



## Review Article

# Long-term size and range changes of the Griffon Vulture *Gyps fulvus* population in the Balkans: a review

DOBROMIR DOBREV<sup>1\*</sup> , RIGAS TSIKIRIS<sup>2</sup>, THEODORA SKARTSI<sup>3</sup>, VLADIMIR DOBREV<sup>1</sup>, VOLEN ARKUMAREV<sup>1</sup>, KALIOPI STARA<sup>4</sup> , ANTON STAMENOV<sup>1</sup>, NIKOS PROBONAS<sup>5</sup>, THEODOROS KOMINOS<sup>6</sup>, ANTONIA GALANAKI<sup>6</sup>, ELZBIETA KRET<sup>3</sup>, BEN HALLMANN<sup>7</sup>, BRATISLAV GRUBAČ<sup>8</sup>, GORAN SUŠIĆ<sup>9</sup>, SAŠA MARINKOVIĆ<sup>10</sup>, IRENA HRIBŠEK<sup>11</sup>, STEFAN SKORIĆ<sup>12</sup>, HANS JERRENTROP<sup>13</sup>, VEDRAN LUCIĆ<sup>14</sup>, SVEN KAPELJ<sup>15</sup>, GEORGI STOYANOV<sup>16</sup>, SYLVIA ZAKKAK<sup>17</sup>, HRISTO HRISTOV<sup>18</sup>, STOYCHO STOYCHEV<sup>1</sup>, LAVRENTIS SIDIROPOULOS<sup>19</sup>, TAULANT BINO<sup>20</sup> and DIMITAR DEMERDZHIEV<sup>1</sup>

<sup>1</sup>Bulgarian Society for the Protection of Birds, Sofia 1111, 71 'Yavorov', etr.4, ap.1; E-mail: [dobromir.dobrev@bspb.org](mailto:dobromir.dobrev@bspb.org).

<sup>2</sup>Forestry Service of Ioannina, M. Kotopouli 62, Ioannina, 45445 Greece.

<sup>3</sup>WWF Greece, 21 Lembesi, 11743 Athens, Greece.

<sup>4</sup>University of Ioannina, Department of Biological Applications and Technology, Laboratory of Ecology, University campus. 45110, Ioannina, Greece.

<sup>5</sup>Hellenic Ornithological Society, Themistokleous 80, 10681, Athens, Greece.

<sup>6</sup>Department of Zoology, School of Biology, Aristotle University of Thessaloniki, GR-54124, Thessaloniki, Greece.

<sup>7</sup>40008 Rapsani, Greece.

<sup>8</sup>Nemanjina 1/14, 35250 Paraćin, Serbia.

<sup>9</sup>Grifon - Birds of Prey Conservation Society, Ornithological station Rijeka CASA, Ružičeva 5/2, HR-51000 Rijeka, Croatia.

<sup>10</sup>Institute for Biological Research "Siniša Stanković", National Institute of Republic of Serbia, University of Belgrade, Bulevar Despota Stefana 142, 11060 Belgrade, Serbia.

<sup>11</sup>Birds of Prey Protection Foundation, Bulevar Stefana 142, 11060 Belgrade, Serbia.

<sup>12</sup>Institute for Multidisciplinary Research, University of Belgrade, Kneza Višeslava 1, 11030 Belgrade, Serbia.

<sup>13</sup>A-2273 Hohenau an der March, Rathausplatz 1, Germany.

<sup>14</sup>HR-10000 Zagreb, Croatia.

<sup>15</sup>Association BIOM/BirdLife Croatia, Preradovićevo 34, HR-10000 Zagreb, Croatia.

<sup>16</sup>Birds of Prey Protection Society, 23 Golyam Bratan Str., 1618 Sofia, Bulgaria.

<sup>17</sup>Management Body of Dadia-Lefkimi-Soufli Forest National Park Dadia, 68400, P.O. 1413 Dadia, Greece.

<sup>18</sup>Rewilding Rhodopes Foundation, Haskovo 6300, 41 Bulgaria Blvd.

<sup>19</sup>Kanari 1 st, 57010, Asvestochori, Greece.

<sup>20</sup>Albanian Ornithological Society, "Ymer Kurti" Street, Olympia Center, 2nd Floor, No. 24, 1001, Tirana, Albania.

\* Author for correspondence; email: [dobromir.dobrev@bspb.org](mailto:dobromir.dobrev@bspb.org)

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## Summary

The Eurasian Griffon Vulture *Gyps fulvus* is a large Palearctic, Indohimalayan and Afrotropical Old-World vulture. The species' range is vast, encompassing territories from the Pyrenees to the Himalayas. We reviewed and analysed a long-term data set for Griffon Vulture in the Balkans to estimate the change in its population size and range between 1980 and 2019. After a large historical decline, the Griffon Vulture population slightly increased in the last 39 years ( $\lambda = 1.02$ ) and reached 445–565 pairs in 2019. We recorded a gradual increase of Griffon Vulture subpopulations in Serbia ( $\lambda = 1.08 \pm 0.003$ ), Bulgaria ( $\lambda = 1.08 \pm 0.003$ ) and Croatia ( $\lambda = 1.05 \pm 0.005$ ) and steep to a moderate decline of the species subpopulations in Greece ( $\lambda = 0.88 \pm 0.005$ ) and North Macedonia ( $\lambda = 0.94 \pm 0.01$ ). However, species range contracted to half of its former range in the same period. It occurred in 42 UTM squares in the 1980–1990 period and only 20 UTM squares between 2011 and 2019 and concentrated into three source subpopulations in Bulgaria, Serbia, and Croatia. Following reintroductions of the Griffon Vulture in Bulgaria, new colonies were formed at three novel localities after 2010. Regular movements of individuals between the different subpopulations exist nowadays. Therefore, preservation of both current and former core areas used for breeding and roosting is essential for species conservation in the region. However, the Griffon Vulture still faces severe threats and risk of local extinction. Various hazards such as poisoning, collision with energy infrastructure, disturbance and habitat alteration are depleting the status of the Balkan population and its full recovery. Further studies should analyse age-specific survival and mortality, recruitment, genetic relatedness, spatial use to inform the viability of this population in the future.

**Keywords:** demography, scavenger, Europe, status, monitoring

## Introduction

Nowadays, scavengers, in particular vultures, face a high risk of extinction due to numerous threats that occur in their breeding, migration, and wintering areas (Buechley and Sekercioğlu 2016, Donázar et al. 2016, McClure et al. 2018). Studying the demography of raptor species is an essential part of the conservation process and is needed to understand their population dynamics (Steenhof and Newton 2007). Estimating population trends in long-lived species with large ranges is a major and complex task (Balmford et al. 2003). The reliability of trend estimates and associated uncertainties is therefore a primary issue in conservation ecology and management (Akcakaya et al. 2000, Rodrigues et al. 2006, Knappe 2016). Vultures inhabit large territories and are limited by the environmental capacity (Donázar 1987). Therefore, a better assessment of the processes occurring in the entire population will be achieved when the larger part of it is studied (Margalida et al. 2020). This is particularly important for vultures because they are long-lived, wander over vast geographic areas, can settle temporarily and exploit spatially unpredictable food resources (Donázar et al. 2016). Such large-scale studies might outline regional demographic differences and reveal their effect on the entire population (Del Moral and Molina 2018). Hence, a comprehensive assessment of vulture population status and trends can support management and inform appropriate conservation measures.

The Eurasian Griffon Vulture *Gyps fulvus* is a large Old-World vulture with a vast range spreading from Portugal to the Himalayan region (Cramp and Simmons 1980, Birdlife International 2017) (Figure 1). The species consumes the carcasses of domestic and wild ungulates and thus provides a paramount ecosystem service (Morales-Reyes et al. 2015). The Griffon Vulture is classified globally as 'Least Concern' with an increasing population and range, abruptly different across geographical regions (BirdLife International 2017, Botha

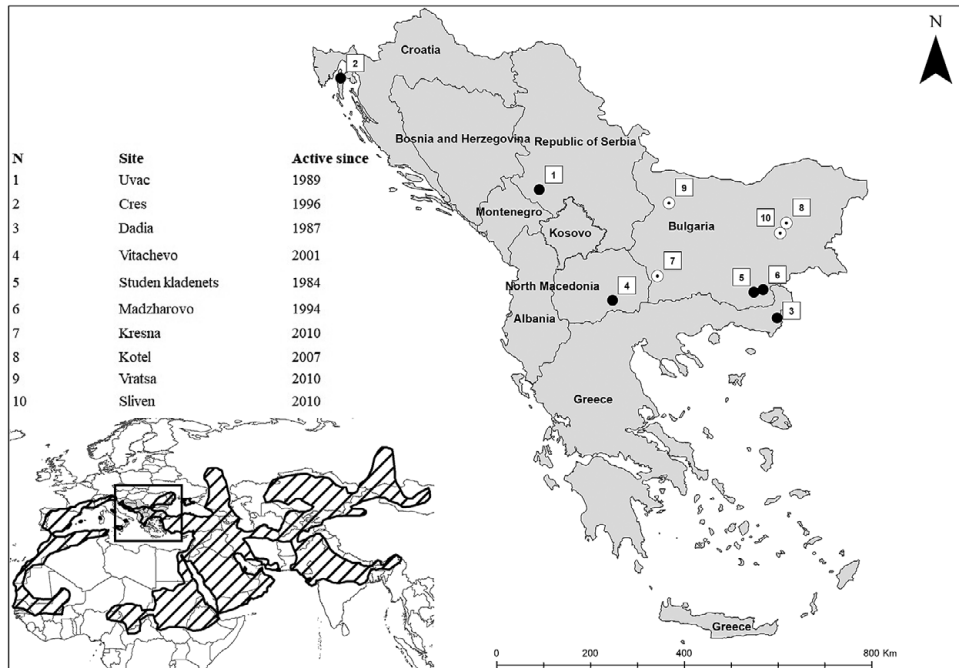


Figure 1. General map of the study area, marked in grey. The hatched area represents the Griffon Vulture population range (Birdlife International 2017) and shows the key location of the Griffon Vulture's Balkan population with respect to species global population range. Black dots represent main operational feeding sites (Azmanis *et al.* 2009, Marinković *et al.* 2020), while the white dots show both main active feeding and reintroduction sites in the Balkans with the start year of their operation.

*et al.* 2017). Over 85% of the European population of the Griffon Vulture is concentrated in Spain, where it has increased substantially in the last few decades and become the most abundant at a global scale (Botha *et al.* 2017, Del Moral and Molina 2018). In contrast, the Griffon Vulture population in the Balkans underwent a large decline during the past century and is thus, considered regionally endangered (Andevski 2013). This population occurs at the crossroads between the Middle East and Africa on one hand and the healthy Western European populations of the Iberian Peninsula and southern France on the other. Therefore, conservation of this bridge population is important to sustain the natural connection between the east and west of the species' range.

Griffon Vulture populations in the Balkans underwent a catastrophic decline during the 1950s–70s due to massive poisoning events that brought the species to local extinction in many areas. As a result, its population dropped to c.500 pairs in the 1990s (Grubach 2005, Bourdakis 2019). This state of emergency brought international attention to the region and intensive conservation actions were applied after 2002 in most Balkan countries (Andevski 2013). In Bulgaria, the Griffon Vulture population numbered no more than a few pairs at the beginning of the 1980s (Demerdzhiev *et al.* 2014a). In Serbia at the same time, its population was estimated at 32 breeding pairs (Marinković *et al.* 1985, Grubach 2014). This population, however, was boosted by recolonization of vultures from Bosnia and Herzegovina, where the breeding sites were abandoned during the war in the 1990s (Marinković *et al.* 2012, Grubach 2014). In Croatia, the population was estimated at 110 pairs in 1983 (Perco 1983). The Griffon Vulture was

Table 1. Status and population estimates per countries for 2019.

Country	Population size, pairs	Range, km <sup>2</sup>	Trend	Status	Year of estimate	Reference
Albania	0	0	N/A	extinct	1996	Andevski 2013
Bulgaria (natal)	96	5,000	increasing	active	2019	Dobrev <i>et al.</i> 2019
Bulgaria (reintroduced)	34	10,000	increasing	active	2019	Stoynov <i>et al.</i> 2018a; Stoynov 2019; greenbalkans.org
Greece (mainland Thrace)	7	5,000	fluctuating	active	2019	Skartsi 2019
Greece (mainland Pindos)	8–19	7,500	decreasing	active	2019	Tsiakiris 2019; Theodoros Kominos unpubl. data
Greece (Aegean)	14	5,000	increasing	active	2019	Nikos Probonas unpubl. data
Greece (Crete)*	250–340	N/A	increasing	active	2019	Xirouchakis 2019
Serbia	164–262	7,500	increasing	active	2018	Grubach <i>et al.</i> 2018; Marinković 2019
North Macedonia	12–13	5,000	decreasing	active	2017	Marinković <i>et al.</i> 2020
Croatia	110–120	2,500	decreasing	active	2019	Peshev <i>et al.</i> 2018
Bosnia and Herzegovina	0	N/A	N/A	extinct	1992	Kapelj and Modric 2017, G. Sušić pers. obs. Marinković 2006
<b>TOTAL BALKANS*</b>	<b>445–565</b>	<b>47,500</b>	<b>Slight increase</b>		<b>2019</b>	<b>This study</b>

\* Excluding Crete population

widespread in North Macedonia in the past, but in the period 1980–2002 numbered no more than 36–38 pairs (Grubach 2014). Greece used to be the stronghold of the species in the Balkans with the largest population, and a number of colonies known from all over the country, including several islands (Handrinos & Akriotis 1997, Theodoros Kominos unpubl. data) and was estimated at 200 pairs in the 1980s (Handrinos 1985, Xirouchakis and Tsiakiris 2009, Sidiropoulos *et al.* 2013). Only the population on the island of Crete was stable and increased recently to 250–340 pairs (Xirouchakis 2019) (Table 1).

Understanding population size and trend, range dynamics, and impact of threats is essential to inform conservation actions and policies across all Balkan countries. Therefore the current study aimed to review and analyse the long-term trend of the Balkan Griffon Vulture population. The objectives of our study were to (1) estimate the population size and trends, (2) review and define the breeding range, (3) review major past and current threats, and (4) suggest conservation measures to support the recovery of the species in the Balkans.

## Methods

### Study area

The study was conducted in south-eastern Europe, encompassing the territory of the Balkan Peninsula (42°N, 22°E; ≈ 438,000 km<sup>2</sup>) (excluding European Turkey, Romania, Slovenia and Crete; Figure 1). We excluded the island of Crete because of the isolation of this population and its lack of

connectivity to the mainland population. The other countries were excluded because of the negligible percentage of their territory falling within the geographical borders of the Balkans and the lack of relevant data and/or contemporary breeding records (Mihelič and Genero 2005).

### Population monitoring

We reviewed published and unpublished sources of information and retrieved data on Griffon Vulture population size, distribution, dynamics, and threats between 1980 and 2019 in five Balkan countries (Table S1 in the online supplementary materials). Our large-scale monitoring study used standardized counts of breeding attempts, without accounting for breeding parameters, repeated over time across the different countries to obtain the best assessment of species status (Sutherland 2000, Keller 2017) (Table 1). Whenever two alternative estimates for the same locality were present, we averaged them to avoid over- or under-parametrization of the sample (Sutherland 2006). We used the population trend index as a measure of population change over the study period because this index is proportional to the change in status when the monitoring programme is irregular or ill-designed (Gregory *et al.* 2004). However, because data were collected with different intensity and survey effort, it is possible that our estimates understate or overstate the real species range and numbers locally. We also collected information on the major threats and provided conservation insights on the Griffon Vulture population (Slotta-Bachmayr *et al.* 2005).

### Estimation of trend, range, and statistical procedures

We estimated the population trend and its percentage change in the study period with 'rtrim' v 2.1.1 (Pannekoek and van Strien 2005, Pannekoek *et al.* 2018) and 'poptrend' v. 0.1.0 packages (Knape 2016) in R Studio v. 3.4.3 (R Core Team 2013). We used site effects in combination with a linear trend effect to handle variation among survey localities and skewness of the data input (Pannekoek and van Strien 2005, Knape 2016). We used model 2 in 'rtrim' to compute the overall Griffon Vulture population trend. We set all years as change points, where in each year the trend changes, to constrain over-dispersion in the model (Pannekoek *et al.* 2018). We further used the 'change' function in 'poptrend' to compute the estimated percentage change in the population between two given time points (Knape 2016).

To measure the species' range, we used the confirmed breeding records obtained by our study to outline Griffon Vulture distribution in four discrete periods: 1980–1990, 1991–2000, 2001–2010 and 2011–2019 (Robertson *et al.* 2010). Each colony between 1980 and 2019 with known size and location was assigned to a UTM reference grid (datum WGS 1984) (Donázar and Genero 1997, Hagemeyer and Blair 1997).

## Results

Griffon Vulture population size on the Balkan Peninsula slightly increased during 1980–2019 ( $\lambda = 1.02 \pm 0.32$ ) and enlarged by 42% (CI: 30%–174%) for the same period. However, the population was in constant sink between 1980 and 1990 ( $-13\%$ ), 1991 and 2000 ( $-19\%$ ) and reverted in 2001–2010. Since that period, it showed a gradual population recovery, very prominent from 2008 onwards and increased by 15% (CI:  $-41\%$ – $129\%$ ) during 2011–2019 but not in all remaining population nuclei (Figure 2). Contrary to the positive general tendency, local extinctions also occurred, for example, in Bosnia and Herzegovina in 1992, in Albania in 1996 and in Montenegro, where the Griffon Vulture was completely extirpated (Figure 4, Table 1). A large decrease was also recorded in Greece ( $\lambda = 0.88 \pm 0.005$ ) and moderate in North Macedonia ( $\lambda = 0.94 \pm 0.01$ ). On the other hand, a stable increase was recorded in Serbia ( $\lambda = 1.08 \pm 0.003$ ), Bulgaria ( $\lambda = 1.08 \pm 0.003$ ) and Croatia ( $\lambda = 1.05 \pm 0.005$ ) (Figure 3). Nowadays, the Serbian subpopulation is the most abundant in the Balkans ( $n = 164$ – $262$  pairs), while the smallest is found in North Macedonia ( $n = 12$ – $13$  pairs). The population size was estimated at 445–565 pairs in the Balkans in 2019 (Table 1).

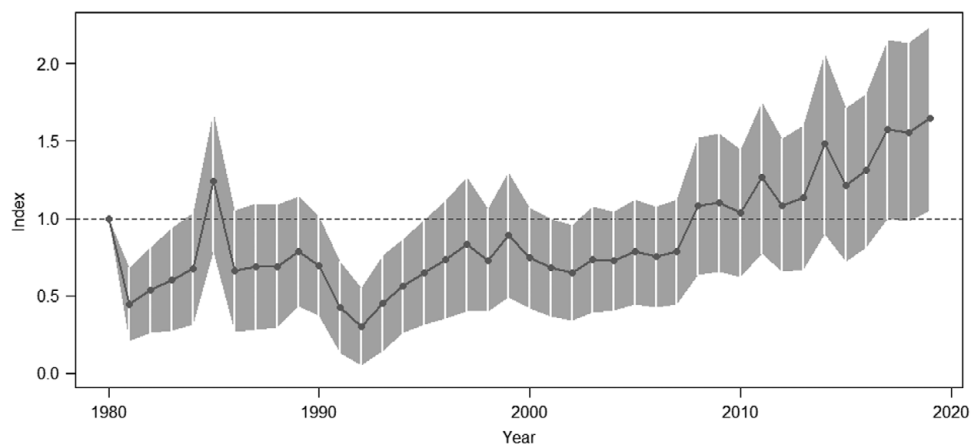


Figure 2. Griffon Vulture population trend in the Balkans between 1980 and 2019. The solid line represents the population size index in the period along with its standard deviations (shaded area).

Griffon Vulture distribution contracted and condensed during 1980–2019 (Figure 4). In the first period (1980–1990), the species was more widely dispersed in smaller numbers across the region, and larger nuclei existed in Greece (42 UTM squares). The estimated range was 105,000 km<sup>2</sup>. The range shrank significantly in the second period when it occurred in 29 UTM squares and occupied 72,500 km<sup>2</sup> (Figure 4). During 2001–2010, Griffon Vultures occurred in 21 UTM squares or at 52,500 km<sup>2</sup>. Despite the population recovery at the end of that decade, the species occurred in its smallest range during 2011–2019 (20 UTM squares; 50,000 km<sup>2</sup>). As a result, the population was condensed into several larger breeding nuclei in Bulgaria, Croatia and Serbia. During the first period, Griffon Vulture breeding range equalled 24% of the Balkans territory compared to 11% today. The species disappeared from Bosnia and Herzegovina and contracted significantly in North Macedonia, Greece, and Croatia. The range expanded only in Bulgaria and Serbia (Figure 4, Table 1).

## Discussion

After the catastrophic crash of the Griffon Vulture in the Balkans (Andevski 2013, Tsiakiris and Pergantis 2019), today the population is slowly recovering at an annual rate of about 1% in almost the last four decades. However, this change was heterogeneous in the different countries. The population increase in the species' stronghold (Serbia, Bulgaria and Croatia) might be a result of a shift of pairs breeding in neighbouring colonies, long-term conservation efforts, reintroduction programmes and reduced mortality (Marinković 1999, Skartsi et al. 2009, Stoynov et al. 2018a). For example, the recent population increase in Bulgaria is thought to be supported by the reintroduction programme, the operation of several supplementary feeding sites (Stoynov et al. 2018a) and long-term conservation efforts for the indigenous population (Dobrev and Stoychev 2013). This possibly affected neighbouring areas, because birds from the reintroduction programme have been observed breeding in other parts of Bulgaria, Greece, and North Macedonia (Zakkak et al. 2015). Hence, intensive conservation programmes and fewer poisoning incidents sustained stable and increasing population cores acting as a source for the periphery of the main colonies in the study area (Skartsi et al. 2009). Meanwhile, several temporary settlement areas in Serbia, Greece and Bulgaria were formed, associated with either operational feeding sites or areas of extensive livestock husbandry, as occurred in the Pindos massif in Greece (Tsiakiris and Pergantis 2019). Supplementary feeding sites, established along with the main surviving breeding nuclei and

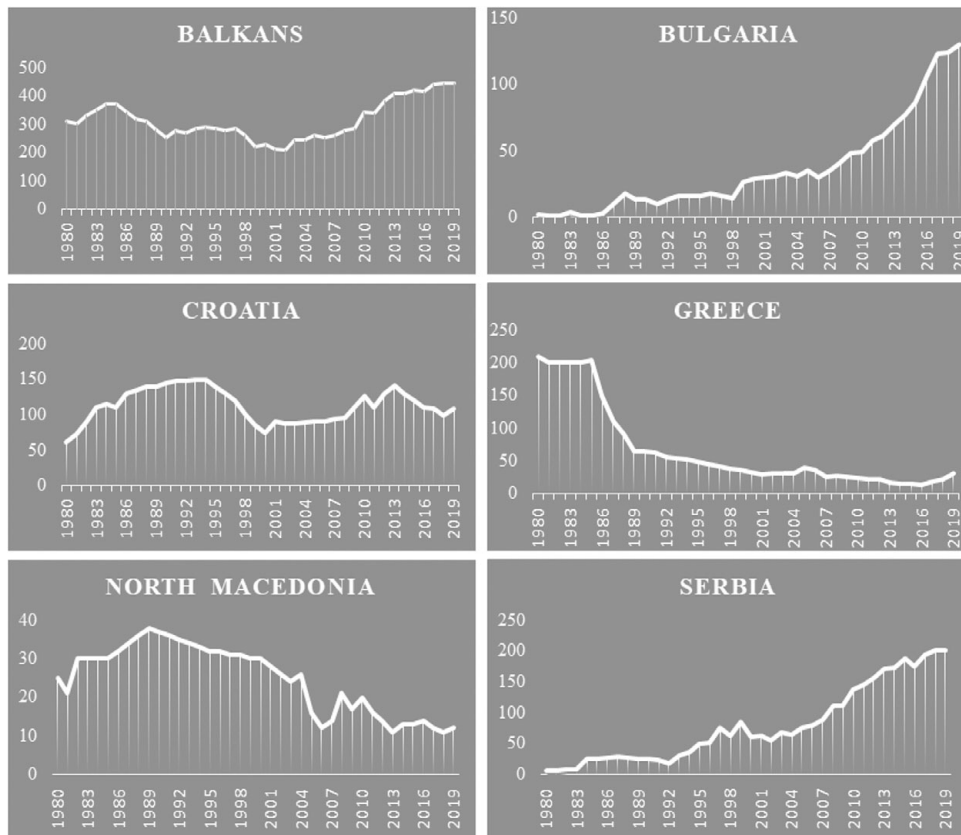


Figure 3. Overall Griffon Vulture population size dynamics in the Balkans in the period 1980–2019 in each country and the Balkans in total. A solid white line represents the number of pairs during the period. Years are given on the X-axis and the number of pairs on the Y-axis.

reintroduction areas, have played an important role in conservation of the species. Moreover, our data from 2012 onwards from Bulgaria, Greece, Serbia, and North Macedonia show a slightly increasing size of the Griffon Vulture population in the pre-breeding season ( $678 \pm 34$  birds per year, min = 562, max = 811) (authors' unpubl. data). We hypothesize that this increase is related to the overall increment of the core population that also activated long-abandoned colonies. For example, a marked individual of Croatian origin has been found breeding in the Aegean islands successfully for several consecutive years (N. Probonas unpubl. data).

While the Griffon Vulture population increased in three of the countries that could be characterised as “Vulture Safe Zones” (IUCN Bangladesh 2016), the population declined in most other areas. Poisoning – accidental and intentional – is considered the most severe threat, with a tremendous impact on vulture populations and range globally (Bijleveld 1974, Stoyanov 2010, Cano *et al.* 2016, Botha *et al.* 2017, Margalida and Mateo 2019). We hypothesize that mass poisoning campaigns linked to human-wildlife conflict and extermination of so-called pest species (wolves, foxes, etc.) (Handrinos 1985, Marinković and Orlandić 1994, Grubach 2005) have resulted in the rapid decline of the Balkan population. For example, nearly 500 individuals were poisoned in the last 20 years in the Balkans (Ntemiri *et al.* 2018, Pantovic and Andevski 2018, Dobrev *et al.* 2019, Kret *et al.* 2019), each incident sometimes involving marked birds from several different countries (R. Tsiakiris pers. obs.). Likewise, vulture populations in Africa decreased by 60% on



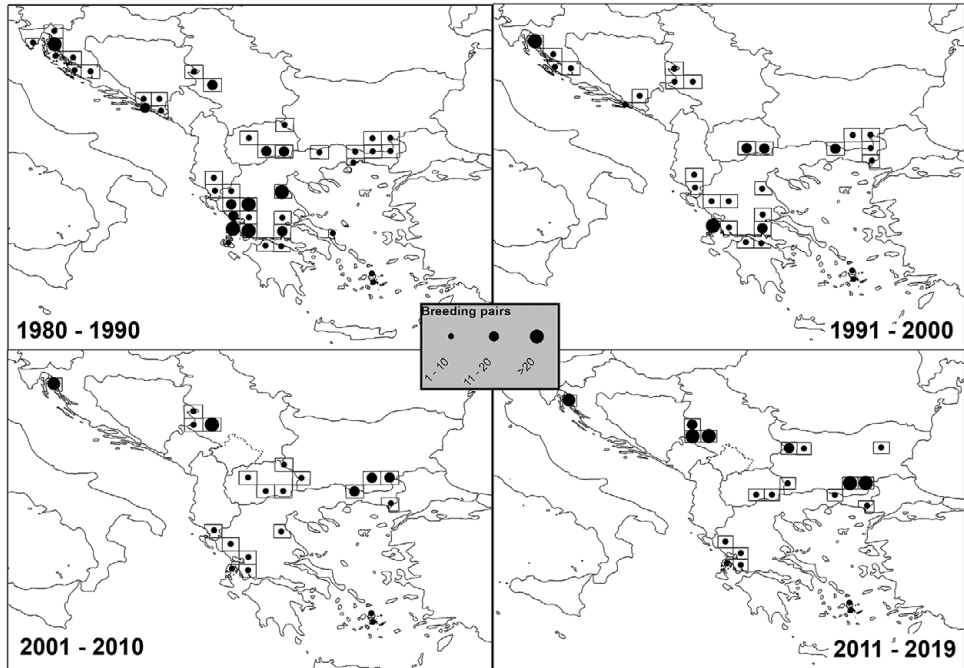


Figure 4. Range of the Griffon Vulture on the Balkan Peninsula and population size (pairs) within each 50x50 km grid cell between 1980 and 2019. Population size represents the maximum number of registered pairs within each square for the given period.

average in the last 30 years (Ogada *et al.* 2015, Botha *et al.* 2017). Therefore, illegal poison baits can easily affect vulture populations and halt recovery (Newton 2008). For example, in 2012 in Nestos (Northern Greece), 40 Griffon Vultures and four Golden Eagles *Aquila chrysaetos* died in one incident. We suggest the magnitude and type of poisoning could be culturally and country-specific, although with the identical motivation (Pantovic and Andevski 2018). However, differences in livestock husbandry practices (Stoynov *et al.* 2014) and the distribution of large terrestrial predators might indicate the areas where most poison baits are used (Angelov *et al.* 2006, Stoynov *et al.* 2015, Ntemiri *et al.* 2018) and explain the different population status among countries.

The regional differences and rates of population recovery in the Balkans might also result from mortality related to energy infrastructure (e.g. power lines and wind turbines) (Carcamo *et al.* 2011, Douteau *et al.* 2011, Vasilakis *et al.* 2016), similar to Spain (Carrete *et al.* 2012) or globally (Ferrer 2012). Griffon Vulture in the Balkans was dependent for centuries on extensive livestock grazing and parts of the historical distribution were associated with transhumance herding routes (Marinković and Karadžić 1999, Tsiakiris and Pergantis 2019). Thus, the loss of traditional pastoral practices may have negatively affected the Griffon Vulture in the long-term (Olea and Mateo-Tomas 2009, Margalida and Colomer 2012). Such changes might also result from military conflicts that directly repel birds, lead to the abandonment of rural areas and the consequent extinction of animal husbandry (Marinković *et al.* 2006). Nowadays, restricted use of animal by-products, removal of dead livestock from the countryside, and EU sanitary regulations have led to an immense change in carcass disposal and have had diverse effects on vulture populations in Spain (Donázar *et al.* 2009, Margalida *et al.* 2018). Consequently, the complicated geographical, political, and social atmosphere in the Balkans can bring more uncertainties in the future regarding EU sanitary regulations (Margalida *et al.* 2010).



We found that the overall population growth rate in our area is notably lower than that recorded in France (Razin *et al.* 2008, Grubach 2014) and Spain (Del Moral and Molina 2018) in the same period. However, these countries are not comparable with the Balkans, because of the size and connectivity of those steeply increasing populations. Spain holds the largest and densest population of the Griffon Vulture at a global scale (>30,000 pairs; Del Moral and Molina 2018) reflecting the great availability of food and nest sites (Parra and Telleria 2004). Decreased mortality rates (Donázar 1987) and the large breeding output of this population can probably explain the difference in the growth rates between the Balkan metapopulation and the Pyrenean–French one, even under a density-dependence scenario. Besides this, such differences might be related to the sympatric presence of vultures and large terrestrial predators (Stoyanov *et al.* 2015) or differences in juvenile survival (Van Beest *et al.* 2008) during migration and wintering (Griesinger 1998). Probably a high percentage of juveniles of Balkan origin spend their first years in the Middle East, Saudi Arabia, Yemen and as far as Africa (Sušić 2000, Tsiakiris *et al.* 2018, Arkumarev *et al.* 2019). Currently, an unknown combination of possible high mortality of juveniles and immature birds in these areas and low emigration (Schaub *et al.* 2013) can affect the slow population recovery in the Balkans. This population is a natural bridge to the species range in Asia and Northern Africa and is thus an important genetic reservoir (Davidović *et al.* 2020). We have recorded constant exchange of birds between the different subpopulations in the Balkans (Sušić 2000, Grubach 2014, Peshev *et al.* 2015, 2018, Tsiakiris *et al.* 2018, Stanković *et al.* 2019, Skartsi 2019) and neighbouring ones (Genero *et al.* 2020). For example, birds from Croatia are breeding on the Aegean Sea islands in Greece (N. Probonas unpubl. data), Serbia (S. Marinković unpubl. data) and Italy (F. Genero pers. obs.). Furthermore, Griffon Vultures originating from Spain have been recorded in Bulgaria (Stoyanov *et al.* 2020), and birds originating from Bulgaria (reintroduced) and Croatia have been observed in France and Spain (Sušić 2013, Green Balkans unpubl. data). This proves that consistent immigration and emigration of Griffon Vultures in our study area still exists, though it could be at a very low rate. These are important population growth factors (Demerdzhiev *et al.* 2015, Lieury *et al.* 2016) and could possibly affect and ease the colonisation of new territories in the future (Borello and Borello 2002).

We found that the species' range in the Balkans contracted significantly in the last 40 years. This phenomenon is also supported by other studies from Spain where the range expanded in certain areas (Mateo-Tomas and Olea 2011), associated with the availability of nesting sites and food abundance (Parra and Telleria 2004). In such a scenario, the species will naturally occupy the high-quality habitats first, as a non-saturated population and lack of density dependence (Sergio and Newton 2003, Demerdzhiev *et al.* 2014a). The same thing could have happened in our area, where the species progressed in the most optimal habitats (Sergio and Newton 2003). Such a fact might explain why the Griffon Vulture is more abundant in certain countries/nuclei, rather than being dispersed over a larger area. This finding implies that the species' range might be defined not only by certain ecological conditions (Mateo-Tomas and Olea 2011), but also by the spatial and temporal distribution of threats. Considering the large spatial and temporal scale of our study, monitoring gaps might also bias results (Baumgart 1974). Therefore, population size, trend, and range should be monitored regularly to inform conservation adequately (Martinez *et al.* 1997, Dobrev and Stoychev 2013). Former breeding sites that were occupied temporarily or used for roosting (especially during pre-breeding) (Mateo-Tomas and Olea 2010, 2011) should be protected as they can support species recovery if suitable conditions persist over time, emigration exists, and major threats are halted, as the recent recolonization of Mt Valtos and Nestos gorge in Greece indicate (Tsiakiris 2019, H. Jerrentrup pers. obs.).

### *Conservation concerns and implications*

Conservation actions can have a positive effect on the survival of birds and may be used successfully in the management of endangered species (Demerdzhiev *et al.* 2014b). Actions against direct and indirect poisoning need to be undertaken immediately, at a large scale and prior to the emergence of poisoning events in the Balkans (Ntemiri *et al.* 2018, Pantovic and Andevski 2018). Poisoning

activities must be recognized by the enforcement agencies across the region and this threat eliminated or minimized. The development of GPS technologies must be used to help to identify vulture core-use areas and poisoning hotspots to focus conservation actions there (Buechley et al. 2018, Stoynov et al. 2018b).

In the short-term, urgent species-specific measures in regard to food provisioning, with operation of more small and non-permanent feeding sites need to be promoted to enhance the conservation of the Griffon Vulture (Azmanis et al. 2009, Moreno-Opo et al. 2015) (Figure 1). In the long-term, the application of EU regulations regarding the in-situ disposal of dead livestock, support for extensive grazing through the CAP, augmentation of wild ungulate herds, promotion of the avian scavenger guild as a provider of vital ecosystem services, and promotion of the species' biocultural significance are recommended to sustain the population recovery (Morales-Reyes et al. 2015, Donázar et al. 2016, Stara et al. 2016). Meanwhile, a strong policy lobby is needed to propose modern and diverse mitigation solutions to combat energy infrastructure casualties (Ferrer 2012, Vasilakis et al. 2016, 2017, Kafetzis et al. 2017, May et al. 2020, Serrano et al. 2020).

Reintroduction can support the recovery of the Griffon Vulture (Peshev et al. 2015, 2018). In Bulgaria, three new breeding nuclei were established in the Balkan Mountains and Pirin Mountains as a result of long-term reintroduction efforts (Stoynov et al. 2018a). Reintroduction programmes have also been successfully applied in Europe (Sarrazin and Barbault 1996, Le Gouar et al. 2008). However, such measures have to be implemented cautiously, especially when the main threats are ongoing (Peshev et al. 2018). More attention should focus on the long-term sustainability of the reintroductions and sound, expert justification before implementation.

The proposed policies and measures need to be implemented widely and become top rank priorities for governments in the region. Thus, when the main threats are reduced to a minimum over a sufficiently large scale, the high breeding rates recorded in the region (Demerdzhiev et al. 2014a) and well-conditioned food habitats can support population recovery in the future. If sustained it will safeguard the connection between the east and the west of species' global range.

## Supplementary Material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0959270921000198>.

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