

# Habitat preferences of the Eurasian Griffon Vulture (*Gyps fulvus*) in Bulgaria to support species management

Dobromir D. Dobrev\* & Georgi S. Popgeorgiev

*D.D. Dobrev, Bulgarian Society for the Protection of Birds, 5 Leonardo da Vinci Str., PO box 562, 4000 Plovdiv, Bulgaria & Plovdiv University, Faculty of Biology, 24 Tzar Assen Str., Plovdiv 4000, Bulgaria \* Corresponding author's e-mail: dobromir.dobrev1@gmail.com*

*G.S. Popgeorgiev, Bulgarian Society for the Protection of Birds, 5 Leonardo da Vinci Str., PO box 562, 4000 Plovdiv, Bulgaria & National Museum of Natural History, Bulgarian Academy of Sciences, 1 Tsar Osvoboditel Blvd., 1111 Sofia, Bulgaria*

*Received 16 December 2020, accepted 31 July 2021*

The Eurasian Griffon Vulture (*Gyps fulvus*) is a large scavenger with a population ranging between Portugal and India. The species is an obligate scavenger with a narrow ecological niche and is therefore particularly dependent on, and limited by habitat availability. The study aimed, for the first time in Eastern Europe, to identify the habitat preferences of the Griffon Vulture at landscape and cliff scales. We used long-term monitoring data between 1987–2018 to analyze habitat preferences of the natal Griffon Vulture population in the Eastern Rhodope Mountains, Bulgaria. We employed single explanatory variable tests to reveal the species habitat preferences at two spatial scales. The results revealed Griffon Vultures' high preferences towards rocky habitats at the landscape level. At a cliff scale, the height and length of the cliff, the distance to the nearest conspecific colony and the distance to the nearest feeding site were the best predictors for the species habitat preferences. We stress the importance of these findings considering the current status of the species within the region. Our results are useful to support the future conservation of the Griffon Vulture population in Bulgaria and provide a starting point for future research in the Balkans and Eastern Europe.



## 1. Introduction

Determining resources available to animals is essential to preserve species and is mandatory to understand their requirements (Manly *et al.* 2002). Resources are not uniform and hence the usage of environmental features by animals through the process of habitat selection and/or preferences is important to study (Johnson 1980). Understanding species distribution at different spatial scales is

necessary because resources may vary (Martínez *et al.* 2003). Therefore, a multi-scale approach has been proposed and used in avian research to identify different factors outlining the relationship between the environment and the spatial distribution of raptors and scavengers (García-Ripollés *et al.* 2005, López-López *et al.* 2006, 2007, Margalida *et al.* 2008, Mateo-Tomás & Olea 2010). These relationships have been broadly examined in the last decades (Guisan & Zimmermann 2000, Guisan & Thuiller 2005, Olea & Mateo-Tomás

2013). The main objectives of most of these studies was to identify the habitat preferences and subsequently to address conservation actions (Martínez *et al.* 2003, Muñoz *et al.* 2005, Mateo-Tomás & Olea 2009, Olea & Mateo-Tomás 2011, Di Vittorio *et al.* 2012, Donázar *et al.* 2016).

The Eurasian Griffon Vulture (*Gyps fulvus*) (hereafter Griffon Vulture) is a large Old-World vulture with a distribution spanning from the Iberian Peninsula to the Himalayan region (Cramp & Simmons 1980). The species plays a key ecological role to recycle animal carcasses, limit the spread of diseases, and maintain the nutrient return in natural ecosystems (DeVault *et al.* 2016, Sebastián-González *et al.* 2020). Griffon Vulture is one of the most prominent providers of multiple natural non-material contributions to people thus also plays a major role in social-ecological systems (Aguilera-Alcalá *et al.* 2020). The most abundant species population at a global scale is found in Spain (Botha *et al.* 2017). The species is classified globally as ‘Least Concern’ with an increasing population and range (Birdlife International 2017). Griffon Vulture was widely distributed across the Balkans in the past with many colonies known from all over the region (Andevski 2013). However, because of the use of poison baits to extirpate large terrestrial predators, the species was brought to the brink of extinction from almost all of the area after World War II (Demerdzhiev *et al.* 2014a). Nowadays the species survives in scattered fragments across five Balkan countries with a population estimate of 445–565 pairs (Dobrev *et al.* 2021b).

In Bulgaria, the Griffon Vulture population showed a steep decline and by the beginning of the 1970s was considered extinct from the country. At the end of that decade, a breeding colony was discovered in the Eastern Rhodope Mountains (Iankov 2007, Demerdzhiev *et al.* 2014a). Since the 1980s, this population was subject to regular and intensive monitoring of its colony occupancy, number of pairs and breeding rates. As a result of numerous conservation activities, such as supplementary feeding, anti-poisoning actions and active work to engage local communities in the protection of the species, the Griffon Vulture population slowly recovered in the last 30 years and reached over 100 pairs recently (Dobrev & Stoychev 2013, Dobrev *et al.* 2019). The

species is also breeding in the Balkan Mountain range and Pirin Mountains as a result of a re-introduction program in Bulgaria, and the national population now numbers 130 pairs distributed in five breeding nuclei (Demerdzhiev *et al.* 2014a, Dobrev *et al.* 2021b).

The relationship between the Griffon Vulture and its habitat requirements at different spatial scales in different areas of the Iberian Peninsula has been well-studied (Parra & Telleria 2004, García-Ripollés *et al.* 2005, Mateo-Tomás & Olea 2010, Morales-Reyes *et al.* 2017). An extensive study conducted in Spain revealed the importance of environmental factors for their distribution at two spatial scales (García-Ripollés *et al.* 2005). At the colony level, the distance to the nearest cottage, the distance to the nearest colony, and the average altitude above sea level were the best predictors of Griffon Vulture preferences for a breeding site. They also found that climatic, geomorphologic, disturbance-related, trophic and vegetation variables were involved in the habitat preferences at the landscape level (García-Ripollés *et al.* 2005). The presence of vultures was related to traditional livestock practices based on the movement of livestock between summer and winter pastures, e.g. transhumance; vultures relied on transhumant animals for up to four months per year in the Cantabrian Mountains (Olea & Mateo-Tomás 2009). Rocky habitats and livestock abundance were the most important variables affecting vulture distribution (Mateo-Tomás & Olea 2010).

In contrast, in the Balkans, the distribution of the Griffon Vulture in respect to habitat preferences and selection is largely unexplored because such ecological surveys are limited in the region (Xirouchakis & Mylonas 2004, 2005). As exceptions, McIntyre (2010) modelled Griffon Vulture distribution relative to food availability in Crete, and Polce (2004) and Dobrev & Popgeorgiev (2021) assessed the species habitat suitability in Romania and Bulgaria, respectively. Only species distribution and population size have been relatively well documented. However, those parameters are insufficient to ensure the conservation of Griffon Vulture breeding and foraging habitat, without being supplemented with studies revealing the species ecological requirements. Therefore, habitat preference studies are urgently

needed to explain species distribution, to evaluate Griffon Vultures habitat carrying capacity and therefore to provide important information for the management and conservation of the species in the light of the current habitat changes and threats (Newton 1979, Dobrev & Stoychev 2013). This knowledge is essential for the future conservation of the species in Bulgaria, but also in the Balkans and Eastern Europe.

The current study aims to identify Griffon Vulture habitat preferences and the specific environmental variables determining its distribution at two spatial scales: landscape and cliff, in the Eastern Rhodopes. We analysed species preferences and discuss our findings broadly to ensure a better understanding of the Griffon Vulture resource selection and to support the conservation management of the species in Bulgaria and other areas of its range.

## 2. Materials and methods

### 2.1. Study area and data collection

The study encompassed the territory of the Eastern Rhodope Mountains, Bulgaria, part of the Rilo-Rhodopean massif (Fig. 1). This low mountainous area (100 to 1463 m a.s.l.) comprises diverse heterogeneous habitats and low-impact human activities, mainly extensive livestock breeding. Over 150,000 cattle, sheep and goats are raised in the territory (BFSA 2018) with the most free grazing for much of the year. The climate is continental-Mediterranean characterized with average January temperatures of 1–2°C and hot and dry summers, with average July temperatures of 24°C. The annual rainfall is 600–800 mm (Koprarev *et al.* 2002). The area hosts the highest diversity of breeding raptors in Bulgaria (23 species) and 171 breeding bird species overall (Stoychev *et al.* 2004).

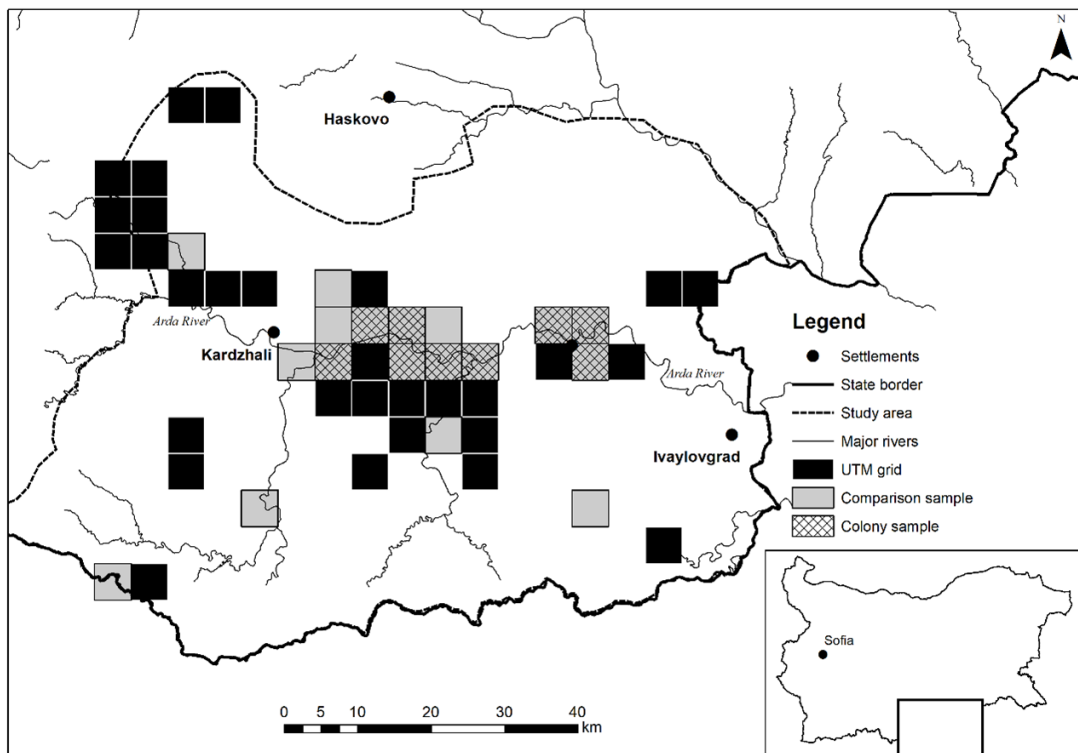


Fig. 1. Map showing the study area and 5 × 5 km cells on the UTM grid used for comparisons between occupied and non-occupied cliffs analysed at two spatial scales.

The data set we used for both cliff and landscape preferences of the species was based on long-term breeding distribution surveys conducted during 1987–2018 (Demerdzhiev *et al.* 2014a, Dobrev *et al.* 2019). The survey was carried out mainly along the Arda River and its tributaries to locate all occupied breeding cliffs by Griffon Vultures. However, more distant cliffs that offered suitable nesting sites were also annually checked within the study area to locate other breeding locations (Demerdzhiev *et al.* 2014a). We monitored the area yearly in January/August with at least four visits to each potential breeding cliff between 1987 and 2018. We used the method for observation from an elevated viewpoint (Bibby *et al.* 1999) and recorded the status of the different Griffon Vulture colonies, following López-López *et al.* (2004). Thereby, species distribution in the study area was determined to adequately qualify presences and absences.

## 2.2 Cliff (colony) and landscape (home range) preferences

All identified Griffon Vulture breeding localities at the cliff and landscape-scale were geo-referenced using GPS and an ortho-photography layer of Bulgaria. Those data were processed in Quantum GIS (QGIS) to match the study design. Thus, the study area was divided into a grid comprising 48 cells of the UTM 5 × 5 km grid using the MGRS naming of cells (UTM zone 35N, datum WGS 1984), containing rocky landscapes and cliffs (Fig. 1), following a stratified random design (Sutherland 2000, Xirouchakis & Mylonas 2004, Di Vittorio *et al.* 2015). The Griffon Vulture has a large home range (Monsarrat *et al.* 2013, Genero *et al.* 2020, Martín-Díaz *et al.* 2020). However, the Griffon Vulture breeding distribution in our area is confined along the Arda river valley between Kardzhali and Madzharovo (Demerdzhiev *et al.* 2014a). Therefore, in our study, we used a 5 × 5 km grid cell to measure species preferences at landscape scale according to the concise distribution of the Griffon Vulture, studied by GPS/GSM transmitters in the Eastern Rhodopes (Arkumarev *et al.* 2021, BSPB/Birdlife Bulgaria unpubl.).

Breeding colonies were identified in nine of the 48 UTM 5 × 5 km grid cells (colony sample).

The same number of non-occupied grid cells ( $n = 9$ , comparison sample) was selected at random from the same grid and compared with each other (analysed sample = 18 cells in total, see Fig.1). Also, colony, climate, disturbance and trophic parameters of the known breeding cliffs ( $n = 16$ ) were compared at this spatial scale with the same number of randomly selected non-occupied cliffs within the analyzed grid cells (García-Ripollés *et al.* 2005). Non-occupied cliffs were selected randomly from a pool of cliffs ( $n = 26$ ) encompassed within the analysed sample. Thus, occupied and non-occupied cells and cliffs were independently sampled to collect information on the colony, climate, disturbance, topography, trophic and habitat variables. The spatial calculations and measurements of these variables for each of the studied cliffs and cells were processed in QGIS (QGIS Development Team 2016). Colony and disturbance related variables were measured based on the ortho-photography layer of Bulgaria (scale 1:2000) (<http://gis.mrrb.government.bg/>) and obtained from field surveys and NSI (2012), respectively. Climate-related variables were obtained from free internet climate databases (rp5.ru, weatheronline.co.uk, stringmeteo.com). Topography features were obtained from a Digital Elevation Model (DEM) of Bulgaria with a 40 m pixel size. Trophic features were obtained from the country's official database, obtained by BFS (2018), and habitat variables were based on 2012 Corine Land Cover layer classification (but see Table 1) (Bossard *et al.* 2000). These variables were selected because they are indirectly related to known breeding habitat preferences of the Griffon Vulture and were expected to affect the realized ecological niche of the species (Guisan & Zimmermann 2000, López-López *et al.* 2007). Thus, our results would be comparable to similar studies in Spain (García-Ripollés *et al.* 2005) and would stem from a standard procedure, useful for future assessment in Eastern Europe.

## 2.3 Statistical procedures

Before starting the statistical analysis, we processed the data for multi-collinearity. We used the Spearman correlation coefficient ( $r$ ) to explore the inter-correlations among the continuous variables

Table 1. Complete list of environmental variables considered in the Griffon Vulture habitat preferences comparison. Variables included in the cliffs analysis are marked with (1) and those included in the landscape analysis with (2).

Abbreviation	Variable description (measurement unit)	Dropped because of correlation ( $r > 0.7$ )
<i>Colony</i>		
CLLE <sup>1</sup>	Linear length of the cliff (m)	No
CLHI <sup>1</sup>	Height of the cliff, measured at the highest point (m). The linear distance between the base and the top of the cliff.	No
CLHIma <sup>1</sup>	Highest (summit) level of the breeding cliff (m)	Yes
NECD <sup>1</sup>	Linear distance to the nearest neighbouring colony (m)	No
CAMA <sup>1</sup>	Aspect of the breeding cliff (degrees). The variable was categorized into 16 categories (per every 22.5°).	No
<i>Climate</i>		
APJA <sup>1,2</sup>	Average rainfall during January (mm)	Yes
<i>Disturbance</i>		
SEDI <sup>1</sup>	Linear distance to the nearest human settlement (m)	No
RODI <sup>1</sup>	Linear distance to the nearest paved road (m)	No
INDE <sup>2</sup>	Inhabitant density in the surveyed grid cell (people/km <sup>2</sup> )	No
POLE <sup>2</sup>	Length of the low and medium voltage grid system $\leq 110$ kV (m)	Yes
<i>Topography</i>		
ASAV <sup>2</sup>	Average aspect of the cell (degrees), created by a triangular irregular network (TIN) method based on vector data of contour lines with 40 m accuracy as the maximum rate of change in exposure across each in the TIN. For the aim of the analysis, the variable was categorized into 16 categories (per every 22.5°).	No
<i>Trophic</i>		
DELI <sup>2</sup>	Density of the livestock in livestock units (LU): (1) 1 cow = 5 LU; (2) 1 sheep/goat = 1 LU; (3) pig = 2 LU. A method to quantify the biomass of the available livestock in the study area, based on Mateo-Tomás & Olea 2010.	No
DIFE <sup>1</sup>	Linear distance to the nearest feeding station (m)	No
<i>Habitat</i>		
PEOH <sup>2</sup>	Area of the open habitats in the cell in hectares (Categories from the Corine Land Cover describing the open habitat types: code 321 – Natural grasslands; 324 – Transitional woodland-shrub; 231 – Pastures; 243 – Land principally occupied by agriculture, with significant areas of natural vegetation; 112 – Discontinuous urban fabric; 333 – Sparsely vegetated areas; 131 – Mineral extraction sites; 142 – Open sports and leisure areas).	No
PERO <sup>2</sup>	Area of rock habitats in the cell in hectares	No

(Table 1). From pairs of variables that showed high correlation ( $r > 0.7$ ), we used only one to be analyzed further on. The decision on which variable to retain was based on the results of a Principal Component Analysis (PCA), selecting the one with a higher factor score. As a result, we removed three variables (CLHIma – highest (summit) level of the breeding cliff; APJA – Average rainfall during January; and POLE – Length of the low and medium voltage grid system  $\leq 110$  kV) and retained 6 variables for the cliff analysis (CLLE – cliff length; CLHI – cliff height; NECD – linear distance to the nearest neighbouring colony; SEDI – linear distance to the nearest human settlement; RODI – linear distance to the nearest paved road; and DIFE – linear distance to the nearest feeding station) and 4 variables for the cell analysis (INDE – inhabitants density in the surveyed grid cell; PEOH – an area of the open habitats in the cell; PERO – an area of rock habitats in the cell; and DELI – density of the livestock in livestock units) from a set of a priori selection (Table 1). Non-parametric tests were applied because data did not approach the normal distribution (Fowler & Cohen 1995). We compared occupied and non-occupied cliffs and grid cells through Mann-Whitney  $U$ -test to search for differences in the medians of the explored variables separately. We further compared the categorical variables (ASAV – aspect of the cell at home range scale and CAMA – aspect of the breeding cliff at colony scale) using the Chi-Square test ( $\chi^2$ ). We separately computed a simple Mantel test ( $Z$ ) with 30 000 permutations to assess the similarity and correlation between the nearest neighbouring conspecifics distances of the occupied and non-occupied cliffs and species presence/absence dissimilarity matrices (Pierre-Rossi 1996, Schick *et al.* 2004). Results with  $p < 0.05$  were considered significant. Statistica for Windows, Release 7 (StatSoft Inc. 2004) and R v.3.6.1 (R Development Core Team 2012) were used for the statistical analysis of the data

### 3. Results

#### 3.1. Habitat preferences at cliff scale

Statistically significant differences ( $p < 0.05$ ) were found between the following variables: cliff

length (CLLE), cliff height (CLHI), nearest neighbouring Griffon Vulture colony distance (NECD) and the distance to the nearest feeding station (DIFE). Cliffs occupied by Griffon Vultures were longer ( $U = 2.13$ ,  $p = 0.03$ ) and higher ( $U = 1.73$ ,  $p = 0.05$ ) in comparison to non-occupied ones. The simple Mantel test showed that occupied and non-occupied cliffs have no similarities in their spatial pattern of distribution (normalized  $Z = 29.27$ ,  $p = 0.85$ ), neither there is a correlation between cliffs distance matrices ( $r = 0.35$ ,  $p = 0.12$ ). Nevertheless, the NECD of occupied cliffs is significantly lesser in comparison to that of non-occupied cliffs ( $U = -3.31$ ,  $p = 0.00$ ) (Fig. 2). The distance to the nearest feeding station was significantly lower in occupied than in non-occupied cliffs ( $U = -4.52$ ,  $p < 0.001$ ). Cliffs occupied by the Griffon Vulture had predominantly southern exposure (CAMA) in contrast to randomly selected cliffs ( $\chi^2 = 12.4$ ,  $p = 0.05$ ).

#### 3.2. Habitat preferences at landscape scale

Cells occupied by Griffon Vultures colonies had a significantly more area of rocky habitats (PERO) than non-occupied ones ( $U = 2.78$ ,  $p = 0.003$ ). We did not find significant differences between the aspect (ASAV) of the occupied and non-occupied cells ( $\chi^2 = 27.46$ ,  $p = 0.3$ ). Density of human population (INDE) ( $U = 1.19$ ,  $p = 0.25$ ), the area of open habitats (PEOH) ( $U = 1.02$ ,  $p = 0.34$ ) and livestock densities (DELI) ( $U = 0.39$ ,  $p = 0.73$ ) did not differ significantly between the occupied and non-occupied cells.

### 4. Discussion

This is the first study aimed at providing prime knowledge for the most important environmental variables affecting the Griffon Vulture's preferences at two spatial scales in Bulgaria and, to a broader extent, in Eastern Europe. The availability of suitable breeding sites is a substantial driver of site occupancy (Newton 1979, Mateo-Tomás & Olea 2011, Di Vittorio & López-López 2014). We demonstrated that variables related to the breeding cliffs have high significance for the habitat preferences of the Griffon Vulture. Cliff height, length

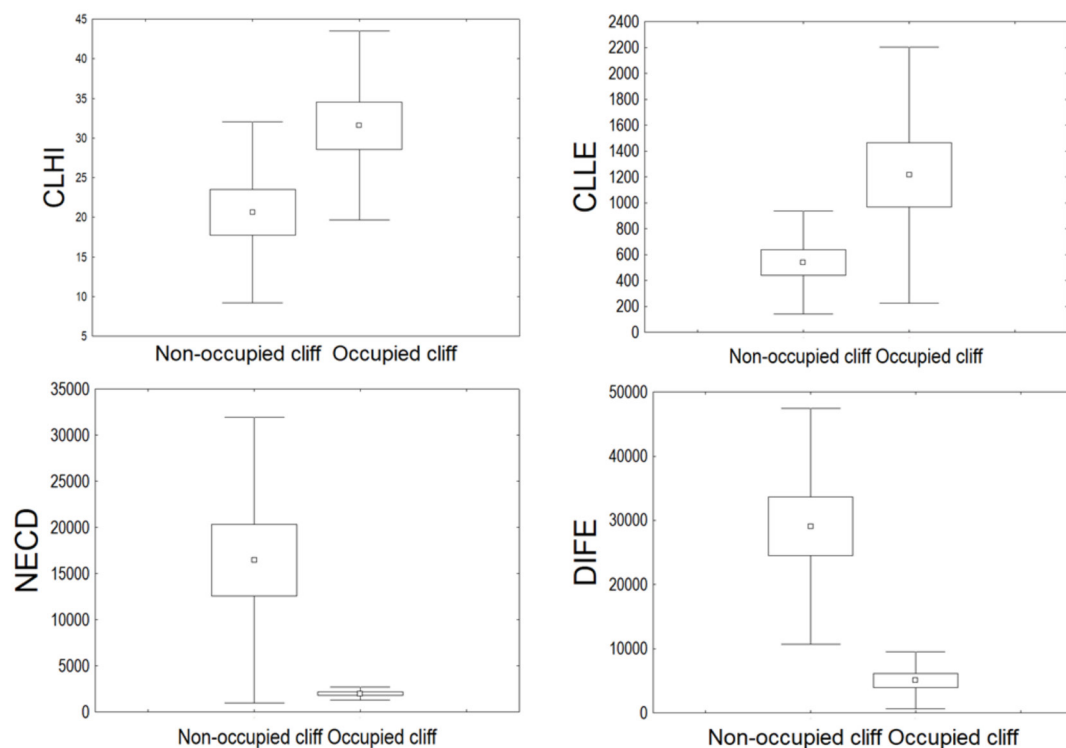


Fig. 2. Box-Whiskers plots presenting the comparison of the variables showing statistically significant differences between occupied and non-occupied cliffs: CLLE – cliff length (m); CLHI – cliff height (m); NECD – Linear distance to the nearest neighbouring colony (m); and DIFE – Linear distance to the nearest feeding station (m) ( $\pm$  standard error presented with  $\square$ , standard deviation presented with  $\top$  and mean, presented with  $\square$ ).

and distance to the nearest conspecific colony were highlighted as important factors for occupancy by other studies as well (Cramp & Simmons 1980, Xirouchakis & Mylonas 2005). Similarly, the best predictors affecting the distribution of large birds of prey such as the Golden Eagle (*Aquila chrysaetos*) and the Bearded Vulture (*Gypaetus barbatus*) were related to topographic features (López-López *et al.* 2007, Margalida *et al.* 2008, Di Vittorio & López-López 2014). The Griffon Vulture, being a large cliff-nesting raptor is highly selective to topographic features too, as highlighted by our and others' results (Parra & Telleria 2004, Xirouchakis & Mylonas 2005). Larger cliffs present more suitable sites for breeding (Mateo-Tomás & Olea 2011). Hence, the Griffon Vultures' cliffs in the study area usually present considerable space, height, and length situated along rivers, steep slopes, and gorges where birds can easily take off and land (Xirouchakis & Mylonas 2005).

Nesting substrate (niche or ledge) may affect species breeding (López-López *et al.* 2004) and occupancy (Iezekiel *et al.* 2004). A previous study in our study area did not find such a relationship (Demerdzhiev *et al.* 2014a). However, the nesting substrate may positively affect Griffon Vulture breeding success and ensure protection from adverse weather conditions (Ceballos & Donázar 1988, Iezekiel *et al.* 2004, Freund *et al.* 2017).

Our results also underline the significance of the nearest colony distance as a major factor affecting species preferences and confirm findings from previous studies (Xirouchakis & Mylonas 2004, Margalida *et al.* 2007, Skartsi *et al.* 2009). The positive trend of any given population is dependent on the surplus of birds immigrating from other populations (Demerdzhiev *et al.* 2014b). The occupancy of new territories is highly dependent and related to neighbouring conspecifics, occupying the high-quality habitats

(Carrete *et al.* 2007). This has been observed in our study area where the newly emerging colonies were always close to the core ones (Demerdzhiev *et al.* 2014a). Thus, occupancy of new territories and the expansion of local range by the Griffon Vulture is strongly dependent on the safe permanence and breeding of neighbour populations.

We revealed that Griffon Vulture has higher preferences towards cliffs with southern exposure. This may be related to climatic factors in our study area, which we accounted for in our analysis but did not show enough statistical power to be studied in detail. However, Griffon Vultures breeding season starts with the egg-laying in January (Ferguson-Lees *et al.* 2001) and thus vultures are particularly dependent on the climatic conditions at that time (Newton 1979, Grande *et al.* 2009). Sudden temperature changes and extreme precipitation can negatively affect incubation and lead to breeding failure (Donázar 1993, Elliott *et al.* 2005). In the Eastern Rhodopes, regardless of the low altitudes, such climatic extremes are not a rare event at the beginning of the breeding season and can ultimately alter reproduction causing failures and/or clutch replacement. Our findings support similar studies, where the Griffon Vulture avoids northern exposure to counteract the fluctuations in the temperatures, precipitation (Demerdzhiev *et al.* 2014a) and wind (Xirouchakis & Mylonas 2005).

We did not find a difference between occupied and non-occupied cells about livestock density, very likely because the density of livestock in our area is high in most of the territory and thus such differences would be difficult to establish on this scale. Nevertheless, livestock abundance shapes the foraging behaviour of Griffon Vulture in our study area (Arkumarev *et al.* 2021). The species is an obligate scavenger, searching food at great distances and is highly dependent on the availability of dead animals and adapted to use carrion as a food source (DeVault *et al.* 2016, Martin-Díaz *et al.* 2020). Therefore, vultures are reliant on livestock abundance and are highly related to agro-pastoral ecosystems (Xirouchakis & Mylonas 2004, Olea & Mateo-Tomás 2009, Donázar *et al.* 2009), including in our area (Hristov 1997, Angelov *et al.* 2006, Arkumarev *et al.* 2021). For example, the Griffon Vulture on Crete is probably one of the most pastoralism-bonded populations in the

whole range of the species (McIntyre 2010). This highlights the strong connection between Griffon Vulture and livestock and supports our statement that food availability and abundance dependent from the extensive livestock husbandry are of key importance for the species presence and distribution (Xirouchakis & Mylonas 2004, Olea & Mateo-Tomás 2009, Mateo-Tomás & Olea 2015, Martin-Díaz *et al.* 2020).

We found a significant positive relationship for Griffon Vultures breeding colonies to be situated closer to feeding stations. This finding supports research in the same study area which reported that Griffon Vultures have high seasonal preferences towards usage of the feeding sites without being entirely reliant on them (Arkumarev *et al.* 2021) in contrast to other areas of the species range (Harel *et al.* 2017). Indeed, the settlement of supplementary feeding stations has become a major conservation and management tool for vulture species in Europe (Cortes-Avizanda & Pereira 2016, Cortes-Avizanda *et al.* 2016) and elsewhere (Brink *et al.* 2020). In Bulgaria, this management tool has been used exclusively to direct the Griffon Vulture population conservation after its re-discovery in Bulgaria at the end of the 1970s (Dobrev & Stoychev 2013). The network of feeding sites in Bulgaria is an important conservation tool for the Griffon Vulture population in the Balkans (Stoynov *et al.* 2017). Besides, our study confirms previous findings where the proximity to the feeding site was determined as one of the best predictors for Griffon Vultures roosting cliff selection in the pre-breeding season (Dobrev *et al.* 2021a). However, the spatial and temporal predictability of the feeding sites can rapidly change vultures' foraging strategies and behavioural responses (Deygout *et al.* 2009, Moreno-Opo *et al.* 2010, 2015, Margalida *et al.* 2014). Consequently, the management of the feeding sites must be species and/or area-specific and considered gently with respect to species conservation (Margalida *et al.* 2014).

Our study in the Eastern Rhodopes complements other studies from Europe for the factors affecting the Griffon Vulture habitat preferences at two spatial scales – landscape and cliff. We confirmed also for an eastern European population that a combination of larger cliffs, the presence of conspecifics and suitable breeding and foraging



habitats explain Griffon Vultures preferences. Territory quality is an important measure of occupancy and fitness (Fahrig 2001, Sergio & Newton 2003). Hence, we recommend conservation of the species' prime breeding habitats, but also territories part of the historical breeding range in Bulgaria (Olea & Mateo-Tomás 2009, Dobrev & Popgeorgiev 2021) that can be used either for roosting (Dobrev *et al.* 2021a), but also re-occupied in future colonisation (Dobrev *et al.* 2021b). Areas of extensive livestock breeding, like the Eastern Rhodopes, must be sustained viable to contribute to vultures' persistence (Mateo-Tomás & Olea 2011, Martín-Díaz *et al.* 2020). The animal husbandry there might be favoured by application of relevant EU agri-environmental measures to support livestock breeders and search regional measures to buffer human-wildlife conflict and the use of poisons. Thereby, vultures will benefit from the availability of safe food and will be possibly less affected and/or exposed to severe threats like poisoning. Furthermore, the protection of the currently occupied breeding cliffs and foraging habitats will ensure population growth in future and its connection to neighbouring breeding population nuclei of the species (Dobrev & Popgeorgiev 2021, Dobrev *et al.* 2021b). We suggest similar studies to be conducted elsewhere in the Balkans and Eastern Europe to bring insight into the species habitat selection process and preferences there. Application of cognate conservation approaches in neighbouring countries may bring homogeneity and consistency at a regional level and possibly ease the Griffon Vulture population recovery. The usage of GPS telemetry must be considered to assist this process and reveal how this reverberates the survival and fitness of the Griffon Vulture.

### **Hanhikorppikotkan elinympäristövaatimukset Bulgariassa – tukena suojelutoimille**

Hanhikorppikotka on kookas haaskalintu, jonka levinneisyys ulottuu Portugalista Intiaan. Lajilla on kapea ekolokero, sillä se käyttää ravinnokseen vain haaskoja, ja täten sen esiintyminen on hyvin rajattu tiettyihin elinympäristöihin. Tässä tutkimuksessa selvitettiin ensimmäistä kertaa hanhikorppikotkan elinympäristövaatimuksia

maisematasolla Itä-Euroopassa. Käytimme pitkäaikaisaineistoa (1987–2018) Bulgariasta Rodopivuorilta. Havaitimme, että maisematasolla hanhikorppikotkat suosivat kivikkoisia habitaatteja. Kalliojyrkänteiden korkeus ja pituus, etäisyys lähimpään hanhikorppikotkakoloniaan sekä etäisyys lähimpään ruokintapaikkaan selittivät parhaiten lajin esiintymistä. Tulokset ovat tärkeitä lajin nykyisen statuksen ymmärtämisen kannalta, auttavat suojelutoimia suunniteltaessa, ja toimivat lähtökohtana tuleville tutkimuksille Itä-Euroopassa.

*Acknowledgements.* The current research was financed by National program “Young scientists and Postdoctoral candidates” funded by the Bulgarian Ministry of Education and Science. We express our gratitude to Hristo Hristov, Dimitar Demerdzhiev, Marin Kurtev, Vladimir Dobrev, Volen Arkumarev, Ivaylo Angelov, Nedko Nedyalkov, Vladimir Trifonov, Stoycho Stoychev, Anton Stamenov, Atanas Delchev, Vera Dyulgerska and Nikolay Terziev for their contribution in collecting monitoring data and support. We are grateful to Yurii Korniliev for providing valuable comments on the edited draft of the manuscript.

### **References**

- Aguilera-Alcalá, N., Morales-Reyes, Z., Martín-López, B., Moleón, M. & Sánchez-Zapata, J. 2020: Role of scavengers in providing non-material contributions to people. — *Ecological Indicators* 117: 106643.
- Andevski, J. (ed) 2013: Vulture Conservation in the Balkan Peninsula and Adjacent Regions. 10 Years of Vulture Research and Conservation. Action Plan for the Recovery and Conservation of Vultures on the Balkan Peninsula and Adjacent Regions. — Vulture Conservation Foundation & Frankfurt Zoological Society, Skopje.
- Angelov, I., Demerdzhiev, D. & Stoychev, S. 2006: Use of carcasses from wolf kills by Griffon Vultures (*Gyps fulvus*) in Eastern Rhodopes, Bulgaria. — In Proceedings of the International Conference on Conservation and Management of Vulture Populations (eds. Houston, D.C. & S.E. Piper). — Natural History Museum of Crete & WWF Greece, Thessaloniki.
- Arkumarev, V., Dobrev, D., Stamenov, A., Terziev, N., Delchev, A. & Stoychev, S. 2021: Seasonal dynamics in the exploitation of natural carcasses and supplementary feeding stations by a top avian scavenger. — *Journal of Ornithology*. DOI 10.1007/s10336-021-01865-1.
- BFSА 2018: Reference at Art.37m, par.3 of the Property and agricultural lands use Act. Downloaded from <http://www.babh.government.bg/en/> on 24/1/2018. (In Bulgarian)

- Bibby, C., Jones, M. & Marsden, S. 1999: Expedition Field Techniques. – Bird Surveys-Royal Geographical Society, London.
- BirdLife International 2017: *Gyps fulvus* (Griffon Vulture). – IUCN Red List for birds. Downloaded from <http://www.birdlife.org/> on 01/01/2020.
- Bossard, M., Feranec, J. & Otahel, J. 2000: CORINE Land Cover Technical Guide-Addendum 2000. Technical report No 40. Copenhagen (EEA). Downloaded from <http://terrestrial.eionet.eu.int>.
- Botha, A.J., Andevski, J., Bowden, C.G.R., Gudka, M., Saford, R. J., Tavares, J. & Williams, N. P. 2017: CMS Multi – species Action Plan to conserve African – Eurasian Vultures. Abu Dhabi, United Arab Emirates: Coordinating Unit of the CMS Raptors MOU. (CMS Raptors MOU Technical Publication No. 5. CMS Technical Series No. 35).
- Brink, C., Santangeli, A., Amar, A., Wolter, K., Tate, G., Krueger, S., Tucker, A. S. & Thomson, R. L. 2020: Quantifying the spatial distribution and trends of supplementary feeding sites in South Africa and their potential contribution to vulture energetic requirements. — *Animal Conservation* 23: 491–501.
- Carrete, M., Grande, J., Tella, J., Sanchez-Zapata, Donazar J., Diaz-Delgado, R. & Romo, A. 2007: Habitat, human pressure, and social behavior: Partialling out factors affecting large-scale territory extinction in an endangered vulture. — *Biological conservation* 136: 143 – 154.
- Ceballos, O. & Donazar, J. 1988: Egyptian vulture (*Neophron percnopterus*) nest-site in Navarra. — *Munibe* 40: 3–8.
- Cortes-Avizanda, A. & Miguel Pereira, H. 2016: Rewilding: Vulture restaurants cheat ecosystems. — *Nature* 540: 525–525.
- Cortes-Avizanda, A., Blanco, G., DeVault, T., Markandya, A., Virani, M., Brandt, J. & Donazar, J. 2016: Supplementary feeding and endangered avian scavengers: Benefits, caveats, and controversies. — *Frontiers in Ecology and the Environment* 14: 191–199.
- Cramp, S. & Simmons, K. 1980: The Birds of the Western Palearctic. — Oxford Univ. Press, Oxford.
- Demerdzhiev, D., Hristov, H., Dobrev, D., Angelov, I. & Kurtev, M. 2014a: Long-term population status, breeding parameters and limiting factors of the Griffon Vulture (*Gyps fulvus*) population in Eastern Rhodopes, Bulgaria. — *Acta Zoologica Bulgarica* 66: 373–384.
- Demerdzhiev, D., Stoychev, S., Dobrev, D., Spasov S. & Oppel, S. 2014b: Studying the demographic drivers of an increasing Imperial Eagle population to inform conservation management. — *Biodiversity and Conservation* 24: 627–639.
- DeVault, T., Beasley, J., Olson, Z., Moleón, M., Carrete, M., Margalida, A. & Sanchez-Zapata, J.A. 2016: Ecosystem Services Provided by Avian Scavengers. — USDA National Wildlife Research Center-Staff Publications.
- Deygout, C., Gault, A., Sarrazin, F. & Bessa-Gomes, C. 2009: Modeling the impact of feeding stations on vulture scavenging service efficiency. — *Ecological Modelling* 220: 1826–1835.
- Di Vittorio, M. & López-López, P. 2014: Spatial distribution and breeding performance of Golden Eagles (*Aquila chrysaetos*) in Sicily: implications for conservation. — *Acta Ornithologica* 49: 33–45.
- Di Vittorio, M., Ciaccio, A., Greci, S. & Luiselli, L. 2015: Ecological modelling of the distribution of the Lanner falcon *Falco biarmicus feldeggii* in Sicily at two spatial scales. — *Ardeola* 62: 81–94.
- Di Vittorio, M., López-López, P. & Sarà, M. 2012: Habitat preference of Bonelli's eagle (*Aquila fasciata*) in Sicily. — *Bird Study* 59: 207–217.
- Dobrev, A., Arkumarev, V., Dobrev, V., Stamenov, A. & Demerdzhiev, D. 2021a: Use and selection of roost sites by Eurasian Griffon Vultures *Gyps fulvus* in Bulgaria. — *Bird Study*. DOI: <https://doi.org/10.1080/00063657.2021.1950122>
- Dobrev, D., Arkumarev, V., Skartsi, T., Stamenov, A. & Kret, E. 2019: Griffon Vulture population trend and size in the Eastern Rhodopes at the crossroads to Asia. — Poster, European vulture conference, Algarve, Portugal.
- Dobrev, D. & Popgeorgiev, G. 2021b: Modeling breeding habitat suitability of Griffon Vultures (*Gyps fulvus*) in Bulgaria and conservation planning. — *North-Western Journal of Zoology* 17(2).
- Dobrev, D. & Stoychev, S. 2013: Vulture conservation in Bulgaria. — *Proceedings of the Griffon Vulture Conference*, 6-8 March 2013, Limassol.
- Dobrev, D., Tsiakiris, R., Skartsi, T., Dobrev, V., Arkumarev, V., Stara, K., Stamenov, A., Probonas, N., Kominos, T., Galanaki, A., Kret, E., Hallmann, B., Grubač, B., Sušić, G., Marinković, S., Hribšek, I., Skorić, S., Jerrentrup, H., Lucić, V., Kapelj, S., Stoyanov, G., Zakkak, S., Hristov, H., Stoychev, S., Sidiropoulos, L., Bino, T. & Demerdzhiev, D. 2021: Long-term size and range changes of the Griffon Vulture *Gyps fulvus* population in the Balkans: a review. — *Bird Conservation International*. DOI: <https://doi.org/10.1017/S0959270921000198>
- Donazar, J.A. 1993: Los buitres ibéricos. *Biología y conservación*. — Reyero J. M., Madrid.
- Donazar, J.A., Avizanda, A., Fargallo, J., Margalida, A., Moleon, M., Morales-Reyes, Z., Moreno-Opo, R., Perez-Garzia, J., Sanchez-Zapata, J., Zuberogoitia, I. & Serrano, D. 2016: Roles of raptors in a changing world: from flagships to providers of key ecosystem services. — *Ardeola* 63: 181–234.
- Donazar, J., Margalida, A. & Campión, D. 2009: Vultures, Feeding Stations and Sanitary Legislation: A conflict and its consequences from the perspective of conservation biology. — *Sociedad de Ciencias Aranzadi San Sebastián, Spain*.
- Elliott, K., Gill, C. & Elliott, J. 2005: The influence of tide and weather on provisioning rates of chick-rearing Bald Eagles in Vancouver island, British Columbia. — *Journal of Raptor Research* 39: 1–10.
- Fahrig, L. 2001: How much habitat is enough? — *Biological*

- Conservation 100: 65–74.
- Ferguson-Lees, J., Christie, D.A., Franklin, K., Mead, D. & Burton, P. 2001: Raptors of the World. — Houghton Mifflin Company, New York.
- Fowler, J. & Cohen, L. 1995: Statistics for Ornithologists: 2nd ed. — BTO, London.
- Freund, M., Bahat, O. & Motro, U. 2017: Breeding success and its correlation with nestsite characteristics: a study of a Griffon Vulture colony in Gamla, Israel. — *Journal of Raptor Research* 51: 136–144.
- García-Ripollés, C., López-López, P., García-López, F., Aguilar, J.M. & Verdejo, J. 2005: Modeling nesting habitat preferences of Eurasian Griffon Vulture *Gyps fulvus* in eastern Iberian Peninsula. — *Ardeola* 52: 287–304.
- Genero, F., Franchini, M., Fanin, Y., Filacorda, S. 2020: Spatial ecology of non-breeding Eurasian Griffon Vultures (*Gyps fulvus*) in relation to natural and artificial food availability. — *Bird Study* 67: 53–70.
- Grande, J.M., Serrano, D., Tavecchia, G., Carrete, M., Ceballos, O., Diaz-Delgado, R., Tella, J. & Donazar, J. 2009: Survival in a long-lived territorial migrant: Effects of life-history traits and ecological conditions in wintering and breeding areas. — *Oikos* 118: 580–590.
- 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.
- Harel, R., Spiegel, O., Getz, W.M. & Nathan, R. 2017: Social foraging and individual consistency in following behaviour: testing the information Centre hypothesis in free-ranging vultures. — *Proceedings of the Royal Society B: Biological Sciences* 284: 10.1098/rspb.2016.2654.
- Hristov, H. 1997: Status, monitoring and supplementation of the vultures in the Eastern Rhodopes. — Eastern Rhodopes reports, BSBDB-BSPB, Sofia. (In Bulgarian)
- Iankov, P. (ed.) 2007: Atlas of Breeding Birds in Bulgaria. — Bulgarian Society for the Protection of Birds, Conservation series, Book 10, Sofia.
- Iezekiel, S., Bakaloudis, D.E. & Vlachos, C.G. 2004: The status and conservation of Griffon Vulture *Gyps fulvus* in Cyprus. — In *Raptors worldwide: proceedings of the 6th World Conference on Birds of Prey and Owls* (eds. Chancellor, R.D. & B.-U. Meyburg). — WWGBP/MME, Budapest, Hungary.
- Johnson, D. 1980: The comparison of usage and availability measurements for evaluating resource preference. — *Ecology* 61: 65–71.
- Koprale, I. 2002: Geography of Bulgaria. Physical and socio-economic geography. — BAS, ForKom, Sofia. (in Bulgarian)
- López-López, P., García-Ripollés, C., Aguilar, J. M., García-López, F. & Verdejo, J. 2006: Modelling breeding habitat preferences of Bonelli's eagle (*Hieraetus fasciatus*) in relation to topography, disturbance, climate and land use at different spatial scales. — *Journal of Ornithology* 147: 97–106.
- López-López, P., Ripollés, C.G., Soutullo, A., Cadahia, L. & Urios, V. 2007: Identifying potentially suitable nesting habitat for golden eagles applied to 'important bird areas' design. — *Animal Conservation* 10: 208–218.
- López-López, P., García-Ripollés, C. & Verdejo, J. 2004: Population status and reproductive performance of Eurasian Griffons (*Gyps fulvus*) in eastern Spain. — *Journal of Raptor Research* 38: 350–356.
- Manly, B., McDonald, L., Thomas, D., McDonald, T., & Erickson, W. 2002: Resource selection by animals. Statistical design and analysis for field studies, 2<sup>nd</sup> edition. — Dordrecht, The Netherlands: Kluwer Academic Publisher.
- Margalida, A., Campion, D. & Donazar, J. 2014: Vultures vs livestock: Conservation relationships in an emerging conflict between humans and wildlife. — *Oryx* 48: 172–176.
- Margalida, A., Donazar, J., Bustamante, J., Hernández, F. & Romero-Pujante, M. 2008: Application of a predictive model to detect long-term changes in nest-site selection in the Bearded Vulture (*Gypaetus barbatus*): conservation in relation to territory shrinkage. — *Ibis* 150: 242–249.
- Margalida, A., García, D. & Cortés-Avizanda, A. 2007: Factors influencing breeding density of Bearded Vultures, Egyptian Vultures and Eurasian Griffon Vultures in Catalonia (NE Spain): management implications. — *Animal Biodiversity and Conservation* 30: 189–200.
- Martin-Díaz, P., Cortés-Avizanda, A., Serrano, D., Arrondo, E., Sánchez-Zapata, J. & Donazar, J. 2020: Rewilding processes shape the use of Mediterranean landscapes by an avian top scavenger. — *Scientific Reports* 10 (1): 2853.
- Martínez, J.A., Serrano, D. & Zuberogoitia, I. 2003: Predictive models of habitat preferences for the Eurasian Eagle Owl *Bubo bubo*: a multiscale approach. — *Ecography* 26: 21–28.
- Mateo-Tomás, P. & Olea, P. P. 2009: Combining scales in habitat models to improve conservation planning in an endangered vulture. — *Acta Oecologica* 35: 489–498.
- Mateo-Tomás, P. & Olea, P.P. 2010: Anticipating Knowledge to Inform Species Management: Predicting Spatially Explicit Habitat Suitability of a Colonial Vulture Spreading Its Range. — *PLoS ONE* 5: e12374.
- Mateo-Tomás, P. & Olea, P.P. 2011: The importance of social information in breeding site selection increases with population size in the Eurasian Griffon Vulture (*Gyps fulvus*). — *Ibis* 153: 832–845.
- Mateo-Tomás, P. & Olea, P.P. 2015: Livestock-driven land use change to model species distributions: Egyptian vulture as a case study. — *Ecological Indicators* 57: 331–342.
- McIntyre, A.L. 2010: Modelling foraging distribution of Griffon Vultures (*Gyps fulvus*) on the island of Crete, Greece. — MSc thesis, University of Twente.

- Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C. & Bouten, W. 2013: How Predictability of Feeding Patches Affects Home Range and Foraging Habitat Selection in Avian Social Scavengers? — *PLoS ONE* 8: 10.1371.
- Morales-Reyes, Z., Pérez-García, J., Moleón, M., Botella, F., Carrete, M., Donazar, J., Cortés-Avizanda, A., Arrondo, E., Moreno-Opo, R., Jimenez, J., Margalida, A. & Sánchez-Zapata, J. 2017: Evaluation of the network of protection areas for the feeding of scavengers in Spain: From biodiversity conservation to greenhouse gas emission savings. — *Journal of Applied Ecology* 54: 1120–1129.
- Moreno-Opo, R., Margalida, A., Arredondo, Á., Guil, F., Martín, M., Higuero, R., Soria, C. & Guzmán, J. 2010: Factors influencing the presence of the cinereous vulture *Aegypius monachus* at carcasses: Food preferences and implications for the management of supplementary feeding sites. — *Wildlife Biology* 16: 25–34. 10.2981/09-037.
- Moreno-Opo, R., Trujillano, A. & Margalida, A. 2015: Optimization of supplementary feeding programs for European vultures depends on environmental and management factors. — *Ecosphere* 6(7): 1–15. 27. 10.1890/ES15-00009.1.
- Muñoz, A.R., Real, R., Barbosa, A.M. & Vargas, M. 2005: Modelling the distribution of Bonelli's eagle in Spain: implications for conservation planning. — *Diversity and Distributions* 11: 477–486.
- Newton, I. 1979: *Population Ecology of Raptors*. — Buteo Books, Vermillion SD, U.S.A.
- NSI 2012: *Population and Settlements Census in 2011, Vol.1: population by regions, municipalities and settlements*, NSI Sofia. (In Bulgarian).
- Olea, P.P. & Mateo-Tomás, P. 2009: The role of traditional farming practices in ecosystem conservation: The case of transhumance and vultures. — *Biological Conservation* 142: 1844–1853.
- Olea, P.P. & Mateo-Tomás, P. 2011: Spatially explicit estimation of occupancy, detection probability and survey effort needed to inform conservation planning. — *Diversity and Distributions* 17: 714–724.
- Olea, P. & Mateo-Tomás, P. 2013: Assessing Species Habitat Using Google Street View: A Case Study of Cliff-Nesting Vultures. — *PLoS ONE* 8: 10.1371.
- Parra, J. & Telleria, J.L. 2004: The increase in the Spanish population of Griffon Vulture *Gyps fulvus* during 1989–1999: effects of food and nest site availability. — *Bird Conservation International* 14: 33–41.
- Pierre-Rossi, J. 1996: Statistical tool for soil biology. XI. Autocorrelogram and Mantel test. — *European journal of soil biology* 32(4): 195–203.
- Polce, C. 2004: Application of Geographic Information Systems to assess environmental suitability for reintroduction of Griffon Vulture (*Gyps fulvus*) in Retezat National Park, Romania. — Report, International Institute for geoinformation science and earth observation Enschede, The Netherlands.
- QGIS Development Team. 2016: *QGIS: Geographic Information System*. — Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>.
- R Development Core Team. 2012: *R: A language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Sebastián-González, E., Morales-Reyes, Z., Botella, F., Naves, L., Pérez-García, J., Mateo-Tomás, P., Olea, P., Moleón, M., Barbosa, J., Hiraldo, F., Arrondo, E., Donazar, J., Cortés-Avizanda, A., Selva, N., Lambertucci, S., Bhattacharjee, A., Brewer, A., Abernethy, E., Turner, K. & Sánchez-Zapata, J. 2020: Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. — *Ecography* 43: 1143–1155.
- Sergio, F. & Newton, I. 2003: Occupancy as a measure of territory quality. — *Journal of Animal Ecology* 72: 857–865.
- Schick, R., Goldstein, J., & Lutcavage, M. 2004: Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). — *Fisheries Oceanography* 13: 225–238.
- Skartsi, T., Vasilakis, D. & Elorriaga, J. 2009: Population trends and conservation of vultures in the National Park of Dadia-Lefkimi-Soufli forest. — In *The Dadia-Lefkimi-Soufli National Park, Greece: Biodiversity, Management and Conservation* (ed Catsadorakis, G.): 183–193. — WWF-Hellas, Athens.
- StatSoft Inc. 2004: *STATISTICA (data analysis software system)*, version 7. — StatSoft Inc., Tulsa, USA: [www.statsoft.com](http://www.statsoft.com).
- Stoychev S., Hristov, H., Iankov, P. & Demerdzhiev, D. 2004: Birds in the Bulgarian part of the Eastern Rhodopes. — In *Biodiversity of Bulgaria. Biodiversity of Eastern Rhodopes (Bulgaria and Greece)* (eds Beron P. & Popov A.): 881–894. — Pensoft & Natural Museum of Natural History, Sofia.
- Stoynov, E., Peshev, H., Vangelova, N. & Grozdanov, A. 2017: Ranging Behaviour of the Griffon Vulture *Gyps fulvus* in Kresna Gorge and South-western Bulgaria. — Technical Report on Action A1 of the LIFE11 NAT/BG/363, Fund for Wild Flora and Fauna, Blagoevgrad. 10.13140/RG.2.2.31588.58242.
- Sutherland, W. 2000: *The Conservation Handbook: research, management and policy*. — Blackwell science, Oxford.
- Xirouchakis, S. & Mylonas, M. 2004: Griffon Vulture (*Gyps fulvus*) distribution and density in Crete. — *Israeli Journal of Zoology* 50: 351–354.
- Xirouchakis, S. & Mylonas, M. 2005: Selection of Breeding Cliffs by Griffon Vultures *Gyps fulvus* in Crete (Greece). — *Acta Ornithologica* 40: 155–161.