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ORIGINAL ARTICLE

# Landscape factors affecting territory occupancy and breeding success of Egyptian Vultures on the Balkan Peninsula

**Steffen Oppel[1] · Vladimir Dobrev[2] · Volen Arkumarev[2] · Victoria Saravia[3] · Anastasios Bounas[3,5] · Aris Manolopoulos[3] · Elzbieta Kret[4] · Metodija Velevski[6] · Georgi S. Popgeorgiev[2] · Stoyan C. Nikolov[2]**

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**Abstract** Avian scavengers are declining throughout the world, and are affected by a large number of threats such as poisoning, electrocution, collision with man-made structures, direct persecution, changes in agricultural practices, landscape composition, and sanitary regulations that can reduce food availability. To formulate effective conservation strategies, it is important to quantify which of these factors has the greatest influence on demographic parameters such as territory occupancy and breeding success, and whether quantitative models can be transferred across geographic regions and political boundaries. We collated territory and nest monitoring data of the endangered Egyptian Vulture *Neophron percnopterus* in the Balkans to understand the relative influence of various factors on population declines. We monitored occupancy in 87 different territories and breeding performance of 405 territory-monitoring years between 2003 and 2015, with an overall territory occupancy rate of 69% and a mean productivity of 0.80 fledglings per occupied territory. We examined which of 48 different environmental variables were most influential in explaining variation in territory occupancy and breeding success in Bulgaria and Greece, and tested whether these models were transferrable to the Former Yugoslav Republic of Macedonia. Territory occupancy and breeding success were affected by a wide range of environmental variables, each of which had a small effect that may not be the same across political boundaries. Both models had reasonably good discriminative ability [area under the receiver-operated characteristic curve (AUC) for territory occupancy = 0.871, AUC for breeding success = 0.744], but were unsuccessful in predicting occupancy or breeding success in the external validation data set from a different country, possibly because the most influential factors vary geographically. Management focussing on a small number of environmental variables is unlikely to be effective in slowing the decline of Egyptian Vultures on the Balkan Peninsula. We recommend that in the short term the reduction of adult mortality through the enforcement of anti-poison laws, and in the long term the adoption of large-scale landscape conservation programs that retain or restore historical small-scale farming practices may benefit vultures and other biodiversity.

**Keywords** Avian scavenger · Raptor · Nesting success · Territory abandonment · Random forest · Machine learning

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✉ Steffen Oppel
steffen.oppel@rspb.org.uk

[1] RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

[2] Bulgarian Society for Protection of Birds/BirdLife Bulgaria, Yavorov Complex, bl. 71vh. 4, PO Box 50, 1111 Sofia, Bulgaria

[3] Hellenic Ornithological Society, Themistokleous 80, 10681 Athens, Greece

[4] WWF Greece, 21 Lambessi, 117 43 Athens, Greece

[5] Department of Biological Applications and Technologies, University of Ioannina, 45110 Ioannina, Greece

[6] Macedonian Museum of Natural History, Blvd. Ilinden 86, 1000 Skopje, Former Yugoslav Republic of Macedonia

## Zusammenfassung

### Der Einfluss von Landschaftsfaktoren auf die Revierbesetzung und den Bruterfolg von Schmutzgeiern auf der Balkanhalbinsel

Die Bestände von Aasfressern nehmen weltweit ab. Viele dieser Arten sind einer grossen Zahl an Bedrohungen ausgesetzt, wie zum Beispiel Giftködern, Stromschlag, Kollisionen mit industriellen Anlagen, direkter Verfolgung, Veränderungen in landwirtschaftlichen Praktiken, der Landschaftsstruktur, oder sanitären Vorschriften welche die Nahrungsverfügbarkeit beeinträchtigen können. Um effektive Schutzstrategien zu entwickeln ist es wichtig zu wissen welche dieser Gefahren den grössten Einfluss auf populationsdynamische Parameter wie die Revierbesetzung und den Bruterfolg haben. Wir stellten Revier- und Nest-Monitoring Daten des bedrohten Schmutzgeiers *Neophron percnopterus* auf dem Balkan zusammen, um den relative Einfluss diverser Faktoren auf den Rückgang dieser Art zu untersuchen. Wir beobachteten die Revierbesetzung in 87 verschiedenen Brutrevieren und den Bruterfolg von 405 Bruten zwischen 2003 und 2015 mit einer Revierbesetzungsrate von 69% und einer durchschnittlichen Produktivität von 0,80 flüggen Jungvögeln pro besetztem Revier. Wir untersuchten welche von 48 verschiedenen Umweltvariablen den grössten Einfluss auf Revierbesetzung und Bruterfolg in Bulgarien und Griechenland hatten, und überprüften ob diese Modelle in die ehemalige jugoslawische Republik Mazedonien übertragbar waren. Revierbesetzung und Bruterfolg wurden durch eine breite Palette von ökologischen Faktoren beeinflusst, von denen jede einzelne nur eine geringe Wirkung hatte die nicht die gleiche über politische Grenzen hinweg sein muss. Beide Modelle hatten einen recht guten Klassifizierungserfolg (AUC für Revierbesetzung = 0871, AUC für Bruterfolg = 0744), konnten aber die Revierbesetzung oder den Bruterfolg in einem externen Validierungsdatensatz aus einem anderen Land nicht erfolgreich vorhersagen, vermutlich weil die wichtigsten Faktoren räumlich variieren. Artenschutzmassnahmen die sich auf eine kleine Anzahl ökologischer Faktoren konzentrieren können den weiteren Rückgang des Schmutzgeiers auf dem Balkan wahrscheinlich nicht aufhalten. Wir empfehlen daher umgehend die Sterberate von Altvögeln zu senken indem bestehende Gesetze, welche die Anwendung von Giftködern verbieten, durchgesetzt werden. Längerfristig könnte die Einführung von grossflächigen Landschaftspflegeprogrammen, welche historische kleinräumige landwirtschaftliche Praktiken erhalten oder wiederherstellen, positive Auswirkungen für Geier und andere Artenvielfalt haben.


## Introduction

Many raptor species around the world are declining, and avian scavengers like vultures are among the most threatened raptor species (Chaudhary et al. 2012; Ogada et al. 2015; Buechley and Şekercioğlu 2016). Many different threats exist for vultures around the world, ranging from poisoning by veterinary drugs (Green et al. 2004; Oaks et al. 2004; Galligan et al. 2014), poison bait targeted at livestock predators (Hernández and Margalida 2008, 2009; Mateo-Tomás et al. 2012), electrocution at electrical infrastructure (Donázar et al. 2002; Boshoff et al. 2011; Angelov et al. 2013), collision with wind turbines (Carrete et al. 2009; de Lucas et al. 2012), to direct persecution (Thiollay 2006; Margalida et al. 2008). In addition to threats causing direct mortality of birds, changes in agricultural practices, landscape composition, and sanitary regulations are known to have more subtle effects on vulture populations, for example by altering food availability and thus leading to lower reproductive output or lower survival probability (Carrete et al. 2007; Donázar et al. 2010; Margalida et al. 2014). Understanding the relative influence of these threats on declining populations is important to develop effective conservation management actions.

Among the four vulture species that breed in Europe, the Egyptian Vulture (*Neophron percnopterus*) is the smallest species with the most precarious conservation status. While populations in western Europe are currently stable or increasing (García-Ripollés and López-López 2006; Lieury et al. 2015; Tauler et al. 2015), the Egyptian Vulture population in Eastern Europe has been declining at a rate of ~7% per year for several decades (Velevski et al. 2015). Territory abandonment and declines in productivity in Spain, which holds the vast majority of the European population, have been related to changes in diet availability and diversity (Margalida et al. 2012), poison use (Sanz-Aguilar et al. 2015), and a complex mixture of various landscape factors affecting habitat suitability (Carrete et al. 2007; Hernández and Margalida 2009; Olea and Mateo-Tomás 2011). For the Balkan population, however, the causes of population declines are still speculative and considerable uncertainty exists as to which conservation management actions might be effective to halt population declines (Grubač et al. 2014; Velevski et al. 2014; Oppel et al. 2016). Although several sources of mortality have been documented for Egyptian Vultures from the Balkans, for example electrocution and natural mortality on migration (Angelov et al. 2013; Oppel et al. 2015), direct persecution on wintering areas (Arkumarev et al. 2014; Oppel et al. 2015), poisoning on breeding areas (Skartsi et al. 2014; Kret et al. 2016; Saravia et al. 2016), and the collection of adult birds and eggs by poachers (Bulgarian

Society for the Protection of Birds, unpublished data), there has been no comprehensive study in the Balkans to understand the factors affecting which territories are abandoned and how productivity is affected. Formulating effective conservation management strategies requires the key factors to be identified, or management to be based on studies from other countries.

Establishing conservation management in the Balkans based on the knowledge that has been accumulated on Egyptian Vulture threats in Spain (Carrete et al. 2007; Mateo-Tomás and Olea 2010; López-López et al. 2014; Sanz-Aguilar et al. 2015) would require that statistical models explaining variation in occupancy and breeding success can be transferred from one country to another (Hothorn et al. 2011; Zurell et al. 2012; Torres et al. 2015). Here we evaluate whether factors affecting occupancy and breeding success of Egyptian Vultures in two countries in the Balkans (Bulgaria and Greece) can be used to explain the same demographic parameters in a neighbouring country [the Former Yugoslav Republic (FYR) of Macedonia]. This work therefore provides a region-specific analysis of the factors affecting a declining population of a globally endangered species, and formally assesses whether regional assessments of threatening factors can be safely transferred across different countries.

We collated data on Egyptian Vulture territory occupancy and breeding success over 13 years from three countries, and compiled 48 different environmental variables that may plausibly affect Vulture distribution in the region. We used a powerful machine-learning algorithm to explore whether any of a wide range of landscape variables had a sufficiently large effect on territory occupancy or breeding success to warrant conservation management in Bulgaria and Greece, and whether these variables could reliably predict occupancy and breeding success in the FYR of Macedonia. This study is the first comprehensive analysis of a large number of potential factors affecting the conservation status of Egyptian Vultures in eastern Europe, and provides a thorough assessment of the generality of the analytical models on which inference and management recommendations will be based.

## Methods

### Nest monitoring

We monitored Egyptian Vulture nests in Bulgaria every year between 2003 and 2015, and in Greece between 2010 and 2015. We visited each breeding territory multiple times per breeding season to confirm if the territory was occupied, and to count the number of raised fledglings (Velevski et al. 2015; Dobrev et al. 2016). A territory was considered occupied if a pair or a single bird was observed with territorial behaviour at the beginning of the breeding season (March/April). Territorial behaviour included courtship flights, aggressive interactions with other birds, or nest-building behaviour. All territories were visited again in May to confirm which of the pairs were breeding, in June and July to confirm the number of hatched chicks, and in August to confirm the number of fledged juveniles. Survey efforts were generally many hours in duration (Oppel et al. 2016), and because multiple surveys were carried out in each territory in each year we do not account for imperfect detection in our analysis because the probability of missing an occupied territory would have been small (Olea and Mateo-Tomás 2011).

Egyptian Vultures can lay two eggs and raise two fledglings. However, the processes determining whether a pair raises one or two fledglings may be fundamentally different from the processes determining whether a pair raises any fledglings or none, and preliminary explorations indicated that none of our environmental variables were able to accurately differentiate between pairs raising one or two fledglings. Hence, for the purpose of this analysis we reduced the data on the number of fledglings to 'breeding success', which considered pairs successful if they raised any fledglings, and unsuccessful if not. We measure breeding success as the proportion of all territories occupied by two adult birds that resulted in at least one fledgling, which accounts for incomplete breeding propensity.

### Environmental variables

Considerable changes in land use, livestock, animal and waste disposal practices have occurred in Bulgaria and Greece over the past decades following the abandonment of socialist farming structures and the adoption of EU regulations, and it is plausible that such changes may have affected the suitability of areas for breeding vultures (Carrete et al. 2007, 2009; Kamp et al. 2011), or affected available food with consequences for productivity (Margalida et al. 2012). We therefore collected information on variables influencing the physical environment, landscape composition, food availability, human disturbance, and intra- and interspecific biological interactions for each territory from a variety of remote sensing and local resources (Table 1). To characterise the environmental conditions of Egyptian Vulture territories, we used a 5-km radius around the nest (Mateo-Tomás and Olea 2015), and we refer to this circular area as 'territory' for the purpose of this analysis. A larger radius, which may have been warranted given that Egyptian Vultures can travel >20 km during foraging excursions and can have fairly large home ranges (Carrete et al. 2007; López-López et al. 2014), was considered impractical for our study due to the large

**Table 1** List and description of 48 environmental predictor variables used to explain variation in Egyptian Vulture territory occupancy and breeding success in Bulgaria and Greece between 2003 and 2015

| Category | Variable | Description | Importance for territory occupancy | AUC reduction territory occupancy | Importance for breeding success | AUC reduction breeding success |
|---|---|---|---|---|---|---|
| Food availability | Distance_food_source | Distance (km) to the nearest reliable food source | 88.1 | 0.024 | 33.7 | 0.005 |
| | n_food_source | Number of reliable food sources in a 5-km radius | 60.4 | 0.016 | 29.2 | 0.004 |
| | n_livestock_owner | Number of livestock owners in a 5-km radius | 21.2 | 0.006 | 0.0 | 0.000 |
| | Number_livestock_2 km | Number of livestock in a 2-km radius | 30.6 | 0.008 | 37.6 | 0.005 |
| | Number_livestock_5 km | Number of livestock in a 5-km radius | 31.5 | 0.009 | 17.9 | 0.003 |
| | Number_poultry_2 km | Number of poultry in a 2-km radius | 2.3 | 0.001 | 5.9 | 0.001 |
| | Number_poultry_5 km | Number of poultry in a 5-km radius | 1.7 | 0.000 | 37.4 | 0.005 |
| | Type_food_source | Type of nearest reliable food source (e.g. slaughterhouse, feeding station, rubbish dump, etc.) | 35.5 | 0.010 | 17.7 | 0.003 |
| Human disturbance | Length_paved 5 km | Total length of paved roads within a 5-km radius around the nest | 24.7 | 0.007 | 36.0 | 0.005 |
| | Length_unpaved 5 km | Total length of unpaved roads within a 5-km radius around the nest | 12.9 | 0.003 | 18.7 | 0.003 |
| | n_villages | Number of villages within a 5-km radius around the nest | 28.1 | 0.008 | 95.1 | 0.013 |
| | n_wind_turb | Number of wind turbines in a 20-km radius | 6.1 | 0.002 | 6.1 | 0.001 |
| | Number_of_people_in_nearest_village | Number of human inhabitants in the nearest village | 8.8 | 0.002 | 11.5 | 0.002 |
| | Poisoning_5 km | Number of known poisoning incidents reported in the past 10 years within a 5-km radius | 14.7 | 0.004 | 5.6 | 0.001 |
| | Total_people_5 km | Total number of human inhabitants within a 5-km radius around the nest | 11.0 | 0.003 | 19.8 | 0.003 |
| Intra- and interspecific interactions | Active_nests_5 km | Number of active Egyptian Vulture nests in a 5-km radius | 24.3 | 0.007 | 19.5 | 0.003 |
| | Alternative_nests | Total number of alternative nest sites used by an Egyptian Vulture in the same territory in other years | 70.8 | 0.019 | 38.8 | 0.006 |
| | EAOW | Presence of an active Eagle Owl nest within a 5-km radius | 10.1 | 0.003 | 6.9 | 0.001 |
| | Griffon | Presence of an active Griffon Vulture nest within a 5-km radius | 10.0 | 0.003 | 19.3 | 0.003 |
| | PEFA | Presence of an active Peregrine Falcon nest within a 5-km radius | 23.5 | 0.006 | 38.3 | 0.005 |
| | Raven | Presence of an active Raven nest within a 5-km radius | 38.5 | 0.010 | 83.0 | 0.012 |
| Land use | Agriculture_5 km | Percent cover of agriculture within a 5-km radius around the nest | 20.7 | 0.006 | 30.5 | 0.004 |
| | Edge_length_5 km | Total length of habitat edges within a 5-km radius around the nest | 11.5 | 0.003 | 61.9 | 0.009 |
| | Grasslands_5 km | Percent cover of grasslands within a 5-km radius around the nest | 82.1 | 0.022 | 13.3 | 0.002 |
| | Habitat_diversity_5 km | Shannon–Wiener index of habitat diversity within a 5-km radius around the nest | 17.5 | 0.005 | 21.4 | 0.003 |

**Table 1** continued

| Category | Variable | Description | Importance for territory occupancy | AUC reduction territory occupancy | Importance for breeding success | AUC reduction breeding success |
|---|---|---|---|---|---|---|
| | Habitat_patches_5 km | Total number of habitat patches within a 5-km radius around the nest | 19.5 | 0.005 | 24.2 | 0.003 |
| | Land_cover_classes_5 km | Number of different coordination of information on the environment (CORINE) land cover classes within a 5-km radius around the nest | 11.2 | 0.003 | 24.5 | 0.003 |
| | Open_ground_5 km | Percent cover of unvegetated soil within a 5-km radius around the nest | 8.0 | 0.002 | 9.2 | 0.001 |
| | Shrubland_5 km | Percent cover of shrub and intermediate succession vegetation within a 5-km radius around the nest | 16.6 | 0.005 | 16.8 | 0.002 |
| | Urban_5 km | Percent cover of urban habitats within a 5-km radius around the nest | 23.6 | 0.006 | 15.8 | 0.002 |
| | Woodland_5 km | Percent cover of forest and tree plantations within a 5-km radius around the nest | 26.1 | 0.007 | 35.4 | 0.005 |
| Physical environment | Cliff_length | Horizontal length of the cliff in which the nest is located (m) | 21.5 | 0.006 | 18.7 | 0.003 |
| | Cliff_orientation | Compass direction into which the cliff faces | 12.7 | 0.003 | 44.1 | 0.006 |
| | Height_cliff_above_nest | Vertical distance from the nest to the top of the cliff (m) | Not included | | 69.2 | 0.010 |
| | Height_nest | Vertical distance from the base of the cliff to the nest (m) | Not included | | 24.0 | 0.003 |
| | Latitude | Latitude of the nest | 31.8 | 0.009 | 13.9 | 0.002 |
| | Length_water5 km | Total length of water courses within a 5-km radius around the nest | 12.0 | 0.003 | 22.0 | 0.003 |
| | Longitude | Longitude of the nest | 28.6 | 0.008 | 45.0 | 0.006 |
| | Max_height_cliff | Maximum height of the nesting cliff (m) | 78.9 | 0.021 | 33.9 | 0.005 |
| | Mean_altitude_terr_5 km | Mean elevation of the territory (m a.s.l.) | 18.4 | 0.005 | 39.4 | 0.006 |
| | Mean_slope_5 km | Mean slope of the terrain across the territory | 19.0 | 0.005 | 43.1 | 0.006 |
| | Nest_orientation | Compass direction into which the nest entrance faces | Not included | | 20.3 | 0.003 |
| | Nest_type | Nest type: cave, ledge, small hole | Not included | | 15.9 | 0.002 |
| | Periphery | Whether the nest was located in the population core (Eastern Rhodopes) or in the periphery (elsewhere in Bulgaria or Greece) | 100.0 | 0.027 | 7.7 | 0.001 |
| | PoolRegion1 | Whether the nest was located in one of five regional sub-populations | 48.5 | 0.013 | Not included | |
| | PPI_5 km | Primary productivity index derived from the normalised difference vegetation index within a 5-km radius | 26.3 | 0.007 | 46.3 | 0.007 |
| | SD_altitude_terr_5 km | Topographical ruggedness expressed as SD of mean elevation in the territory | 23.4 | 0.006 | 100.0 | 0.014 |
| | SD_slope_5 km | Topographical ruggedness expressed as SD of mean slope of the territory | 22.6 | 0.006 | 61.7 | 0.009 |
| | Water_5 km | Percent cover of open water bodies within a 5-km radius around the nest | 17.3 | 0.005 | 59.4 | 0.008 |

Relative importance and area under the receiver-operated characteristic curve (*AUC*) reduction after permutation are derived from a conditional inference random forest model

overlap in territories and the effort required in obtaining relevant data (Table 1) across such spatial scales.

We first measured several physical variables that have been associated with territory occupancy or nest success in past studies (Liberatori and Penteriani 2001; Carrete et al. 2007; Olea and Mateo-Tomás 2011), such as cliff height, exposition, and the precise location of the nest on the cliff (Table 1). Cliff height was measured using a tape measure attached to a rope connecting the top and the bottom of the cliff in a straight line. We also mapped the location of all reliable food sources, such as slaughterhouses, rubbish dumps, vulture restaurants, chicken farms, and other places with regular food available for vultures using handheld global positioning system devices or satellite images. Because wind turbines can cause mortality of adults and lead to nest or territory abandonment (Carrete et al. 2009), we also recorded the location of all wind turbines in the study area. We then used a geographic information system (ArcGIS 10; ESRI, Redlands, CA) to measure the distance from vulture nests to food sources and count the number of food sources and wind turbines within each territory.

We used monitoring data of Egyptian Vultures and other raptors to create indicator variables reflecting the potential for intra- and interspecific interactions. Specifically, we used the monitoring data to assess the number of alternative nesting sites in the same territory as an index of territory quality (Newton 1994, 2010), because alternative sites allow birds to establish nests at sites with less disturbance (Carlon 1998). We also determined whether an active Eurasian Griffon Vulture *Gyps fulvus*, Peregrine Falcon *Falco peregrinus*, Eagle Owl *Bubo bubo*, or Common Raven *Corax corax* nest existed within the territory. These species were chosen because they are known to interact with Egyptian Vultures and may affect occupancy or breeding success (Margalida et al. 2003; Bertran and Margalida 2004; Brambilla et al. 2004).

Relief variables such as elevation, slope, and ruggedness of the landscape (expressed as the SD of elevation over the territory) were derived from a digital elevation model with 30-m resolution for Bulgaria (European Environment Agency 2013) and for Greece (obtained from the Hellenic Mapping and Cadastral Organization).

Land use was expressed as the proportion of the territory that was covered in major land use categories, such as grassland, agricultural areas, forest, shrubland and water (Table 1). The land use coverage was calculated from global remote sensing products at a resolution of 100 m [Coordination of Information on the Environment (CORINE) land cover 2012, available at: http://land.copernicus.eu/pan-european/corine-land-cover/clc-2012]. In addition to the proportional coverage of certain land use types, we also used the CORINE land cover data to calculate metrics characterising the patchiness of the landscape, such as the number of distinct land use patches, the total length of habitat edges, and a habitat diversity index based on the number and extent of different habitat patches (Rotenberry and Wiens 1980; Nikolov 2010; Cord and Rödder 2011). We further considered the primary productivity index, a metric that uses the maximum monthly values of the normalised difference vegetation index (NDVI) within each territory as a general metric that may reflect food availability for opportunistic raptors (Seoane et al. 2003; Carrete et al. 2007). This index was derived from monthly averages of NDVI obtained from remote sensing (TERRA-MODIS, http://reverb.echo.nasa.gov). Basic geographic variables such as the length of the road network were extracted from standard topographic maps (Table 1).

We also contacted relevant authorities to obtain variables relating to food availability and human pressures within each territory. The number of livestock as a measure of food abundance was obtained from official records from the Bulgarian Ministry of Agriculture and Foods and the Greek Payment Authority of Common Agricultural Policy Aid Schemes supervised by the Hellenic Ministry of Rural Development and Foods (Table 1). The number of human inhabitants and human settlements was provided by the National Statistics Institute of Bulgaria and the Hellenic Statistical Authority of Greece to quantify the amount of human disturbance, an important factor in the distribution of vultures (Grubb and King 1991; Richardson and Miller 1997; Krüger et al. 2015). Since poisoning is a potentially important driver of population declines in the Balkans (Velevski et al. 2015; Oppel et al. 2016; Saravia et al. 2016), we obtained official records of all poisoning incidents in the last 10 years in the study area (Skartsi et al. 2014), but we acknowledge that these records may not capture all illegal uses of poison that may affect vultures.

## Model construction and assessment of variable importance

We analysed the influence of environmental variables on three demographic processes that are relevant for conservation: whether formerly occupied Egyptian Vulture territories were abandoned at any time and were no longer occupied between 2011 and 2015 (hereafter referred to as 'territory abandonment'); (2) whether territories were occupied on an annual basis (hereafter referred to as 'occupancy'); and (3) whether pairs bred successfully given that a pair occupied a territory (hereafter referred to as 'breeding success', see above). Our measure of breeding success encompasses pairs that may not have initiated a nesting attempt, and is therefore an overall metric that accounts for incomplete breeding propensity.

Because of the large number of potential direct and indirect threats that may affect vulture presence and breeding success, and the fact that some of these variables may be correlated, we chose an analytical approach that can accurately identify the relative importance of variables under these conditions (Cutler et al. 2007; Hochachka et al. 2007; Strobl et al. 2008). We used a powerful random forest algorithm to relate occupancy and breeding success to the landscape and nest variables to identify which variables had the greatest influence and determine the direction and size of effects. A random forest is a machine learning algorithm based on ensembles of regression trees that can accommodate a large number of predictor variables and yields highly accurate predictions (Breiman 2001; Cutler et al. 2007; Hochachka et al. 2007), and this approach has recently been used to model the spatial distribution of vultures elsewhere (Mateo-Tomás and Olea 2015; Milanesi et al. 2016). Because a random forest does not assume that data are independent or follow a specified statistical distribution, the approach was useful to analyse repeated observations from the same territories, where pseudoreplication is avoided by specifying the re-sampling structure for internal cross-validation (Karpievitch et al. 2009; Buston and Elith 2011). We considered the territory as the unit of replication in all analyses, rather than individual nest sites, because pairs can use different nest sites within the same territory in different years.

We used a random forest model based on a conditional inference framework to account for correlated predictors and

**Table 2** Summary of sample sizes and reproductive performance of Egyptian Vultures in Bulgaria and Greece between 2003–2015

| | Bulgaria | | Greece | |
|---|---|---|---|---|
| Territory-monitoring years[a] (*n*) | 523 | | 297 | |
| Territory-monitoring years occupied by two adults (*n*) | 349 | 66.7% | 180 | 60.6% |
| Occupied territory-monitoring years with information about breeding (*n*) | 349 | | 56 | |
| Occupied territory-monitoring years with breeding (*n*) | 264 | 75.6% | 47 | 83.9% |
| Occupied territory-monitoring years with successful breeding (*n*) | 223 | 84.5% | 27 | 57.4% |
| Successfully breeding territory-monitoring years raising two young (*n*) | 66 | 29.6% | 8 | 29.6% |
| Productivity[b] | 0.83 ($n = 349$) | | 0.63 ($n = 56$) | |
| Fledging rate[c] | 1.30 ($n = 223$) | | 1.30 ($n = 27$) | |

[a] Annual observation of Egyptian Vultures in one of 87 physical territories

[b] Average number of fledglings produced across all territory-monitoring years occupied by two birds

[c] Average number of fledglings produced by successfully breeding pairs

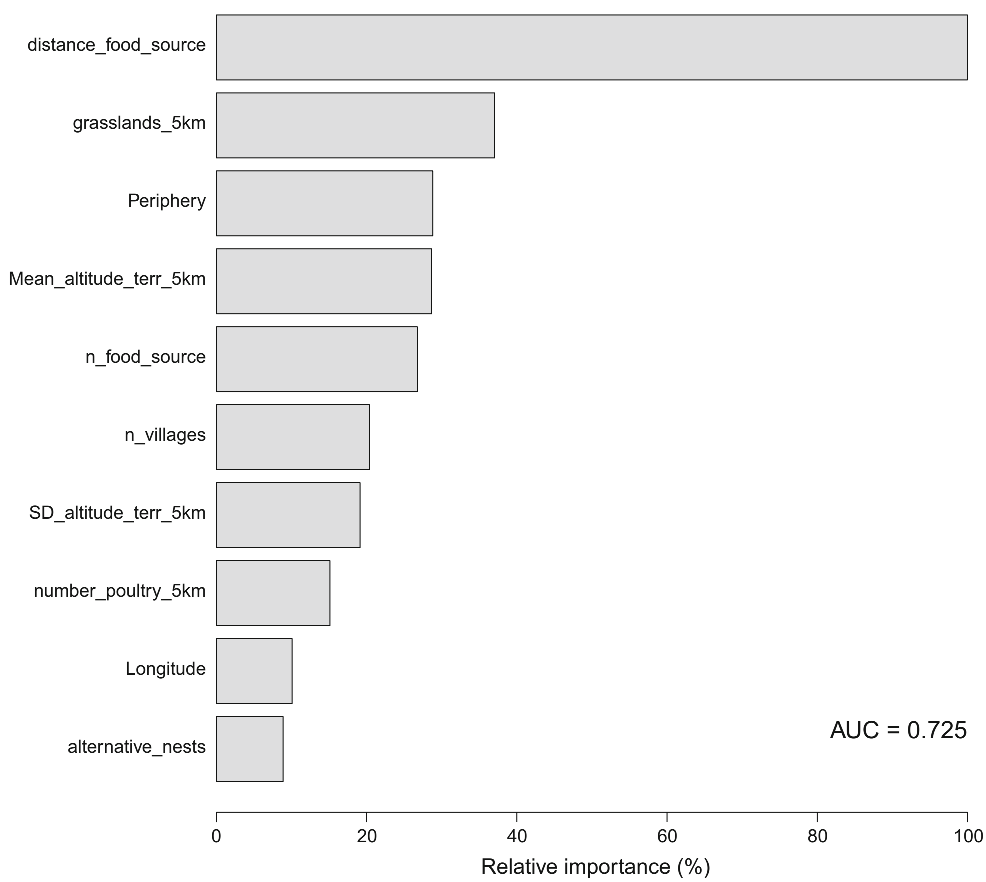


**Fig. 1** Relative variable importance of the ten most important predictor variables influencing whether Egyptian Vulture territories on the Balkan Peninsula were abandoned between 2003 and 2015. Variable importance was derived from a permutation procedure quantifying the reduction in discriminative ability of a random forest model. *AUC* Area under the receiver-operated characteristic curve

for missing data (Hothorn et al. 2006b; Strobl et al. 2008; Hapfelmeier et al. 2012). We fitted this model in a regression framework with the R package party (Hothorn et al. 2006a) and manually specified the internal cross-validation structure to ensure that observations from the same territories were not simultaneously used to fit and evaluate trees in the forest, which is equivalent to incorporating a territory-specific random effect in a linear modelling framework (Buston and Elith 2011). To evaluate the discriminatory ability of the model we used the area under the receiver-operated characteristic curve (AUC) of internally cross-validated data calculated with the package Presence Absence (European Environment Agency (2013) in R 3.2.5 (R Core Team 2016).

To assess which variables had the greatest influence on our response variables, we used a permutation procedure that assesses the loss in predictive accuracy (based on AUC) of the random forest model after randomly permuting a given variable (Strobl et al. 2007; Janitza et al. 2013; Hapfelmeier et al. 2014). We implemented this assessment using the R function varimpAUC with 100 permutations per variable and present results as relative variable importance, with the most important variable (greatest reduction in AUC after permutation) assigned a value of 100%.

Because a random forest is a non-parametric algorithm, the direction and size of effects by given variables cannot be expressed with numeric parameter estimates. For the most important variables we therefore produced partial dependence plots which show the direction and magnitude of the effect of an environmental variable on territory abandonment, annual occupancy, and breeding success after accounting for the effects of all other variables in the model (Cutler et al. 2007; Strobl et al. 2008).

### Model evaluation with independent data from FYR of Macedonia

While machine learning algorithms can overcome many shortcomings of traditional regression analyses, they may overfit the data leading to poor transferability of models and limited predictive ability to data not used for model construction (Oppel et al. 2012; Zurell et al. 2012; Torres et al. 2015). The reliability of complex models to capture broad ecological patterns should therefore be assessed using external validation data from another region (Elith and Leathwick 2009; Hothorn et al. 2011). We collated similar data as in Bulgaria and Greece for 585 territory-monitoring years from 65 territories relating to occupancy and 161 breeding attempts from 30 territories over the time frame from 2006 to 2012 in the FYR of Macedonia (Grubač et al. 2014), and predicted the occupancy and breeding success in those territories with the models constructed from data in Bulgaria and Greece. The FYR of Macedonia is geographically adjacent to Bulgaria and Greece, but does not belong to the EU and is therefore not subject to EU-wide agricultural and nature conservation policies. The validation using independent data from another country provides a true test of the generality of the models used to explain variation in occupancy and breeding success.

## Results

We used data from 87 different territories that were monitored in up to 13 years between 2003 and 2015, resulting in 820 territory-monitoring years for which reliable information on the occupancy status was available. Because not all monitoring efforts were sufficiently intensive to assess reproductive output, our assessment of factors influencing breeding success was based on 405 territory-monitoring years from 64 different territories that were occupied by two adult birds (Table 2).

Of the 87 originally occupied territories that were monitored during our study, 35 had been abandoned by

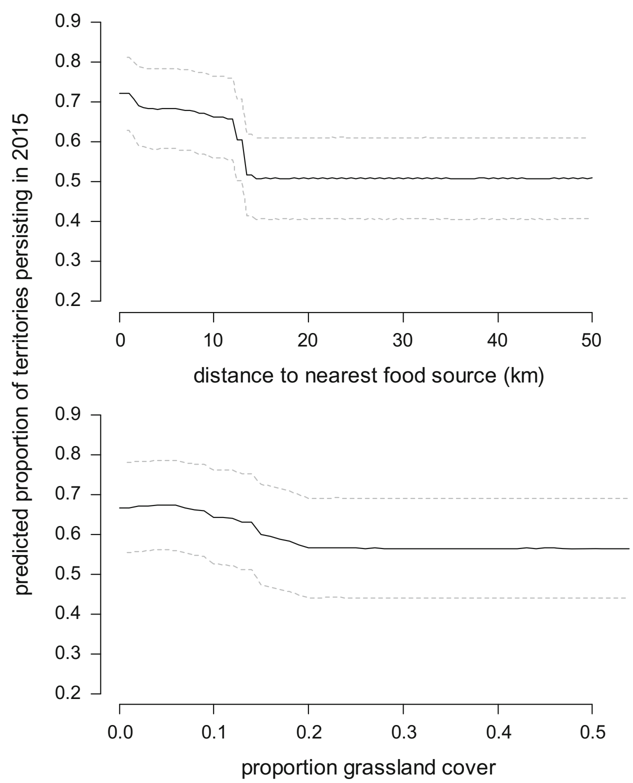


**Fig. 2** Relationships between the two most influential environmental variables and the proportion of Egyptian Vulture territories that were predicted to persist on the Balkan Peninsula between 2003 and 2015 if all other variables were held at their actual values. *Dashed grey lines* indicate the SD around the predicted mean

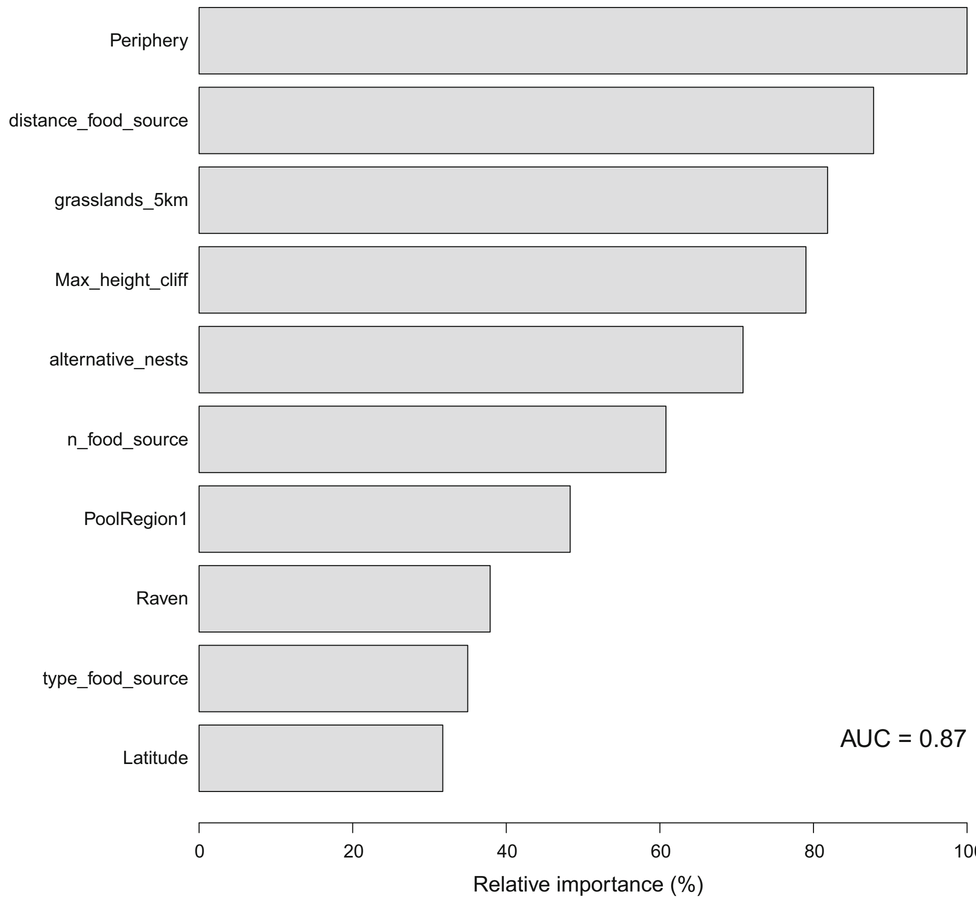


**Fig. 3** Relative variable importance of the ten most important predictor variables influencing the annual occupancy of Egyptian Vulture territories on the Balkan Peninsula between 2003 and 2015. Variable importance was derived from a permutation procedure quantifying the reduction in discriminative ability of a random forest model. *AUC* Area under the receiver-operated characteristic curve

2015 (40%). The model examining the influence of environmental variables on territory abandonment had reasonable discriminative ability (AUC = 0.725 ± 0.058), and indicated that territories that were closer to a reliable food source and with a lower proportion of grassland within 5 km of the nest were more likely to have persisted until 2015 (Figs. 1, 2).

Of the 820 territory-monitoring years available during the study period, 529 (64.5%) found the territory occupied by two birds, and a further 37 (4.5%) indicated that the territory was occupied by only one bird. Annual occupancy ranged from 100% of all monitored territories in 2003 ($n = 17$) to 47% of all monitored territories in 2013 ($n = 86$). The model examining the influence of environmental variables on annual occupancy had good discriminative ability (AUC = 0.871 ± 0.013), and indicated that variables relating to food availability, geographic structure, and suitable nest locations were the most influential in distinguishing between occupied and unoccupied territories (Fig. 3). Eleven variables achieved a relative variable importance of >30%, but no single variable reduced the discriminative ability of the model by >0.03 AUC units when randomly permuted (Table 1). Consequently, the change in the predicted probability of occupancy was relatively small across the scale of even the most important variables (Fig. 4).

Despite the successful discrimination of training data in Bulgaria and Greece, the random forest model was unable to accurately predict the occupancy of Egyptian Vulture territories in the FYR of Macedonia (AUC = 0.519 ± 0.021).

Of the 529 territory-monitoring years that were occupied by two birds, 405 (76.6%) were monitored with sufficient effort to determine breeding propensity and success. No breeding attempt was discovered in 94 occupied territories (23.2%; Table 2), and breeding success ranged from a minimum of 47.4% (in 2005) to a maximum of 76.5% (in 2008). Overall productivity (number of fledglings per occupied territory) was 0.80 (±0.73 SD), and the average number of fledglings per successful pair was 1.30 (± 0.46 SD) and ranged from 1.19 (in 2010) to 1.50 (in 2006; Table 2). The model examining the influence of environmental variables on breeding success had a reasonable discriminative ability (AUC = 0.744 ± 0.025). The variables with the greatest explanatory power related to topography, disturbance, and landscape structure (Fig. 5; Table 1). Similar to the model describing occupancy, seven variables achieved a relative variable importance of >50%,

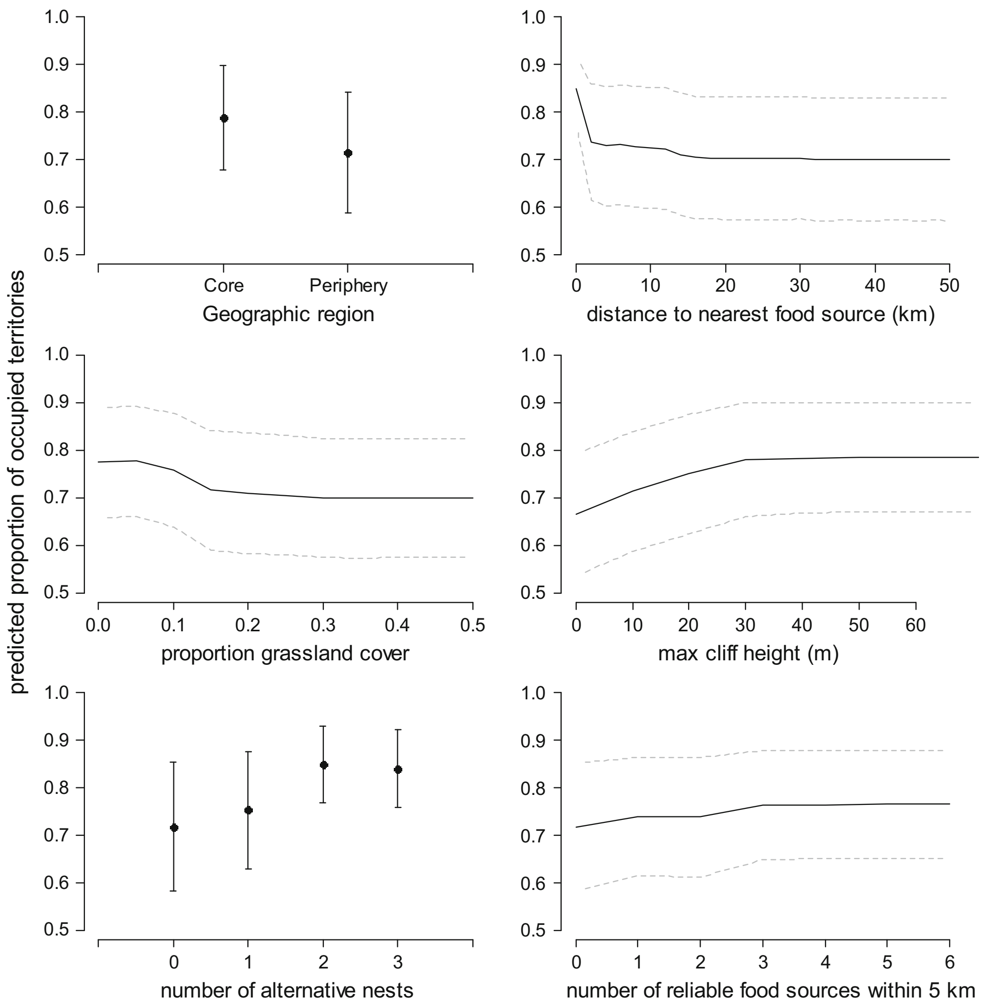


**Fig. 4** Relationships between the six most influential environmental variables and the proportion of Egyptian Vulture territories that were predicted to be occupied on the Balkan Peninsula between 2003 and 2015 if all other variables were held at their actual values. *Dashed grey lines* indicate the SD around the predicted mean

but no single variable reduced the discriminative ability of the model by >0.02 AUC units when randomly permuted (Table 1). Consequently, the increase in predicted breeding success was relatively small across the scale of the most important variables (Fig. 6).

Similar to the model determining occupancy, the random forest model predicting breeding success based on data in Bulgaria and Greece had limited ability to predict breeding success of Egyptian Vultures in the FYR of Macedonia (AUC $= 0.620 \pm 0.048$).

## Discussion

Territory occupancy and breeding success of Egyptian Vultures on the Balkan Peninsula are affected by a wide range of environmental variables relating to food availability, disturbance, topography, and suitable cliffs with ledges or cavities for nesting, each of which has a small effect that may not be the same across political boundaries. As a consequence, simple approaches to modify habitats or manage resources based on a small number of environmental variables are unlikely to be effective conservation management approaches that will considerably slow the decline of the species.

During the 13 years of monitoring covered here, at least 40% of Egyptian Vulture territories were abandoned, despite reproductive output being generally similar to stable or increasing western Palaearctic populations (García-Ripollés and López-López 2006; Lieury et al. 2015; Tauler et al. 2015). We found that territory abandonment was only partially predictable and that territories closer to a core population in the Eastern Rhodopes and within close proximity to a reliable food source were the most likely territories to persist. The lack of very strong drivers affecting territory abandonment and annual

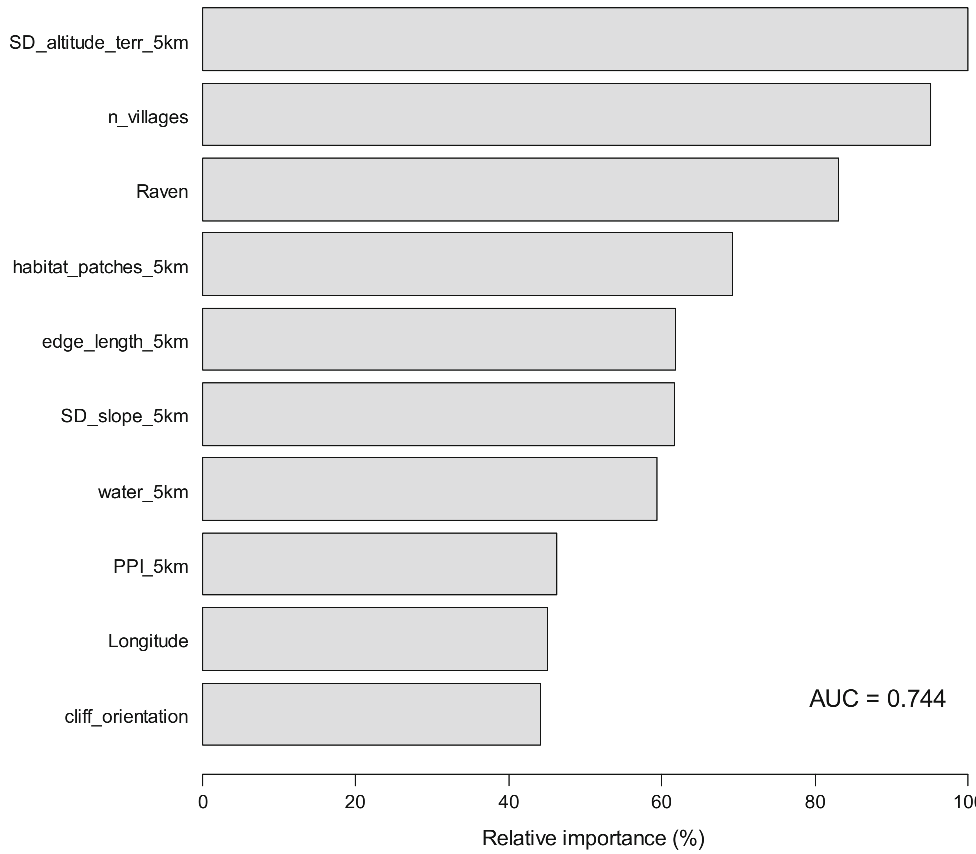


**Fig. 5** Relative variable importance of the ten most important predictor variables influencing the breeding success of Egyptian Vultures on the Balkan Peninsula between 2003 and 2015. Variable importance was derived from a permutation procedure quantifying the reduction in discriminative ability of a random forest model. *AUC* Area under the receiver-operated characteristic curve

occupancy may indicate that population declines could be caused by stochastic adult and juvenile mortality that is poorly captured by the available environmental variables. Egyptian Vultures may suffer considerable mortality during migration (Grande et al. 2009; Angelov et al. 2013; Oppel et al. 2015), and some territory abandonment could be a consequence of random mortality outside the breeding season. Alternatively, territory abandonment could also result from mortality during the breeding season, for example through the illegal use of poison (Skartsi et al. 2014; Oppel et al. 2016), the direct persecution of raptors, or accidental mortality in wind turbines (Carrete et al. 2009). Although numerous Egyptian Vultures have been found poisoned in our study area (Saravia et al. 2016), the number of publicly reported poisoning incidents in a vulture territory had very low explanatory power in our analysis (Table 1). Because the use of poison to kill wildlife is illegal, the knowledge about the frequency of such events is poor and the number of reported incidents may not be an adequate index describing the exposure risk to vultures. Nonetheless, the poisoning problem is pervasive: for example, between 1990 and 2010 there were >8000 reported incidents that killed at least 366 Egyptian Vultures in Spain (Margalida 2012). Given that our analysis did not identify any outstanding environmental factors that could be managed to improve the conservation status of Egyptian Vultures, we recommend that addressing the issue of illegal poisoning should be the highest priority for governments and conservation managers (Margalida et al. 2013; Sanz-Aguilar et al. 2015; Oppel et al. 2016).

Territory abandonment in Egyptian Vultures has previously been described as a consequence of various landscape factors (Carrete et al. 2007; Hernández and Margalida 2009; Olea and Mateo-Tomás 2011; Mateo-Tomás and Olea 2015), and our analysis supports these general findings. We found that the most influential variables affecting annual occupancy related to a territory's location in the core area of distribution (Velevski et al. 2015), and to food availability and the availability of suitable nesting sites. The distance to the nearest reliable food source and the number of reliable food sources within a 5-km radius both had a positive influence on occupancy, because they increase availability and accessibility of food and may thus favour the selection of territories (Margalida et al. 2007; López-López et al. 2014). Territories were also more likely to be occupied if they contained higher cliffs with a larger number of alternative nest sites, which reflects the availability of suitable nesting substrate for individual birds to select (Liberatori and Penteriani 2001; Donázar et al. 2002; Mateo-Tomás et al. 2010). However, the distance and number of reliable food sources may be effects

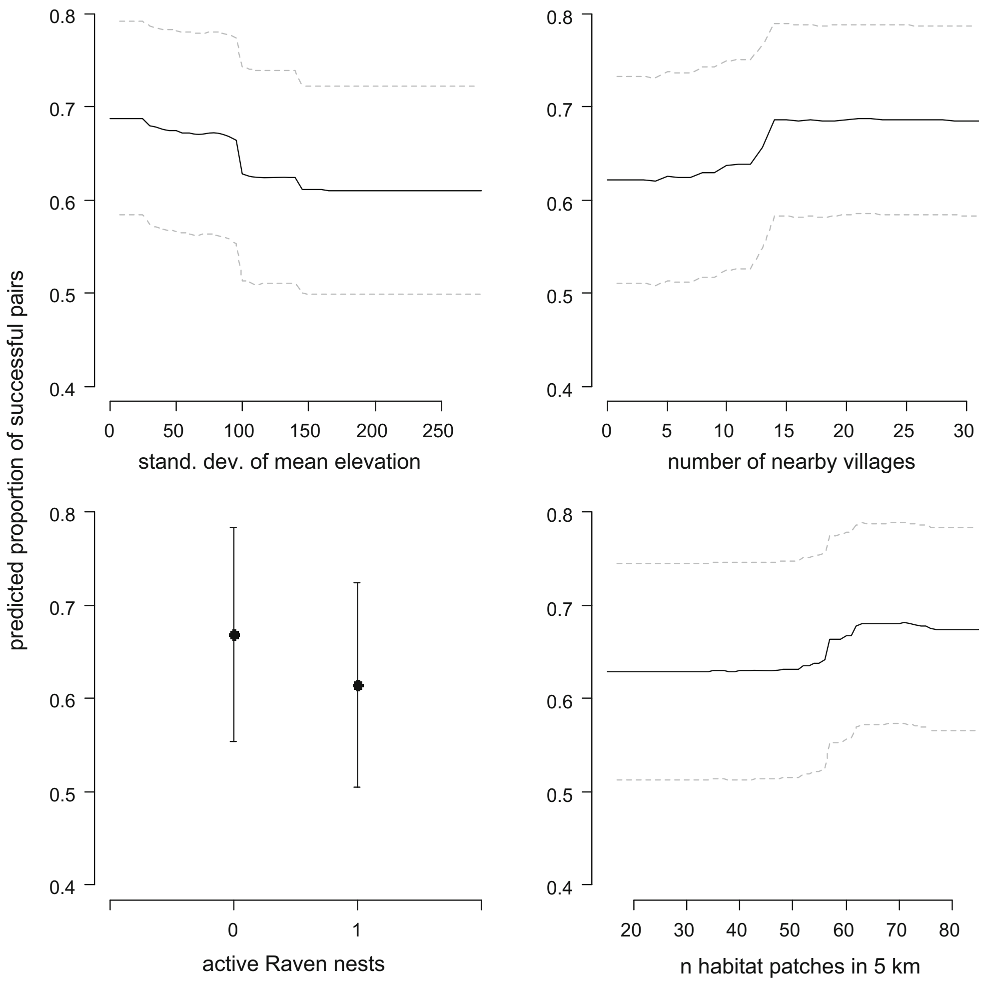


**Fig. 6** Predicted relationships between the four most influential environmental variables and the proportion of Egyptian Vulture pairs that were predicted to successfully raise at least one fledgling on the Balkan Peninsula between 2003 and 2015 if all other variables were held at their actual values. *Dashed grey lines* indicate the SD around the predicted mean

rather than causes of persisting territories: several of the reliable food sources are supplementary feeding stations created by conservation managers in territories that are considered highly valuable (Oppel et al. 2016), and there are no identical 'control' territories to test whether territories would have been abandoned without the establishment of supplementary feeding stations.

Human disturbance has been recognised as a prominent factor for territory abandonment of Vultures (Carrete et al. 2007; Zuberogoitia et al. 2014; Krüger et al. 2015). We found little evidence that measurable factors associated with human pressure influenced the occupancy of territories, and found that breeding success actually increased with a larger number of villages in a 5-km radius around the nest. Although the number of settlements and human disturbance have been shown to explain territory abandonment of vultures in South Africa (Krüger et al. 2015) and decrease breeding success in Spain (Zuberogoitia et al. 2014), a larger number of villages may be reflective of traditional rural landscapes with many small livestock farms that are a more suitable cultural landscape than larger and increasingly urbanised human population centres. Because many small villages have been abandoned in Bulgaria, the attraction of remaining small livestock herds which can act as local food sources may be stronger than the repelling nature of human disturbance. Egyptian Vultures are frequently observed feeding on scraps in small farm yards, and the remains of small-scale livestock farming in rural villages can likely be used by vultures to feed chicks and therefore increase breeding success. However, we found some evidence that disturbance by another cliff-nesting species, the Common Raven, may reduce breeding success of Egyptian Vultures. Ravens are known for their aggressive and kleptoparasitic abilities, and can reduce breeding success of raptors (Bertran and Margalida 2004; Brambilla et al. 2004). Because neither of the most important variables explaining breeding success had a very strong effect, and neither is amenable to management, designing efficient conservation management to increase the productivity of Egyptian Vultures on the Balkan Peninsula will be challenging (Oppel et al. 2016).

Our models were generally successful in distinguishing between occupied and unoccupied territories in Bulgaria and Greece, but the models were not successful in predicting occupancy or breeding success in an external validation dataset from the FYR of Macedonia. The Egyptian Vulture population in the FYR of Macedonia has undergone similar population declines to those in Bulgaria and Greece (Velevski et al. 2015), and exhibits similar rates of occupancy and breeding success (Grubač et al. 2014). The poor predictive performance of our models is therefore unlikely due to a different population status, but could be due to small differences in the collection and aggregation of landscape variables between the two focal countries and the FYR of Macedonia. Alternatively, our powerful algorithmic model may provide a too close fit to the training data, which would result in poor transferability to other regions (Heikkinen et al. 2012; Wenger and Olden 2012; Zurell et al. 2012). Similar poor transferability has been found for other algorithmic models when modelling the distribution of far-ranging species (Oppel et al. 2012; Torres et al. 2015), and we caution practitioners to carefully evaluate whether models can be generalised beyond the focal area from where data were collected to construct the models.

In summary, Egyptian Vultures on the Balkan Peninsula are affected by a broad suite of landscape variables that influence the availability of food and nesting sites, but the complex interaction between a large number of different factors renders it unlikely that targeted action to manage certain aspects of the landscape will have immediate and substantial success in reverting population declines. We recommend action on multiple fronts, in particular a stronger enforcement of anti-poison regulations in the short term, and the conservation of traditional rural farming landscapes with many small livestock holders in the long term (Sanz-Aguilar et al. 2015; Oppel et al. 2016). A heterogeneous and patchy landscape with many small feeding stations where animal carcasses are regularly disposed of to replicate the historical patchy spatiotemporal distribution of prey might be the most suitable landscape for Egyptian Vultures to persist in once the main mortality threats have been sufficiently reduced.

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