting presence-only models with plot abundance data. — Scientific Reports 8: 1003.

Gottschalk, K.T., Ekschmitt, K., Isfendiyaroglu, S., Gem, E. & Wolters, V. 2007: Assessing the potential distribution of the Caucasian black grouse *Tetrao mlokosiewiczi* in Turkey through spatial modelling. — Journal of Ornithology 148: 427–434.

Guisan, A. & Thuiller, W. 2005: Predicting species distribution: offering more than simple habitat models. — Ecology Letters 8: 993–1009.

Guisan, A. & Zimmermann, N.E. 2000: Predictive habitat distribution models in ecology. — Ecological Modelling 135: 147–186.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis–Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald–Madden, E., Mantyka–Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S. a., Elith, J., Schwartz, M.W., Wintle, B. a., Broennimann, O., Austin, M.P., Ferrier, S., Kearney, M.R., Possingham, H.P. & Buckley, Y.M. 2013: Predicting species distributions for conservation decisions. — Ecology Letters 16: 1424–1435.

Habibzadeh, N. Karami, M. & Tarinejad, A. 2010: Micro-

Habitat Characteristics of Breeding display Sites (Leks) of Caucasian Black Grouse (*Tetrao mlokosiewiczi*) in Arasbaran Region, East Azerbaijan, Iran. — Russian Journal of Ecology 41(5): 450–457.

Habibzadeh, N. Karami, Alavipanh, S.K. & Riazie, B. 2013: Landscape requirements of Caucasian grouse (*Lyrurus mlokosiewiczi*) in Arasbarn region, east Azerbijan, Iran. — Wilson Journal of Ornithology 125(1): 140–149.

Habibzadeh, N. & Rafieyan, O. 2016: Land cover patterns surrounding Caucasian grouse (*Lyrurus mlokosiewiczi*) leks in Arasbaran region, East Azerbaijan, Iran. — Wildlife Research 43: 267–275.

Habibzadeh, N., Storch, I. & Ludwig, T. in press: Differential habitat associations in peripheral populations of threatened species: the case of the Caucasian grouse. — Ecological Research. doi: 10.1002/1440-1703.1068

Hijmans, R.J., Phillips, S., Leathwick, J., & Elith, J. 2017: dismo: Species distribution modeling. R package version 1.1–4. Available at https://cran.r-project.org/package= dismo (Accessed 13 April 2017).

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C.F. & Guisan, A. 2006: Evaluating the ability of habitat suitability models to predict species presences. — Ecological Modelling 199: 142–152.

Isfendiyaroğlu, S., Welch, G., & Ataol, M. 2007: The Caucasian black grouse *Tetrao mlokosiewiczi* in Turkey: Recent survey results and conservation recommendations. — Wildlife Biology 13: 13–20.

Jamieson, I.G. & Allendorf, F.W. 2012: How does the 50/500 rule apply to MVPs? — Trends in Ecology and Evolution 27: 578–584.

Johnston, A., Fink, D., Reynolds, M.D., Hochachka, W.M., Sullivan, B.L., Bruns, N.E., Hallstein, E., Merrifield, M.S., Matsumoto, S. & Kelling, S. 2015: Abundance models improve spatial and temporal prioritization of conservation resources. — Ecological Applications 25: 1749–1756.

Kahler, B.M. & Cavalieri, V.S. 2014: Modelling Great Lakes Piping Plover habitat selection during the breeding period from local to landscape scales. — Upper Mississippi River and Great Lakes Region Joint Venture Technical Report No. 2014–1, Bloomington, MN, USA.

Khaleghizadeh, A., Scott, D.A., Tohidifar, M., Musavi, S.B., Ghasimi, M., Sehhatisabet, M.E., Ashori, A., Khani, A., Bakhtiari, P. Amini H., Roselaar, C., Aye, R., Ullman, M. Nezami, B. & Eskandari, F. 2011: Rare birds in Iran in 1980‒2010. — Podoces 6: 1–48.

Klaus, S., Bergmann, H.H., Marti, C., Müller F., Vitovic, O.A. & Wiesner, J. 1990: Die Birkhühner. — Ziemsen Verlag, Wittenberg Lutherstadt, Germany. (In German).

Klaus, S. & Vitovich, A.V. 2006: Clarifying the status of the Caucasian Black Grouse *Tetrao mlokosiewiczi* – methodical approach. — Newsletter of the WPA/BirdLife/IUCN/SSC Grouse Specialist Group 31: 11–15.

Lobo, J.M, Jiménez–Valverde, A. & Real, R. 2008: AUC: a misleading measure of the performance of predictive distribution models. — Global Ecology and Biogeography 17: 145–151.

Lomba, A., Pellissier, L., Randin, C.F., Vicente, J., Moreira, F., Honrado, J. & Guisan, A. 2010: Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. — Biological Conservation 143: 2647–2657.

Masoud, M. 2004: The analysis of distribution of a Caucasian black grouse population (*Tetrao mlokosiewiczi*) in East Azerbaijan Region. — The Environment Protection Society of East Azerbaijan, Iran (In Persian).

McGarigal, K., Cushman, S.A. & Ene, E. 2012: FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. — Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at https://www.umass.edu/landeco/research/fragstats/downloads/fragstats_downloads.html (Accessed 18 November 2015).

Muñoz, A.R., Jiménez–Valverde, A., Márquez, A.L., Moleón, M. & Real, R. 2015: Environmental favourability as a cost efficient tool to estimate carrying capacity. — Diversity and Distributions 21: 1388–1400.

Naimi, B. 2015: usdm: Uncertainty analysis for species distribution models. https://CRAN.R-project.org/package=usdm

O'brien, R.M. 2007: A caution regarding rules of thumb for variance inflation factors. — Quality and Quantity 41: 673–690.

Pacifici, K., Reich, B.J., Miller, D.A.W., Gardner, B., Stauffer, G., Singh, S., McKerrow, A. & Collazo, J.A. 2017: Integrating multiple data sources in species distribution modeling: a framework for data fusion. — Ecology 98: 840–850.

Parsa, V.A., Yavari, A. & Nejadi, A. 2016: Spatio-temporal analysis of land use/land cover pattern changes in Arasbaran Biosphere Reserve: Iran. — Modelling Earth Systems and Environment 2: 178.

Perry, T.E., & Wilson, J.S. 2010: Evaluating the vulnerability of Maine forests to wind damage. — In: Advances in threat assessment and their application to forest and rangeland management (. Pye, J.M., Rauscher, H.M., Sands, Y., Lee, D.C., Beatty, J.S.). –246. U.S. Department of Agriculture, Forest Service, Pacific Northwest and Southern Research Stations.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. 2006: Maximum entropy modeling of species geographic distributions. — Ecological Modelling 190: 231–259.

Potapov, R. L. 1985. Birds. Order Galliformes, Part 2, Family Tetraonidae. Fauna of the USSR, vol. 3. — Science Institute, Leningrad, Russia, 683 pp. (In Russian).

Potapov, R. L. 2008: On the time and routes of the penetration of the Caucasian black grouse's ancestor into the Caucasus. — Russian Journal of Ornithology 437: 1295–1307.

Putland, D. 2005: Problems of studying extinction risks. — Science 310: 1276.

QGIS Development Team 2014: QGIS Geographic Information System. — Open Source Geospatial Foundation Project. Available at http://qgis.osgeo.org (Accessed 03 May 2014).

R Development Core Team 2014: R: a Language and Environment for Statistical Computing. — R Foundation for Statistical Computing: Vienna. Available at http://www.R-project.org (Accessed 7 October 2014).

Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G. Hauenstein S., Lahoz-Monfort, J.J., Schröder, B.,Thuiller, W., Warton, D.I., Wintle, B.A., Hartig, F. & Dormann, C.F. 2017: Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. — Ecography 40: 913–929.

Scott, D.A. 1976: The Caucasian Black Grouse *Lyrurus mlokosiewiczi* in Iran. — World Pheasant Association Journal 66–68.

Shokri, M., Safaian, N., Ahmadi, M.Z.T. & Amiri, B.J. 2004: A second look on biogeographical province of Miankaleh Biosphere Reserve. — Applied Ecology and Environmental Research 2(1): 105–117.

Starling, A.E. 1992: The Ecology of black grouse *Tetrao Tetrix* in North-east England. PhD Thesis. — University of Newcastle upon Tyne. 347 pp.

Stockwell, D.R. & Peterson, A.T. 2002: Effects of sample size on accuracy of species distribution models. — Ecological Modelling 148:1–13.

Storch, I. 2007: Grouse: Status survey and conservation action plan 2006–2010. — Gland, Switzerland: IUCN and Fording bridge, UK: World Pheasant Association. 114p.

Storch, I. 2000: Grouse status survey and conservation action plan 2000–2004. — WPA/Birdlife/SSC Grouse Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK and the World Pheasant Association, Reading, UK.

Swets, J. 1988: Measuring the accuracy of diagnostic systems. — Science 240: 1285–1293.

Tashakori, G.M. 2008: Developing concepts for sustainable management of forest resources (SFM) in north western forests of Iran (Arasbaran). — University of Natural Resources and Applied Life Sciences, Vienna Department of Forest and Soil Sciences Institute of Silviculture, 389 pp.

Thuiller, W., Lafourcade, B., Engler, R. & Arau'jo, M.B. 2009: BIOMOD _ a platform for ensemble forecasting of species distributions. — Ecography 32: 369–373.

Vaughan, I.P. & Ormerod, S.J. 2005: The continuing challenges of testing species distribution models. — Journal of Applied Ecology 42: 720–730.

Valavi, R., Elith, J., Lahoz–Monfort, J.J. & Guillera–Arroita G. 2018: blockCV: an R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. — bioRxiv 357798, doi:10.1101/357798.

VanDerWal, J., Shoo, L.P., Johnson, C.N. & Williams, S.E. 2009: Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. — The American Naturalist 174: 282–291.

Vaz, S., Martin, C.S., Eastwood, P.D., Ernande, B., Carpentier, A., Meaden, G.J. & Coppin, F. 2008: Modelling species distributions using regression quantiles. — Journal of Applied Ecology 45: 204–217.

Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S. H. M., Joppa, L., Alkemade, R., Di Marco, M., Santini, L., Hoffmann, M., Maiorano, L., Pressey, R. L., Arponen, A., Boitani, L., Reside, A. E., van Vuuren, D. P. & Rondinini, C. 2016: Projecting global biodiversity indicators under future development scenarios. — Conservation Letters 9: 5–13.

Weber, M.M., Stevens, R.D., Diniz–Filho, J.A.F., & Grelle, C.E.V. 2016: Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. — Ecography (Cop) 40:817–28.

Wenger, S.J. & Olden, J.D. 2012: Assessing transferability of ecological models: an underappreciated aspect of statistical validation. — Methods in Ecology and Evolution 3: 260–267.

Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J. 2007: Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the Continental Slope. — Marine Geodesy 30: 3–35.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. & Guisan, A. 2008: Effects of sample size on the performance of species distribution models. — Diversity and Distributions 14: 763–773.

Yin, D. & He, F. 2014: A simple method for estimating species abundance from occurrence maps. — Methods in Ecology and Evolution 5: 336–343.

Zuur, A., Ieno, E.N. & Smith, G.M. 2007: Analysing Ecological Data. — Springer Science, United States. 686 p.

Online supplementary material

Fig, S1. Correlation matrix and histograms used for modelling the distribution of Caucasian grouse in Iran

Fig. S2. Contribution of environmental variables in Ensemble of Small Models.