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THE LONG-TERM TREND, REPRODUCTIVE PERFORMANCE AND COLONY SHIFTING OF THE EURASIAN GRIFFON *Gyps fulvus* IN CROATIA

Dugoročni trend, reprodukcijski parametri i pomicanje kolonija bjeloglavog supa Gyps fulvus u Hrvatskoj

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ABSTRACT

The Eurasian Griffon population in Croatia declined during most of the 20th century. Here the results related to the population trend and reproduction parameters and phenomena called colony shifting based on a 40-year research (1981 – 2021) are presented. The population declined from about 110-150 pairs in 10 colonies in 1981 to 78-95 pairs in 6 colonies in 1999, and subsequently increased to 141-150 pairs in 6 colonies in 2013. Since 1999, there have been no Griffons nesting in Paklenica, and it is possible that they all shifted to Kvarner, where 13% increase was recorded in 2000. In 2021, the total number was about 120 pairs on 5 islands: Cres, Plavnik, Krk, Prvić and Pag. Population density was estimated at 32.5 adult individuals/100 km^2 and 13.75 breeding pairs/100 km^2. Detailed population surveys were conducted during 15 years (2000 – 2014) to document cliffs' saturation/occupancy, inter- and intra-colony nest movements, and for 10 years, to calculate reproductive parameters: breeding success Bs = 0.60 ± 0.059 and productivity Pd = 0.55 ± 0.054. The nest site occupation was very low (M = 15.05%), implying that carrying capacity was not determined by cliff availability, and population is still far from saturation level. Six Kvarner islands' colonies are functionally one single colony with many nest-clusters on the same or on different

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islands, annually pulsating with numbers of active nests on cliffs and regularly shifting from cliff to cliff and back.

Keywords: population status, reproductive parameters, coloniality, nest-site movements, vultures.

INTRODUCTION

The Eurasian Griffon (shorter name: Griffon) *(Gyps fulvus*) is a colonial, cliff-nesting raptor specializing in feeding on mammals' carcasses (Johnson *et al.* 2006) distributed all over the western Palearctic, from the Mediterranean countries to India and Central Asia, and the north of Africa (Orta 1994, Birdlife International 2017, Botha *et al.* 2017, Dobrev *et al.* 2021). It has a long lifespan, delayed maturity, and low reproductive rates (Cramp & Simmons 1980, Ferguson - Lees & Christie 2001, García-Ripollés *et al.* 2011). The core range of the species in Europe is in the Mediterranean region, including several island populations: Sardinia and Sicily in Italy, Crete and Naxos in Greece, Cyprus, Mallorca in Spain, and Kvarner Archipelago in Croatia (Botha *et al.* 2017). The population in Europe is significantly increasing mainly due to the implementation of conservation measures (Botha *et al.* 2017), and has been estimated at 32,400 - 34,400 pairs (Birdlife International 2017), with more than 90% of them in Spain (Del Moral & Molina 2018). Recent estimation for Balkan countries analysed the change in its population size and range between 1980 and 2019 (Dobrev *et al.* 2021). After a major historical decline, the Griffon population slightly increased in the last 39 years and reached 445-565 pairs in 2019. There was a gradual increase in the Griffon subpopulations in Serbia, Bulgaria, and Croatia and steep-to-moderate decline in the species subpopulations in Greece and North Macedonia. The species range contracted to half of its former range in the same period (Dobrev *et al.* 2021).

Distribution and threats in Croatia

The Eurasian Griffon was once a widespread and common species in Croatia, nesting in continental part near the rivers Sava and Dunav (on trees, in the nests of Black vultures *Aegypius monachus* and/or White-tailed Eagles *Haliaeetus albicilla*), recorded at altogether 30 breeding localities (Sušić 2013a). It was distributed along the mainland coast from Istria to Dubrovnik (at the beginning of the 1980s, there were colonies in the Zrmanja, Krnjeza and Krka River canyons, on the Učka, Velebit, Biokovo and Mosor mountains, as well as on the mountains near Dubrovnik), as well as on 11 Adriatic islands (on Cres, Lošinj, Plavnik, Krk, Prvić, Rab, Sv. Grgur, Goli, Pag, Dugi otok and Brač). Its population has been declining during the most of the 20th century, and today the Griffon in Croatia breeds only on five islands in the Kvarner Archipelago, in north Adriatic (Cres, Plavnik, Krk, Prvić and Pag) (Sušić 2013a). Recent data on an isolated Griffon nest close to Senj (Döldmayr 2003) proved to be the outcome of a wrong determination, i.e. the author saw the nest of the Golden Eagle *Aquila chrysaetos* (pers.observ.).

The main threats to the Griffon population in Croatia include the use of poisons (mainly for the eradication of large carnivores), food shortage (the loss of traditional farming practices), veterinary and public health measures (which require the incineration or burying dead livestock), electrocution, direct persecution and recently windfarms (Sušić 2013a). As the Griffon in Croatia breeds on island cliffs, sometimes less than 10m above the sea level (7m, e.g., Schwammer 1988, or 8m, e.g., Perco *et al.* 1983), disturbance by growing recreational tourist activities (tourist boats intentionally approaching too close to breeding cliffs to observe Griffons, or organized groups diving in the sea just below the cliffs with nests) have a negative influence on population productivity (Perco *et al.* 1983, Sušić 2002, Sušić 2004). In the course of several years, up to 25 juveniles (almost 30% of all fledglings) had been found floating or drowned in the sea during summer months (Sušić & Radek 2013). Within 20 years (1996 – 2016), 162 injured, exhausted, or poisoned Griffons as well as young birds that fell into the sea during their first flights, were kept in the Recovery centre, and 138 were successfully released back into the nature (Sušić & Kruchten 2017, Sušić 2020).

With the increase of tourism and related industries, the interest in agricultural activities diminished. This resulted in a relative decline in pastureland and less manpower in traditional extensive method of sheep raising, and thus, in an increase in the forest (maquis) surface area (Perco *et al.* 1983). the Kvarner Archipelago is one of the last areas in Croatia continuing a long tradition of extensive sheep husbandry. Today there are less than 40,000 sheep in the Primorje-Gorski kotar County (which includes the Kvarner Archipelago), with the declining trend (Krvavica *et al.* 2021). The karst landscape and relatively mild climate were the most adequate for sheep husbandry. This resulted in keeping sheep outside all year round, with livestock mortality up to 10%. Any sheep that died in the field were traditionally left out, so their remains were available for Griffons' consummation (Rebrović 2017).

The island population of Griffons in Croatia is genetically separated from the western Mediterranean and other Balkan populations (Le Gouar *et al.* 2006, Le Gouar *et al.* 2008, Davidović *et al.* 2020).

Movements

In 1990, a programme of ringing and wing-tagging started, when the first ever wild Griffon was wing-tagged (Sušić 1994). Over 32 years, more than 1090 Griffons have been marked (with green PVC rings and/or wing-tags, as well as metal rings). Breeding adults are largely sedentary, but 90% of juveniles migrate for long distances in all directions: spring records are from Slovenia, north Italy, France, Bulgaria, Romania, and Greece. Summer records are from north Slovenia, Italy, Austria, France, Poland, Hungary, and Russia. Autumn records are from Slovenia, Spain, France, Poland, Bulgaria, Greece, Romania, Turkey, Ukraine, Israel, Chad, and Niger. Winter records are from northern, central, and southern Italy, Serbia, Spain, France, Greece, Turkey, and Israel (Sušić 1994, Sušić 2000, Sušić 2013b).

Supplementary feeding

The first Vulture restaurant (not only in Croatia, but in the Balkan area) opened on the island of Cres in 1982 (Sušić 2020). The supplementary feeding to support the Griffon population intensified in 2001, when 60 tons of carcasses and slaughterhouse offal were provided. The quantity of food provided yearly averaged at 10 tons in the period 2003 – 2012, and there were four Vulture restaurants (mainly two at the same time) on the island of Cres (Sušić 2020). In the period 2013 – 2019 there was no supplementary feeding in the area; it subsequently started again on two localities: Cres and Učka Mtn.

Definition of a colony

The reason why Griffons are colonial breeders is explained by the theory of colonies as "information centres" (Krebs 1974). The hypothesis suggests that individuals benefit from nesting in colonies, because they can learn about good feeding areas by following other birds from the nesting colony to the feeding grounds. In this way, the colony acts as an "information centre", and birds mainly copy their near neighbours. The accepted definition of a colony is: a place where several pairs nest at a centralized location, from which they recurrently depart in search of food (Wittenberger & Hunt 1985). Several authors (Sarrazin *et al.* 1996, following by, for example Del Moral & Marti 2001, Lopez-Lopez *et al.* 2004, Zuberogoitia *et al.* 2009, Del Moral 2009, Xirouchakis & Mylonas 2010, Zuberogoitia *et al.* 2011, Demerdzhiev *et al.* 2014, Zuberogoitia *et al.* 2019) agree that a Griffon's nesting cliff is considered a colony when it is occupied by at least two pairs, at a distance of at least 1000 m from the neighbouring occupied cliff, whilst isolated pairs are those that breed on their own, more than 1000 m from the nearest colony.

Colony shifting

Studying colonisation is crucial to understand metapopulations, their dynamics and evolutionary ecology (Payo-Payo *et al.* 2017). It is well known that vultures of the genus *Gyps* often desert their traditional sites and shift into new locations, such as in the south of Africa (Verdoorn & Becker 1992, Borello & Borello 2002, Whittington-Jones *at al.* 2011) or on Crete (Xirouchakis & Mylonnas 2005b, Xirouchakis 2010). The cause of "colony switching" (Piper 2004) remains unclear, as sometimes optimal sites may be abandoned, whereas others with high breeding failure continue to be occupied (Borello & Borello 2002).

Study objectives

This paper presents the results related to the population trend of the Griffon in Croatia based on a 40-year survey (1981 – 2021). Detailed population surveys were conducted for a 15-year period (2000 – 2014) on the island of Cres to document the cliffs' saturation, as well as inter- and intra-colony nest movements, and for a 10 year-period (1994-2005) on the islands of Cres and Plavnik to calculate the main reproductive parameters. Cliff's occupation has been studied for 15 years (2000 – 2014) on all Kvarner islands.

The main objectives of the present study were: (1) to analyse the population trend of Griffons in Croatia during the period of 40 years (1981 – 2021); (2) to give baseline information about nest site suitability as possible deterministic factor in population growth; (3) to assess their breeding success and productivity; and (4) to show how colony shifting affect the existing definition of a term "colony".

MATERIAL AND METHODS

Study area

The study area covered the Kvarner Archipelago territory in the northern Adriatic (from 45°15′02.40″ to 44° 29′55.46″ N and from 14°16′38.50″ to 15°03′06.47″ E), which includes 9 islands with cliffs: Cres, Lošinj, Plavnik, Prvić, Krk, Goli, Sv.Grgur, Rab, and Pag (Figure 1), as well as two canyons in the Paklenica National Park: Mala Paklenica (44° 17′21.53″ N; 15°30′40.46″ E) and Velika Paklenica (44°17′59.05″ N and 15°28′10.47″ E), which Grffons abandoned in 1997 and 1999, respectively (Lukač 2011).

Presently Griffons breed on Cres (405.78 km^2, 3,184 inhabitants), Plavnik (8.6 km^2, not inhabited), Prvić (12.8 km^2, not inhabited), Krk (405.78 km^2, 17,860 inhabitants), and Pag (284.56 km^2, 8,398 inhabitants) (Statistički ljetopis 2005). Ecological characteristics of the study area were described in detail by Perco *et al.* (1983). The Archipelago consists of limestone, which is dominant on all the islands. Almost all colonies (about 85% of all nests) are on steep cliffs in the NE parts of the islands, exposed to gusts of the bora, katabatic strong dry, cold, fall wind that blows from the NE onto the Adriatic Sea regions of Italy, Slovenia, and Croatia, reaching wind velocities over 15 m/s, frequently in winter (Yoshino 1976). Only 15% of nesting cliffs on Kvarner are facing to the SW.

The islands are marked by high ridges along the major axis. Due to the direction and length of the reliefs, they face strong wind and generate rising air currents along the slopes. The peaks are often bare, and the slopes are covered with vegetation. Hill-thermal currents are formed due to differences at which the two adjacent areas warm up. The currents can be driven by the winds away from their original site to create a path of thermal currents. These conditions are of importance for flight, i.e., for the Griffons' foraging (Pennycuick 1972, Pennycuick & Pennycuick 2015).

The NE coastline of all islands is distinguished by craggy appearance due to the stratigraphic shape of the islands. The exposure of the nesting cliffs generally follows the orientation of the coastline cliff wall, without the possibility to avoid adverse weather conditions. The exposure of nesting cliffs on Crete, as well as among the Griffon colonies in continental Europe, is mainly to the south, to avoid north winds (Xirouchakis & Mylonnas 2005a, Marinković *et al.* 2020), contrary to Kvarner, where 85% of the nests are on cliffs facing the NE.

The straits separating islands from one another, and the mainland, are narrow, not more than 5 km (Figure 1). This does not constitute a major obstacle to the Griffons' movement from one island to another, or from an island to the mainland. In fact, the absence of vegetation cover over vast areas of the islands assists the formation of periodical sea winds, and takes on a certain importance in the movements of these birds during foraging and/or inter-colony communication (Perco *et al.* 1983).

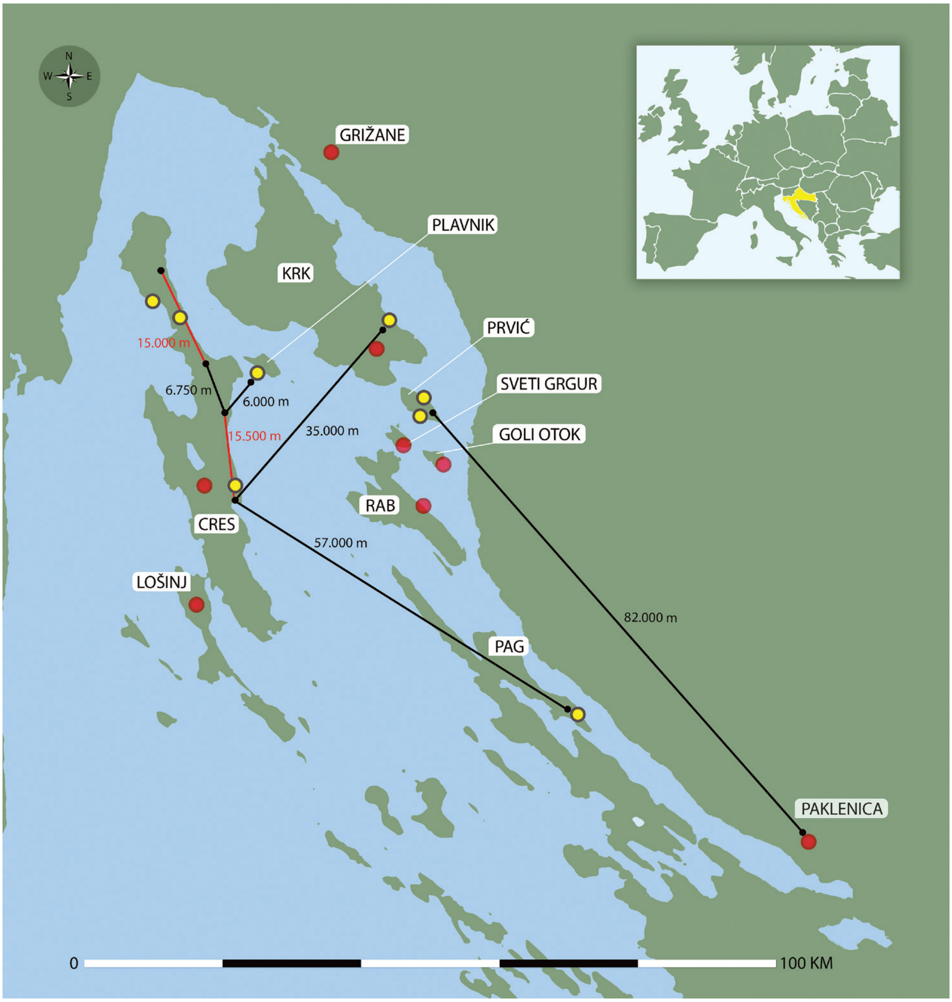

Figure 1. The study area: the Kvarner Archipelago and the Paklenica National Park (Northern Adriatic, Croatia).
Yellow dots: cliffs with active nest-clusters. Red dots: historical nesting cliffs. Black lines show the distances between nest-clusters on cliffs, and red lines the dimension of the northern (15,000 m) and the southern (15,500 m) nesting cliffs on Cres**.**

Slika 1. *Područje istraživanja: Kvarnersko otočje i Nacionalni park Paklenica (sjeverni Jadran, Hrvatska). Žute točke: litice s aktivnim grupama gnijezda. Crvene točke: povijesne gnijezdeće litice. Crne linije pokazuju udaljenosti između gnijezdećih litica, a crvene duljinu litica s grupama gnijezda na sjevernom (15.000 m) i južnom (15.500 m) dijelu otoka Cresa.*

Field survey procedure and data collection

In the period 1981 – 2021, the Eurasian Griffon colonies were monitored during the breeding season between December and June. In the Kvarner Archipelago, colonies are located on coastal cliffs, but as nests are on cliffs directly over the sea, it makes monitoring quite demanding, as it requires a boat and steady weather conditions (e.g., Kapelj & Modrić 2017). A minimum of four visits were made to each colony: during the period before incubation to detect total number of pairs; then during early laying period to detect the number of incubating pairs; during late chick-rearing period to detect the hatching success; and finally during the fledging period to detect failures, second clutches and fledging success (Leconte 1985). Each nest position was recorded every year, individually codified, its position on cliff photographed, so it could be monitored during the future surveys. Observations from a boat were made on clear, rainless days with calm sea conditions, using the Zeiss 10 × 40 binoculars and the Canon SX 420 IS camera.

At the beginning of the study, coastal cliffs with nests on the islands of Cres and Plavnik, with a distance between them of minimum 1 km, were identified and named A-Z. There were 11 such cliffs in the northern part, two on Plavnik and 15 in the southern part of Cres. A comparison of breeding parameters during a 15-year period (2000 – 2014) was made for two nesting cliffs of similar size: cliff P = 755 m and cliff X = 735 m; distance from one another = 1350 m, in the southern part of the island of Cres. The level of nest-site occupation of each cliff (comparing fluctuations of nesting densities) was measured through an index of saturation (S_i). It was calculated using the total number of nesting sites occupied during the whole study period (theoretical maximum) and correcting it by the number of breeding pairs/occupied nests recorded each year, following the proposed methodology of Zuberogoitia *et al.* (2019).

The mean height of the nest in the northern part of Cres was M_1 = 28.71 m (SD = 11.04), and in southern part, it was M_2 = 21.14 m (SD = 12.03). The lowest nest was at 8 m above the sea level. There was no statistically significant difference in the nest height over the sea level on the nesting cliffs in both parts of the island (Sušić 1985). During the study period, the number of abandoned sites and the colonization of new ones (saturation of previously active cliffs or shifting a group of nests to a new, previously never used cliff) were recorded.

The first visit was conducted between 15th December and 15th January. A pair was considered to be an active breeding pair if they were building a nest or incubating (López-López *et al.* 2004). The second visit occurred between 15th February and 15th March, as about 71% of hatchings occurred between 15th February and 15th March, and 60% of all were in February. Less than 10% of incubations started in March and April (Perco *et al.* 1983); these were usually replacement clutches.

The third visit occurred between 5th May and 15th May to record the number of hatchlings and the absence of the previously detected non-breeding pairs, which failed during incubation or after hatching. The fourth visit occurred in June to record the number of fledglings, the presence of late clutches, breeding success (Bs) and productivity (Pd). Griffons on Kvarner are birds whose breeding cycle lasts almost 10 months (from November to September - the last feeding of the chick in the nest was recorded on 17th September).

The following reproductive parameters were calculated for all colonies: productivity Pd = fledged chicks/detected (territorial) pairs; breeding success Bs = fledged chicks/active breeding pairs; and hatching success Hs = hatched chicks/active breeding pairs (Del Moral & Marti 2001; López-López *et al.* 2004). All breeding parameters were calculated for all nest-clusters on the island of Cres and two nest-clusters on the island of Plavnik, during the period of 10 years (1995 – 2004). The chicks that disappeared after 100 days of age were considered to have fledged, even if later found drowned, as any deaths after that date affected the first-year survival rather than the breeding success or the productivity (Sarrazin *et al.* 1996). Population density was calculated as the number of individuals and breeding pairs on the possible foraging area, excluding human settlements (in 100 km^2). Theoretical population density for the whole Kvarner Griffons' theoretical foraging distribution, or total foraging islands' area was calculated following the methodology of Xirouchakis & Mylonnas (2005b).

Each year, after counting all the nests, it was necessary to estimate the number of pairs missed while conducting the census. Depending of the quality of the census (weather, sea condition, number of days spent in counting, etc.), the difference between the total number of counted pairs and number of estimated pairs varied.

RESULTS

Population development

The estimated population size of the Eurasian Griffon in Croatia in 1981, when there were colonies on the Kvarner islands, the Paklenica National Park and southern Dalmatia, was 120 pairs. Just few years later, in 1985, after Dalmatia's colonies disappeared, there were 110 breeding pairs. In 1999, colonies in Paklenica ceased to exist, leaving 105 pairs on Kvarner only, but in next 20 years numbers increased to 120 breeding pairs (Table 1). Strong decline in the number of breeding pairs on Krk and Prvić was recorded in 2002 (Figure 2 and 3), while on Prvić, the minimum lasted six years (Figure 2). When comparing trend of Prvić and Krk with Cres/Plavnik (Figure 4), it becomes clear that during the same period when the number of nests on Krk and Prvić declined, it increased on Cres/Plavnik.

Table 1. The population size of the Eurasian Griffon in Croatia in a period of 40 years (1981 – 2021).

Tablica 1. *Veličina populacije bjeloglavog supa u Hrvatskoj u razdoblju od 40 godina (1981. – 2021.)*

Colony	Year	Number of pairs (counted)	Total number of pairs (estimated)
KVARNER & PAKLENICA & DALMATIA	1981	100	120
KVARNER & PAKLENICA	1985	99	110
KVARNER & PAKLENICA	1995	95	105
KVARNER	1999	78	95
KVARNER	2002	87	94
KVARNER	2006	88	92
KVARNER	2009	101	110
KVARNER	2012	120	130
KVARNER	2013	141	150
KVARNER	2017	108	115
KVARNER	2021	110	120

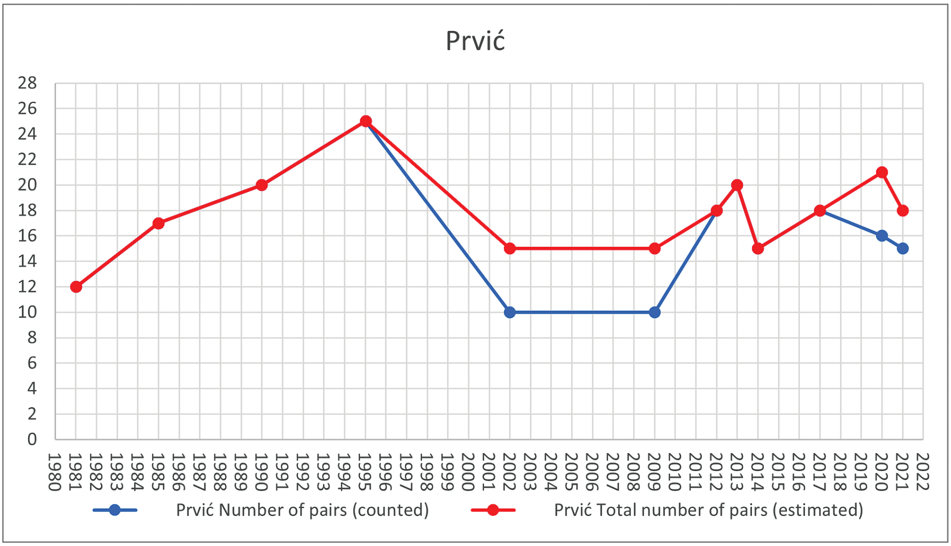

Figure 2. The population trend of the Eurasian Griffon on the island of Prvić in 40 years (1981 – 2021). Data for 2017 are from Kapelj & Modrić (2017).

Slika 2. *Trend populacije bjeloglavog supa na otoku Prviću u razdoblju od 40 godina (1981. – 2021.). Podatci za 2017.g. su iz Kapelj & Modrić (2017).*

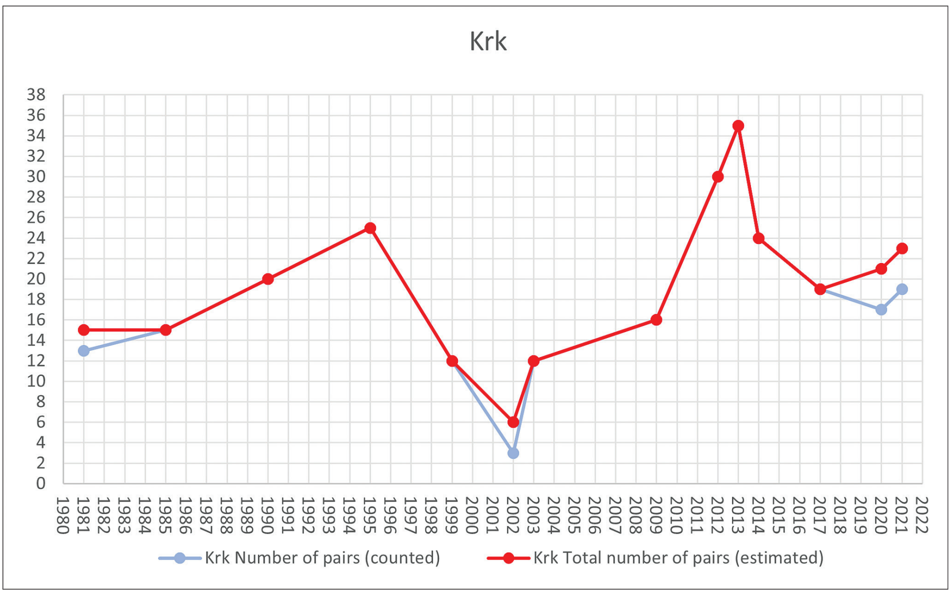

Figure 3. The population trend of the Eurasian Griffon on the island of Krk in 40 years (1981 – 2021). Data for 2017 are from Kapelj & Modrić (2017).

Slika 3. *Trend populacije bjeloglavog supa na otoku Krku u razdoblju od 40 godina (1981. – 2021.). Podatci za 2017.g. su iz Kapelj & Modrić (2017).*

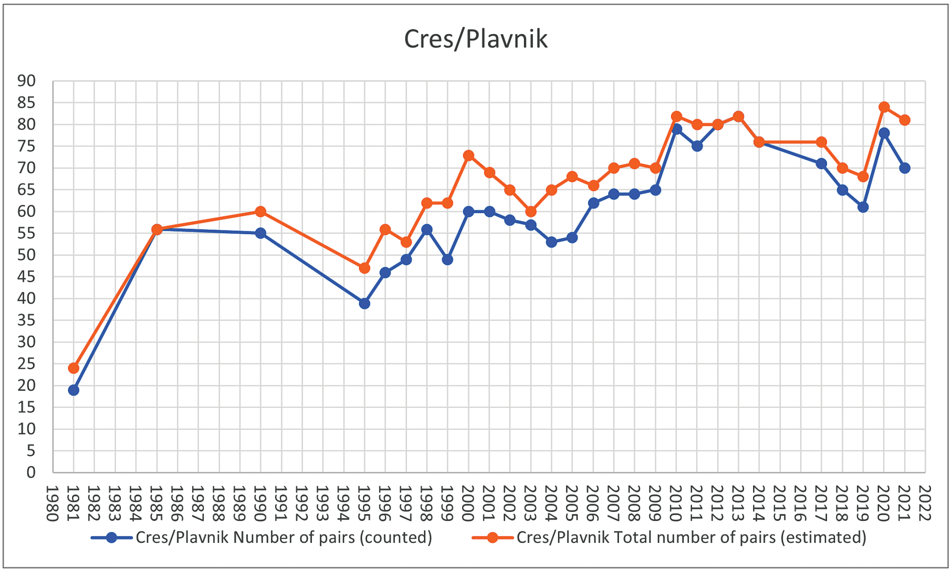

Figure 4. The population trend of the Eurasian Griffon on the Cres and Plavnik islands in 40 years (1981 – 2021). Data for 2017 are from Kapelj & Modrić (2017).

Slika 4. *Trend populacije bjeloglavog supa na otocima Cresu i Plavniku u razdoblju od 40 godina (1981. – 2021.). Podatci za 2017.g. su iz Kapelj & Modrić (2017).*

Reproductive performances

The productivity of the Eurasian Griffon at all nest-clusters on cliffs on the Cres and Plavnik islands in 10 years period varied from 0.46 to 0.63 (0.55 ± 0.054, mean ± SD) (Table 2). During that period griffons produced 369 fledglings, their breeding success varied from 0.51 to 0.69 (0.60 ± 0.059), and hatching success from 0.79 to 0.95 (0.86 ± 0.052) (Table 2, Figure 5). Population density was estimated at 32.5 adult individuals/100 km^2 and 13.75 breeding pairs/100 km^2., for a possible foraging area on the islands of 800 km^2. Theoretical population density for the total foraging area on all Kvarner islands (1214.28 km^2, including areas of former colonies at Goli, Sv. Grgur and Rab which Griffons regularly forage) was 5 individuals/100 km^2.

Table 2. The reproductive performance of the Eurasian Griffon at all nest-clusters on cliffs on the Cres and Plavnik islands in 10 years (1995 – 2004).

Tablica 2. *Reprodukcijski parametri bjeloglavog supa u svim gnijezdećim klasterima na Cresu i Plavniku tijekom 10 godina (1995. – 2004.).*

Year	Total no. pairs/nests	Active nests	No. fledglings	Hatching success	Breeding success	Productivity
1995	52	47	26	0.83 (83%)	0.55 (55%)	0.50 (50%)
1996	62	56	35	0.82 (82%)	0.63 (63%)	0.57 (57%)
1997	58	53	34	0.93 (93%)	0.59 (59%)	0.59 (59%)
1998	67	62	39	0.90 (90%)	0.63 (63%)	0.58 (58%)
1999	67	62	37	0.79 (79%)	0.60 (60%)	0.55 (55%)
2000	76	73	40	0.82 (82%)	0.55 (55%)	0.53 (53%)
2001	76	69	39	0.87 (87%)	0.57 (57%)	0.51 (51%)
2002	72	65	45	0.89 (89%)	0.69 (69%)	0.63 (63%)
2003	66	60	41	0.95 (95%)	0.68 (68%)	0.62 (62%)
2004	72	65	33	0.82 (82%)	0.51 (51%)	0.46 (46%)
Mean	**66.8**	**61.2**	**36.9**	**0.855 (86%)**	**0.599 (60%)**	**0.553 (55%)**
SD	**7.8**	**7.7**	**5.2**	**0.052**	**0.059**	**0.054**

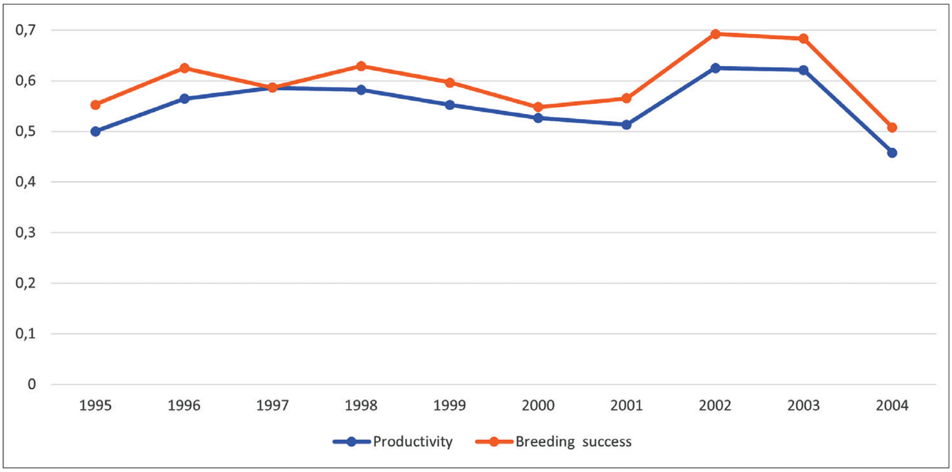

Figure 5. The productivity and the breeding success of the Eurasian Griffons breeding on the Cres and Plavnik islands in 10 years (1995 – 2004).

Slika 5. *Produktivnost i uspješnost gniježđenja bjeloglavog supa na Cresu i Plavniku tijekom 10 godina (1995. – 2004.).*

The saturation of previously used and later abandoned nests-clusters

Nest-clusters P and X on neighbouring, approximately 750 m-long cliffs (distance between them is 1350 m), were situated at the high central part of the steep 15 km-long coastal nesting cliffs area of the island of Cres. In the study period there were 51 used nest locations on cliff P, and 36 nest locations on cliff X (Figure 6).

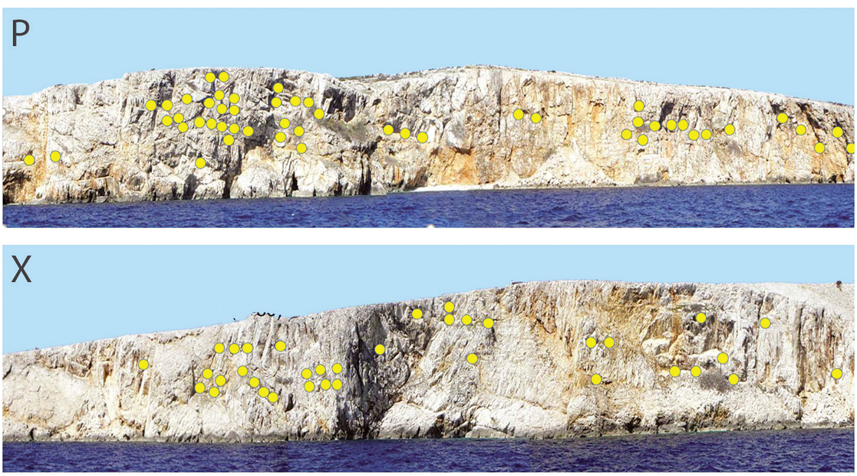

Figure 6. All nest locations (yellow dots) used on cliff P (above) and cliff X (below) in 40 years (1981 – 2021).

Slika 6. *Sve gnijezdeće pozicije (žute točke) korištene na litici P (gore) i litici X (dolje) u 40 godina (1981. – 2021.).*

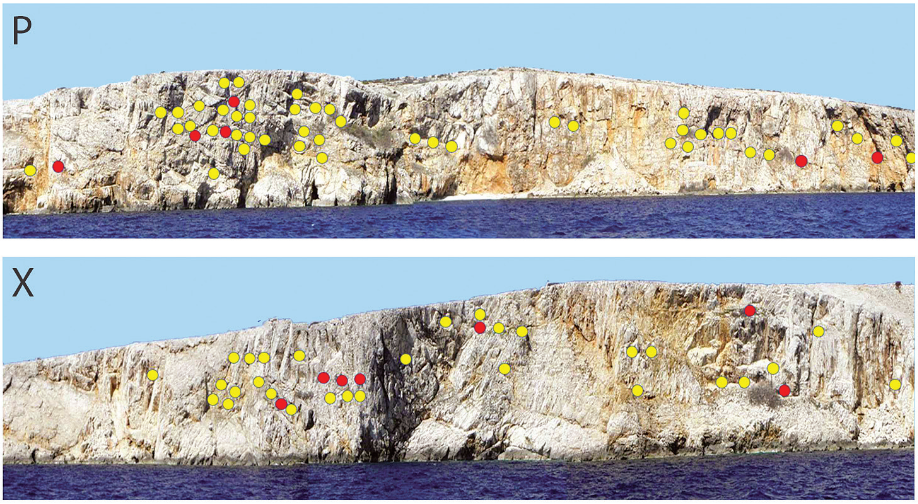

Figure 7. Nest locations used on cliff P (above) and cliff X (below) in 2000. Red dots = nests used in 2000. Yellow dots = nest used in other years during the study period.

Slika 7. *Gnijezdeće lokacije korištene na litici P (gore) i litici X (dolje) u 2000. godini. Crvene točke = gnijezda korištena u 2000.g. Žute točke = gnijezda korištena u ostalim godinama tijekom razdoblja istraživanja.*

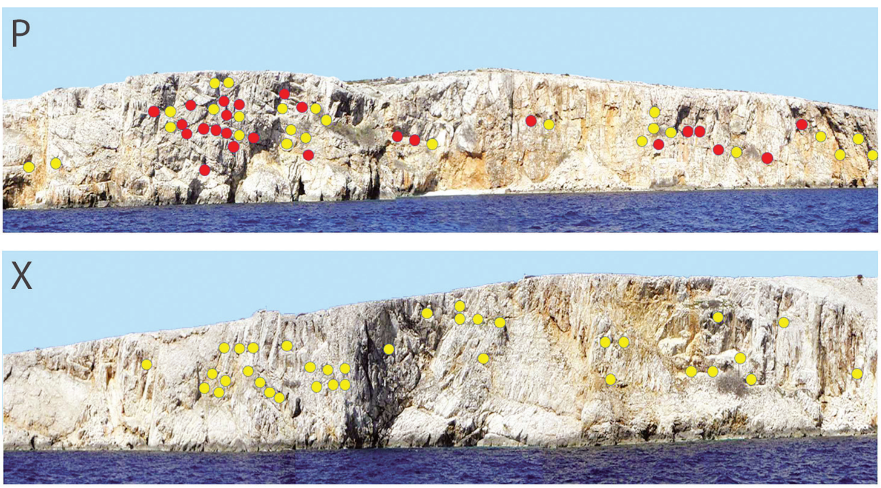

Figure 8. Nest locations used on cliff P and cliff X in 2006. Red dots = nests used in 2006. Yellow dots = nests used in other years during the study period.

Slika 8. *Gnijezdeće lokacije korištene na liticama P i X u 2006. godini. Crvene točke = gnijezda korištena u 2006.godini. Žute točke = gnijezda korištena u ostalim godinama tijekom istraživanja.*

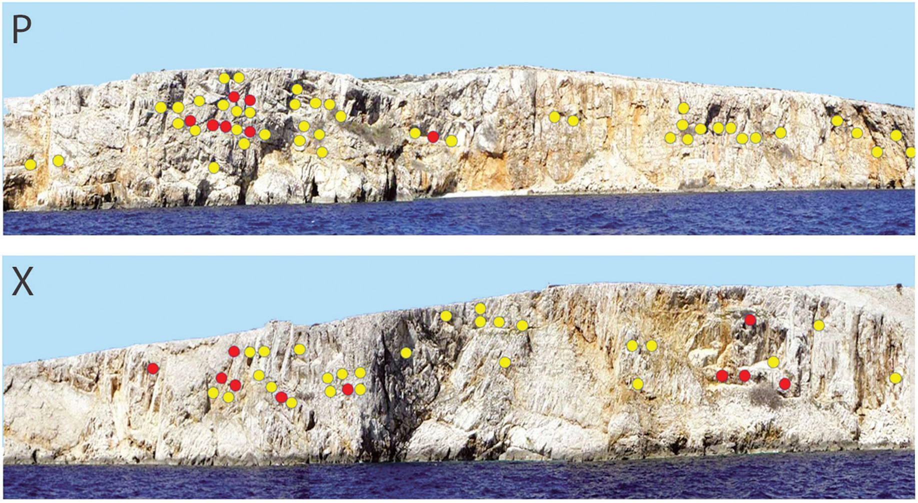

Figure 9. Nest locations used on cliff P and cliff X in 2014. Red dots = nests used in 2014. Yellow dots = nests used in other years during the study period.

Slika 9. *Gnijezdeće lokacije korištene na liticama P i X u 2014.godini. Crvene točke = gnijezda korištena u 2014. godini. Žute točke = gnijezda korištena u ostalim godinama tijekom istraživanja.*

In 2000, both cliffs were almost equally occupied, with similar numbers of active, i.e., occupied nests (cliff P: $N = 6$; $S_i = 0.12$ and cliff X: $N = 7$; $S_i = 0.2$) (Figure 7). In the following six years (2000 – 2006), cliff P was saturated from $N = 6$ in 2000 to $N = 25$ nests in 2006 ($S_i = 0.49$), while cliff X was totally abandoned ($N = 0$). ($S_i = 0$) (Figure 8). In the following eight years (2007 – 2014), 18 nesting sites were abandoned on cliff P ($S_i = 0.14$), while cliff X was saturated from 0 to 10 nests ($S_i = 0.28$) (Figure 9).

In 15 years, 152 chicks were fledged (2.98 chicks/nest) on cliff P, and 44 chicks (1.22 chicks/nest) on cliff X. Cliff P produced almost 2.5 times more chicks per active nest than cliff X. Figure 10 shows how saturation index increased on the 2.5 times more successful cliff P, while on cliff X, it declined. Cliff X was abandoned completely when cliff P was at its saturation maximum of almost 50% ($S_i = 0.49$).

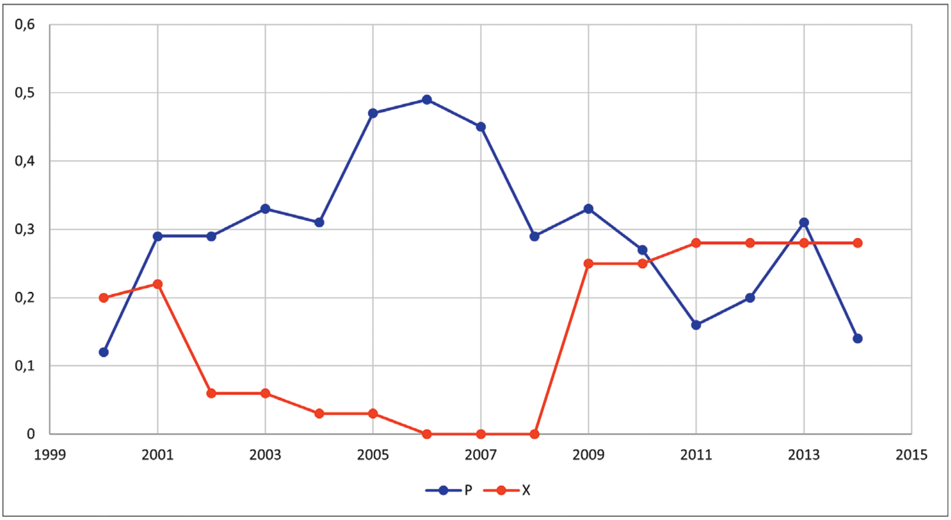

Figure 10. The saturation of nest-clusters on cliffs P and X during a 15-year period.
Slika 10. *Saturiranje grupa gnijezda na liticama P i X tijekom 15 godina.*

Nest-cluster pulsations (NcP)

Nest-cluster shifting and NcP on cliffs in the southern part of the island of Cres was studied in a period of 15 years (2000 – 2014). In Figure 11 a-c, it is clearly visible that the number of nests in each nest-cluster varied from year to year. There were years when some nest-clusters disappeared completely, whereas in other years, the same nest-clusters saturated and became some of the largest of all neighbouring nest-clusters. Comparing years from 2000 to 2005 (Figure 11a) we can see decline both in the number of nest-clusters and in the number of active nests in each nest-cluster; however, by 2010, nest-clusters were saturated again (Figure 11b). In a period of 15 years, clusters of nests (i.e. breeding pairs) were in a dynamic long-term process of *pulsation*, i.e. saturation-abandonment-saturation (Figure 11 a-c).

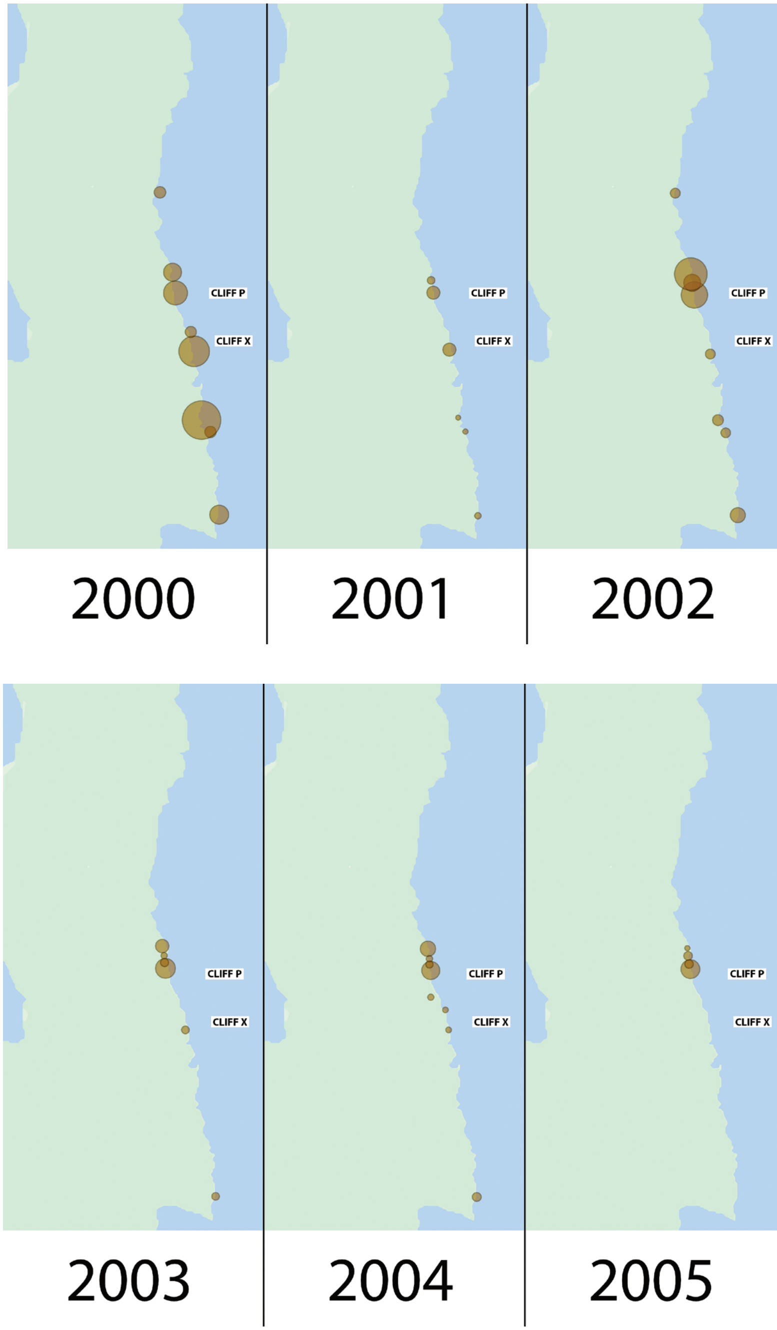

Figure 11. a (2000-2005)
***Slika 11. a** (2000.-2005.)*

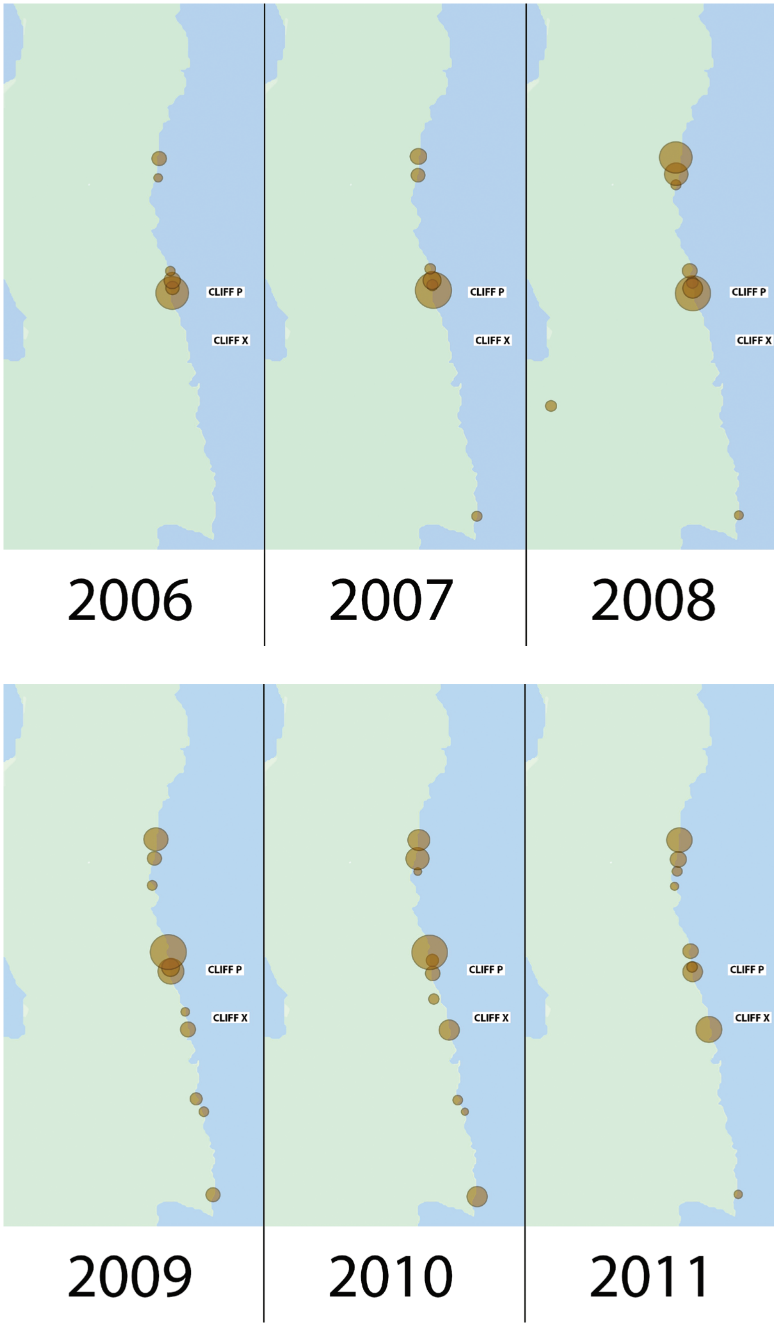

Figure 11. b (2006-2011)
Slika 11. b *(2006.-2011.)*

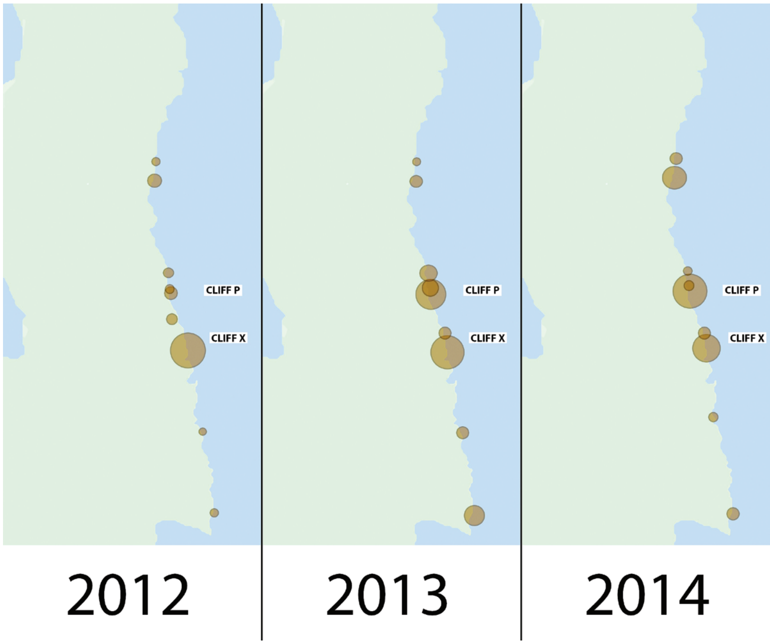

Figure 11.c (2012-2014)
***Slika 11.c** (2012.-2014.)*

Figure 11. a-c Nest-cluster shifting and NcP on cliffs P and X and neighbouring nest-clusters. The size of a brown circles corresponds to the number of active nests in the nest-cluster in a consecutive year.

***Slika 11. a-c** Premještanje i pulsiranje gnijezdećih klastera na liticama P i X, te obližnjih gnjezdećih klastera. Veličina smeđeg kruga odgovara broju aktivnih gnijezda u klasteru u pojedinoj godini.*

Nest occupancy

Figure 12 shows the proportion of active nests on all cliffs in Kvarner in one study year, compared to the total number of available nest sites, used in any year. In a period of 15 years, the occupation of all cliffs in the Kvarner Archipelago varied, depending on a study year, between 9.83% and 22.6% (M = 15.05%). Such a low rate of occupation was a result of annual nest-movements, and it shows low nest-site fidelity.

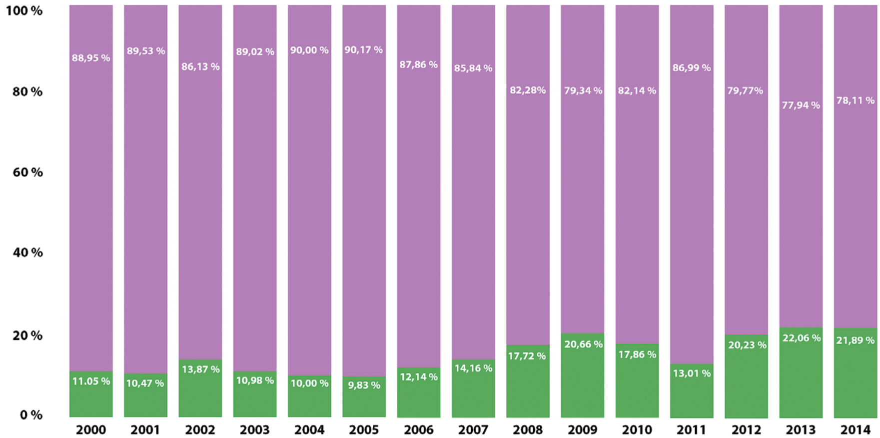

Figure 12. The mean annual percentage of nest-occupancy (green = % of occupied nests; violet = % of not occupied nest sites) in all nest-clusters in the Kvarner Archipelago in a period of 15 years (2000 – 2014).

Slika 12. *Prosječni % godišnje zauzetosti gnijezda (zeleno = % zauzetih gnijezda; ljubičasto = % nezauzetih gnijezda) u svim gnijezdećim klasterima na Kvarneru u razdoblju od 15 godina (2000. – 2014.)*

Out of 15 nest-clusters in the southern part of Cres, only on three of them (M, P and X), more than 10% (14, 17 and 21%) of nest sites were occupied in a period of 15 years. In the same period, but considering however the whole Kvarner population, the mean number of occupied nests varied from 9.83% to 22.6% (M = 15.05%) (Figure 12).

Thus, although nest-clusters on cliffs M, P and X were saturated close to the average of all Kvarner nest-clusters, they were the densest saturated cliffs, not only along the 15,000 m of southern coast with 15 nest-clusters, but even among all 28 nest-clusters on the Cres and Plavnik islands (Figure 13).

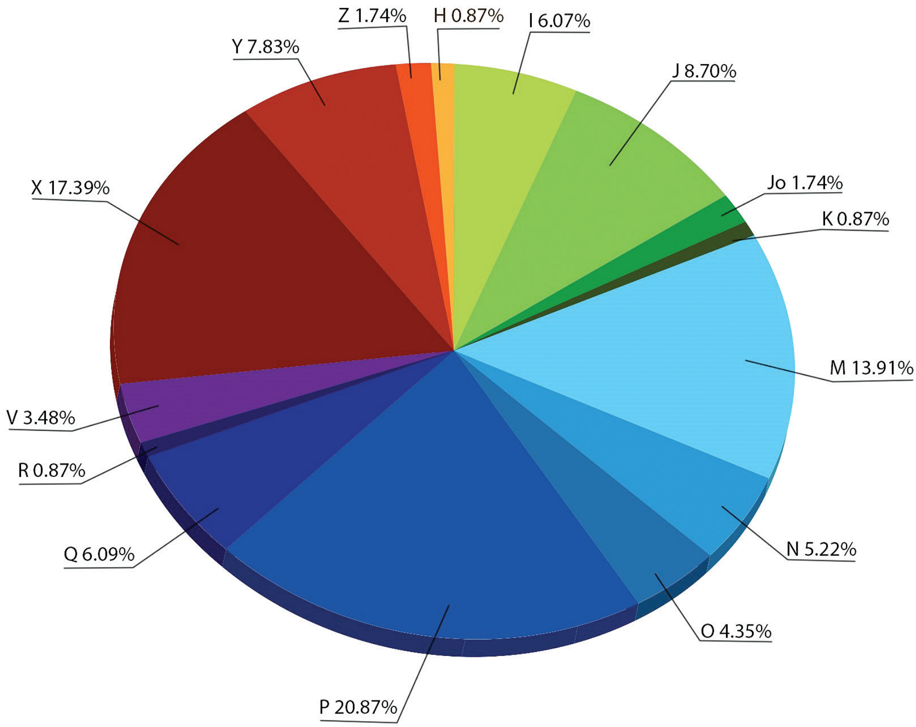

Figure 13. The mean nest occupation of different nesting cliffs/nest-clusters in the southern part of the island of Cres in a period of 15 years (2000 – 2014).

Slika 13. *Prosječna zauzetost gnijezda pojedinih gnijezdećih litica/gnijezdećih klastera na južnom dijelu otoka Cresa u petnaestotogodišnjem razdoblju (2000. – 2014.).*

In a period of 40 years more than 1090 nests were visited in the Kvarner area for ringing Griffon's chicks. The clutch with two eggs laid was recorded only once, on the island of Cres, but the second egg did not hatch (Figure 14).

Figure 14. The clutch with two eggs laid.
Slika 14. *Polog s dva jaja u gnijezdu.*

DISCUSSION

Population trend

At the beginning of the study in 1981, there were 60 breeding pairs in the Kvarner Archipelago, as well as about 20 detected non-breeding pairs (Perco *et al.* 1983), 15 breeding pairs in the Paklenica National Park (Lukač *et al.* 2003), with 5 more non-breeding pairs estimated, and in several smaller nest-clusters in Dalmatia, the maximum of about 20 pairs was estimated. The total number of 120 pairs was estimated for Croatia at the beginning of study period (Table 1). Since 40 years ago, there was the same number of breeding pairs in Croatia as in 2021, we might get the wrong impression that "nothing happened" in the meantime.

Nevertheless, the estimation of 120 pairs from 1981 included nest-clusters from the Kvarner islands, the canyons of Paklenica, Zrmanja, Krnjeza and Krka, as well as mountains near Dubrovnik. From 1999 onwards, after almost all nesting areas had disappeared, there were no other colonies in Croatia except in the Kvarner Archipelago. Thus, if the year 1999 is used as the starting year for Kvarner, there was an increase from 78-95 in 1999 to 141-150 pairs in 2013, and then again a decline to 110-120 pairs in 2021 (Table 1).

The possibility that the increase in the total number of pairs in Kvarner from 78 in 1999 to 87 in 2002 was a result of shifting of the nest-clusters from Paklenica to Kvarner, ought not to be eliminated. In the autumn of 1997, in one month, the number of individuals in Paklenica decreased from 22-24 to only 6-8, and the last three pairs disappeared in 1999 (Lukač *et al.* 2003). Such rapid decline was never fully explained. The most probable existing explanation is that there had been a poisoning accident, although no dead birds were ever found (Lukač *et al.* 2003, Lukač 2011). Before the disappearance of all Griffons, there were about 15 breeding pairs in two canyons of the Paklenica National Park. As the distance between Kvarner and Paklenica is less than 90 km, it is probably more than a coincidence that the increase in the number in Kvarner occurred at the same time when the numbers in Paklenica waned. The same happened between the Potberg and Little Karoo colonies in South Africa (Scott 1997), and between the Popovo polje (Bosnia and Herzegovina) and Uvac colonies (Serbia), where the distances between deserted colonies and colonies with simultaneously increased numbers of breeding birds were larger than between Kvarner and Paklenica (Robertson 1984, Marinković *et al.* 2007; 2012). The triggers might have been conspecific attraction and food availability in Kvarner when food shortage in Paklenica area increased to critical level. The GPS locations and movements show that Griffons from any island regularly explore areas of other islands (Genero 2017, Genero *et al.* 2020); currently, the coastal part of the Velebit mountain is included as well (pers. unpubl. data).

The theoretical population density for the total foraging area on all Kvarner islands (1214.28 km^2, including areas of former colonies at Goli, Sv. Grgur and Rab, which Griffons regularly forage) was 5 individuals/100 km^2, almost the same as Xirouchakis & Mylonnas (2005b) estimated for the island of Crete (8261 km^2), where theoretical population density was 4.6 individuals/100 km^2.

Reproductive performances

The average breeding success on Cres/Plavnik in a ten-year period (1995 – 2004) was Bs = 0.60 ± 0.059 (mean ± SD), varying from 0.51 to 0.69. Comparing the breeding success of the Kvarner nest-clusters with other European colonies, it was lower than in any other country: Serbia (0.81), Portugal (0.69), the French

Alps (0.7), Bulgaria (0.77), Crete (0.74), Cyprus (0.74), the French Pyrenees (0.76), Spanish Pyrenees (0.77), and Sardinia (0.77) (Leconte 1985; Sarrazin *et al.* 1996; López-López *et al.* 2004; Iezekiel *et al.* 2004; Aresu & Schenk 2005; Terrasse 2006; Beest *et al.* 2008; Del Moral 2009; Xirouchakis 2010; Demerdzhiev *et al.* 2014; Marinković *et al.* 2020). This variation in the breeding success among areas might be explained by differences in food availability, intra-specific competition (density of breeding pairs), or climate (Beest *et. al* 2008). Moreover, large year-to-year variation was recorded for the Cape Vulture *(Gyps coprotheres*) as well, with breeding (fledging) success varying from 0.64-0.75 to 0.27-0.43, depending on study year (Borello & Borello 2002). The productivity on the Kvarner islands, depending on study year, varied from 0.46 to 0.63, the breeding success from 0.51 to 0.69, and the hatching success from 0.79 to 0.95 (Table 2).

The earliest recorded egg-laying was on 10th December. This is one of the earliest beginnings of incubation in Europe, as in Spain, it was recorded at the end of December (Leconte 1985). The median egg laying date varied in the Kvarner population between 7th and 22nd January (Sušić & Grbac 2002), which is earlier than on Crete, where the median laying date was 28th January, and the earliest was on 25th December (Xirouchakis 2010). The start of the nesting season partly varies depending on latitude, but generally, the reproductive cycle of Griffons is determined by egg-laying, so that the young fledge when food availability reaches its maximum (Houston 1989). Traditional sheep husbandry on the Kvarner islands includes planning of sheep lambing to take place very early, so lambs would be of optimal size for human consummation at Easter. Griffons-shepherds' coexistence in Kvarner has lasted for more than 1000 years (Sušić & Grbac 2002), so Griffons have had enough time to adapt and adjust the hatching date with the lambing period, i.e. the peak of sheep mortality. Thus, they are not adapted depending on the fledging, but rather on the hatching period. This might be the reason why the Kvarner population starts incubation earlier than other Mediterranean (on Crete or in Spain) or other populations at the same latitude, such as Serbian (Marinković *et al.* 2020).

Nevertheless, the reproductive rate does not seem to be the central demographic parameter influencing the population dynamics of Griffons. It is believed that species with a large body size, a low reproduction, and a long-life expectancy depend heavily on high adult survival for their population success. Parra & Telleria (2004) showed that fluctuations in the number of the Griffon breeding pairs were positively correlated with changes in livestock abundance, supporting a functional relationship between food availability and vulture abundance (Beest *et al.* 2008). When the recorded 12% of increase of Cres/Plavnik nest-clusters in 2000 were compared to 1999 (because of possible nest-cluster shifting from the Paklenica National Park canyons), the breeding success declined from Bs = 0.60 to Bs = 0.55. The lower breeding success may have been caused by the newly arrived pairs being relegated to marginal or suboptimal places (Wittenberger & Hunt 1985), as it was their first year in a new area. However, after we had added 60 tons of supplementary food at the feeding place in 2001, the breeding success and productivity increased from Bs = 0.57 and Pd = 0.51 in 2001 to Bs = 0.69 and Pd = 0.63 in 2002. Both the breeding success and the productivity values were the highest in 2002 for the whole 10 year-period of measuring the breeding performance in these nest-clusters. In the years when the biggest number of pairs started the breeding season (76 pairs in 2000 and 2001 and 72 pairs in 2002 and 2004), the breeding success was the lowest (Bs = 0.51) or nearly the lowest (Bs = 0.55 and Bs = 0.57) (Table 2). The exception was the year 2002, when the breeding success and productivity were the highest (Bs = 0.69 and Pd= 0.63), although 72 pairs started the breeding season, probably as a result of immense quantity of supplementary food available during the previous year. A subsequent decline in 2004 was probably a result of lowering the quantity of supplementary food to 10 tons per year from 2003 onwards, yet from 2005 onwards, the population trend started to increase again.

Colony shifting

It has been generally accepted by several authors (Sarrazin *et al*. 1996, Zuberogoitia *et al.* 2011, Zuberogoitia *et al.* 2019) that there are two Griffon colonies in case the distance between them is more than 1 km without eyries. Following these criteria, if we want to study colony parameters and compare them, we may not state there is one single colony on the island of Cres, as the cliffs with nest-clusters are distributed along the 15 km long coastal area, where there are 28 cliffs separated, with the distance between them from 1350 to 5000 m (Figure 1). Every one of them should thus be named (and studied as) a separate colony, since such distance between the cliffs makes them separate colonies, and not clusters of nests on cliffs inside one big colony, according to the currently accepted definition (e.g. Sarrazin *et al.* 1996, Del Moral & Marti 2001, Zuberogoitia *et al.* 2011, Zuberogoitia *et al.* 2019). Following the actual definition, there would be about 40 colonies in the Kvarner Archipelago. Clusters of active nests in the 15,500 m long southern part of the island of Cres were shifted regularly, so that each year, the saturation of new nest-clusters (or the previously existed nest-clusters, abandoned in the meantime) was observed (Figure 11 a-c). When comparing the neighbouring cliffs P and X, it becomes evident that the dynamics of the abandonment of cliff X follows that of the saturation of cliff P (Figure 8, Figure 11 a-b).

Population surveys for 15 years (2000 – 2014) documented colony occupancy and turnover in nest usage, the number of abandoned sites and colonization of new ones (saturation of previously active cliffs or shifting a group of nests to a new cliff, never used previously, at least during 40 years of study). A comparison of the breeding parameters was made in that period for two breeding cliffs of similar size (Figure 6-10; Figure 11 a-c), of nest-clusters in the southern part of the island of Cres. During these 15 years, cliff P produced almost 2.5 times more chicks per active nest than cliff X. If cliff P was saturated with more experienced pairs from cliff X, which than shifted to cliff P attracted by successful conspecific breeding pairs, the success of the nest-cluster on cliff P would increase with saturation until reaching the optimum (or maximum) threshold in colony size (Xirouchakis & Mylonnas 2005b). On the contrary, consequently, at the nest-cluster on cliff X, the remaining pairs were unexperienced and produced at the end of the 15-years cycle 2.5 times less chicks than the nest-cluster on cliff P. Shifting from the less to the more successful nesting cliff may hence be easily explained. Nevertheless, the question remains: what triggered the shifting of breeding pairs from the more successful cliff P in the middle of the saturation period? During the following 8 years 18 active pairs deserted cliff P and reduced the cliff saturation to $S_i = 0.14$. In the same period, the less successful nest-cluster on cliff X was saturated from 0 to 10 breeding pairs and increased the cliff saturation from $S_i = 0$ to $S_i = 0.28$. Why did the abandonment start, when we know that at its saturation maximum, nesting cliff P was saturated less than 50% ($S_i = 0.49$) (Figure 9)? Is 50% an optimal saturation for 25 breeding pairs on a cliff 755 m long? Cliff P was clearly not too saturated when breeding pairs decided to start abandoning it, move back and re-saturate their previous cliff X or some other neighbouring nest-cluster (Figure 11 b-c). It seems that intraspecific competition started to regulate nest density on the cliff when the saturation level increased up to half of the theoretical maximum carrying capacity of that nesting cliff.

It is well known that vultures of the genus *Gyps* very often desert their traditional sites and shift into new locations. This is well documented in south Africa, where the complete abandonment of one colony and the resettlement of the birds at other sites occurred (Verdoorn & Becker 1992, Borello & Borello 2002). as well as on Crete (Xirouchakis & Mylonnas 2005b, Xirouchakis 2010). Sarrazin *et al.* (1996) found that 41.5% of 89 pairs changed their nest sites, and concluded that pairs that changed nest sites after a nesting failure had a higher breeding success in the following year, so breeding dispersal on local scale (i.e. intra-colony nest movements) seemed to be a good strategy. For Piper (2004), the cause of colony switching remains unclear, as optimal sites may occasionally be abandoned, whereas others with low breeding success may be occupied. Griffons at several nest-clusters in Kvarner abandoned optimal nesting cliffs and occupied new sites, only to leave them again after several years and move to another nesting cliff or re-occupy the previous one. Cliffs P and X were both in the centre of the 15 km-long coastal area with nesting cliffs, and were the most occupied cliffs of all the nest-clusters on the island of Cres. A high annual intra-nest-cluster movements of breeding pairs and large-scale shifting of active nest-clusters between them (in other papers called: inter-colony nest movements) have been recorded (see Figure 11 a-c). This might suggest that changes of the nesting clusters' size were adjusted to reduce the intra-specific competition, similar as on Crete (Xirouchakis & Mylonnas 2005b). Human disturbance and food availability could not explain why Griffons would abruptly abandon their traditional cliffs on the Kvarner islands, as they usually re-saturated the same cliffs (even the same nest-sites, but there is no certainty whether by the same individuals) after approximately 10-15 years. As Griffons sometimes forage in great distances from their colonies, birds from different nest-clusters should forage in the same areas (Xirouchakis & Mylonnas 2005b), and it is known that Griffons use both personal and social information while foraging (Cortes-Avizanda *et al.* 2014). A relatively small foraging range is available to individual nest-clusters on each of the Kvarner islands; thus, they all very often forage other islands and coastal part of mainland, i.e. they exploit the same food resources (Perco *et al.* 1983, Genero 2017, Genero *et al.* 2020, pers. unpubl. data). Another argument in favour of our hypothesis is that all nest-clusters from different islands belong to one large colony. What we used to call „colonies" are in reality clusters of nests (breeding pairs) in a dynamic long-term process of *pulsation*, i.e. saturation-abandonment-saturation (Figure 11 a-c). The pulsation of nest-clusters cannot be explained in terms of nest-clusters' fitness, in which case they should be triggered when an optimum threshold in nest-cluster size has been reached, and the extant breeding group is unprofitable for its members, as Xirouchakis & Mylonnas (2005b) proposed. The number of available nest sites is not a factor limiting the number of breeding pairs in the Kvarner Archipelago, as shown by a low mean occupancy/saturation rate; consequently, the carrying capacity of cliffs seems to be at least several times bigger than the current number of active nests would suggest. Food availability could not explain the abrupt abandonment of their traditional cli*ff*s, as it was the case on Crete (Xirouchakis & Mylonnas 2005b). Their final conclusion that „colony switching should be viewed in terms of the colonies' fitness and should be triggered when an optimum threshold in colony size is passed and the extant breeding group is unprofitable for its members", could not explain the pattern in our research area. Data during the period of 15 years showed that there was never a maximum threshold reached in the nest-cluster size, because there was never a single cliff saturated up to its theoretical maximum (i.e. if we count all the previously used active nest locations as the saturation maximum). It is more probable that the trigger for the abandonment of a previous nesting cliff is based on social information and conspecific attraction (Mateo-Tomas & Olea 2011), after an individual decision-making process conditioned by a still unknown reason. After several pairs (or just one or two in the first year) decide to change the half (or even less) saturated nesting cliff, forced to move and use poorer nesting areas, others follow, driven by conspecific attraction. Consequently, in 6-8 years a new cliff is saturated and the previous one abandoned again. The three-phase pattern after the abandonment of a Griffon colony (nest-cluster), studied by Xirouchakis & Mylonnas (2005b) on Crete were: (1) the formation of a new colony in a new site; (2) a shift of individuals to a new site; and (3) the abandonment of a colony, accompanied by an increase in population size in proximate ones. We might add phase (4): when after several years (6-8), an abandoned nest-cluster ("colony") starts saturating again, it reaches the saturation maximum (optimum?) after about 15 years. The process is regular, and during saturation, nest-clusters become mixed with breeding pairs from other nest-clusters, conspecifically attracted by saturation itself. On the island of Cres, such pattern is seen in Figures 8-10, and clearly recognisable for other nest-clusters as well (see Figure 11 a-c). It was recorded on every island in the Kvarner Archipelago, and the proposed name for such pattern would be *nest-cluster pulsation (NcP).*

Most of the population was concentrated in small-sized nest-clusters (most of them with 10 pairs or less, only a few nest-clusters with 10-25 pairs), and all cliffs showed low occupancy rate (Figure 13 and Figure 14). Nests movements to new cliffs could not be provoked by local food abundance, as food is equally dispersed along the islands (and nest-clusters' shifting and individual nest shifting between the clusters mostly occurred inside a 15 km-long series of nest-clusters' cliffs), except for the year 2001, when we added 60 tons of supplementary food on the island of Cres. The following year, strong decline in the number of breeding pairs at Krk and Prvić was recorded, while concurrently the number of pairs increased on Cres/Plavnik. This might be explained as nest-cluster shifting from Krk and Prvić to Cres/Plavnik, provoked by local food abundance. In the following ten years, supplementary food was available on regular basis on the locations of two Vulture restaurants on the island of Cres, and the number of breeding pairs increased on each island. In 2013, supplemental feeding stopped, which resulted in a decline in the population.

Nests in the southern part of Cres were distributed over a wide area (cliff area 500-1000 m long for 2-50 nest sites, constantly fluctuating on an annual basis in numbers of occupied nests). As the annual occupancy level of previously used nests was low, as well as was the re-usage rate of such nests, contrary to the conclusion of Xirouchakis & Mylonnas (2005b) for Crete, there was no long-term site fidelity on the Kvarner islands. In support thereto, some Griffons hatched on the island of Cres as adults used to breed on the island of Krk and opposite, and some in other countries, such as several pairs in Italy (Genero 2017) or Serbia (Marinković *et al.* 2020). The conclusion that philopatry to the natal cliffs may simply result from conspecific attraction alone was made by Sarrazin *et al.* (1996), and has been confirmed by the results of this study.

Zubergoitia *et al.* (2019) analysed factors affecting the colonial Griffon population regulation, and suggested that at higher densities, breeding pairs are forced to move and use poorer nesting areas, but again, their methodology was biased by the "1 km distance" definition of a colony, which cannot be applied in the Kvarner nest-clusters shifting inside one large colony. Accepting the actual definition, when nest-cluster of one nesting cliff is colony, there have been more than 40 colonies in the Kvarner Archipelago, changing their number and the number of breeding pairs in each of them each year. If some future study of the comparison of the breeding success between these two colonies lasts 4-5 years, it will be highly biased, as nest-cluster shifting will not be registered, and the absence of active nests in one year would be explained as a results of nesting failures, rather than nest movements.

Payo-Payo *et al.* (2017) concluded, after 34 years of studying the temporal evolution of Audouin's gull colonisation, that personal information must be crucial in decision making, and colonisers were mostly experienced individuals gaining higher breeding success in the new colony. This study does not support their conclusion, since in the Kvarner Archipelago, Griffons that took intra- or inter-nest-cluster shifting did not have any higher breeding success at the newly established breeding nest-clusters („subcolonies"). Quite the opposite, the conspecific attraction maintains the aggregation of pairs on the previously abandoned, less successful cliff. Contrary to the conclusion of Sarrazin *et al.* (1996), this study determined that nesting failures did not favour movements. Adult and successful pairs saturated the less successful cliff and abandoned the more successful one. This agrees with the conclusion of Payo-Payo *et al.* (2017) that for those pairs that started abandoning the successful cliff, personal information must be crucial in decision making, but why it is triggered when breeding pairs' density in nest-cluster reaches only 50% of saturation capacity, still remains to be discovered.

Colony capacity

During a ten-year period, the mean annual occupation of nest sites in a population varied during between 9.83% and 22.6% (M = 15,05%), while in the western Pyrenees, it was 53% during six years (Leconte 1985). Comparing cliffs P and X in a period of 15 years, the following pattern was recorded: after reaching almost 50% of the maximum nest saturation, the breeding pairs on cliff P decided to start the abandonment process, and saturating the previously abandoned and less successful cliff X. When cliff P reached its mean saturation (S_i = 0.21, where % of cliff occupation = S_i x100, see Figure 13,), the number of occupied nests started to become stabilised. The mean saturation level of cliff X was 0.17 (Fig 13), but saturation continued to a higher level, and for two years (in 2011 and 2012), cliff X was even more saturated than the 2.5 times more successful cliff P.

The most successful nest-cluster (cliff P) reached the maximum occupation capacity when almost a half of all the ever-used sites (S_i = 0.49 of theoretical maximum) were occupied. As on average only 15% of all the previously used nest sites were occupied each year (Figure 13), the large Kvarner colony is far from reaching an optimum threshold in colony size. However, if all the *ever-used nest sites* become active, the population will become more than 6 times larger than today, which means that the carrying capacity of the existing nest-cluster's cliffs is at least 800 breeding pairs. If we add historical nest-clusters in the area that could be saturated too (see Figure 1), we may estimate that possible total number on Kvarner is more than 1000 breeding pairs. Of course, in such a scenario of reaching the carrying capacity of the environment, the deterministic factor will not merely be the availability of food and cliffs with suitable nest-sites, but density-dependent factors as well (Fernandez *et al.*1998). If nest-cluster shifting and nest movements between nest-clusters start when the saturation of a new cliff reaches 50% (as shown between cliffs P and X), then the carrying capacity of the Kvarner islands is highly determined by density-dependent forces. In such a case, the breeding pairs' capacity in the Archipelago could not reach 1000, but rather closer to 500 breeding pairs. It is well known that food availability is not always the deterministic factor in population growth (Newton 1979), and in the case of cliff nesting species as Griffons, nest suitability may be more influential in determining their distribution and density (Newton 2013). On the Kvarner it was not the case during the survey period, just on the contrary, the main deterministic factor were clearly the amount of available food, and socially conditioned forces. Density-dependent factors were probably equally important, and nest availability a much less important factor.

As on three nest-clusters on the southern part of Cres (cliffs M, P and X), nest occupation varied from 13.9% to 20.9% (M=17.4%), and on other 12 cliffs it was less than 10% (varied from 0.9% to 8.7%, M=4%), we may consider those three cliffs the centre of all nest-clusters in that part of the island, and the other 12 satellite nest-clusters. If cliffs M, P and X, as the most successful ones, are the centre of all nest-clusters, and the others are satellite nest-clusters, then the whole area (which is 15.5 km long area of coastal cliffs) should be considered the set of nest-clusters, and not 15 different colonies. The Kvarner colony had more than 40 (up to 47, depending on the year of study) neighbouring nest-clusters. It is still not clear what the distance between them is when breeding pairs form another nest-cluster. This conclusion is supported by the inter- and intra-nest-cluster movements of breeding pairs, i.e. the NcP process (Figure 11a-c), as well as nest-cluster shifting between nest-clusters on different Kvarner islands.

CONCLUSIONS

The modest population growth of the Griffon population on Kvarner at the beginning of the 2000s was generally contributed by the implementation of extensive conservation measures. It seems that it was only partially true, since the increase in years 1999 – 2002 (from 78 to 87 pairs) could have been a result of the shifting of 15 breeding pairs from the Paklenica National Park to Kvarner between 1998 and 2000. All the colonies on the islands of Cres, Plavnik, Krk, Prvić and Pag are nest-clusters of one large Kvarner colony with regular intra- and inter-nest-cluster movements, as well as nest-cluster shifting. There is regular genetic exchange between breeding units, and they all use the same foraging area. It has been proposed that such annually regular nest movements between nest-clusters on different nesting cliffs might be called *nest-cluster pulsation* (NcP). This is one of the characteristic features of the Kvarner islands' Griffon population. It implicates the new approach to future studies of the Griffon breeding parameters and the comparison of parameters between nest-clusters or studies of nest-cluster fidelity, since without a high proportion of individually recognizable adults within each nest-cluster, such detailed studies will not be accurate.

Finally, we need a new definition for a colony in the Eurasian Griffon, as the current definition (a nesting cliff is considered a colony when occupied by at least two pairs, at a distance of at least 1000 m from the neighbouring occupied cliff) is not functionally appropriate. A better term for a Griffon colony (than in the previous definition), might be a nest-cluster. The distance from the neighbouring occupied nesting cliff depends on evident environmental differences between them (part with too low cliffs etc.), and it may be either less or more than 1000 m. It is important to analyse all nest-clusters' properties, in order to be sure what the size of a colony constituing them is.

The productivity and breeding success were stable and moderate during the whole study period, implying that the population has not approached the saturation level yet. The same conclusion could be made by a low occupancy rate at on all active nesting cliffs. There was no long-term nest site fidelity on Kvarner. The nest suitability is not a determining factor in the population growth of the Kvarner colony; the food availability and social, i.e. density dependent forces are. The empowering of free-range livestock farming and the returning to the traditional method of disposing of dead cattle as well as new supplementary feeding sites could enable further growth of the Griffon population in Croatia.

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References

Aresu, M., Schenk, H. (2005): Status e conservacione del Grifone *(Gyps fulvus)* in Sardegna. pp 30-39 In: Avesani, C. (ed.) Il Grifone in Italia. Verona: Parco Natura Viva.

Beest, F., Bremer, L., Boer, W., Heitkönig, I., Monteiro, A. (2008): Population dynamics and spatial distribution of Griffon Vultures *(Gyps fulvus)* in Portugal. Bird Conservation International 18:102-117.

Birdlife International (2017): *Gyps fulvus* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2017: e.T22695219A118593677.

Borello W.D., Borello R.M. (2002): The breeding status and colony dynamics of Cape Vulture *Gyps coprotheres* in Botswana. Bird Conservation International 12:79-97.

Botha, A. J., Andevski, J., Bowden, C. G. R., Gudka, M., Safford, R. J., Tavares, J., Williams, N. P. (2017): Multi-species Action Plan to Conserve African-Eurasian Vultures. CMS Raptors MOU Technical Publication No. 5. CMS Technical Series No. xx. Abu Dhabi: Coordinating Unit of the CMS Raptors MOU.

Cortes-Avizanda, A., Jovani, R., Donazar, J.A., Grimm, V. (2014): Bird sky networks: How do avian scavengers use social information to find carrion? Ecology 95: 1799-1808.

Cramp, S., Simmons, K. E. L. (eds.) (1980): The Birds of the Western Palearctic, Vol. II. Oxford: Oxford University Press.

Davidović, S., Jelić, M., Marinković, S., Mihajlović, M., Tanasić, V., Hribšek, I., Sušić, G., Dragičević, M, Stamenković-Radak, M. (2020): Genetic diversity of the Griffon vulture population in Serbia and its importance for conservation efforts in the Balkans. Scientific Report 10:20394. https://doi.org/10.1038/s41598-020-77342-1

Del Moral J. C. (ed.) (2009): El buitre leonado en España. Población reproductora en 2008 y método de censo. Madrid: SEO/BirdLife.

Del Moral, J. C., Martí, R. (eds.) (2001): El Buitre Leonado en la Península Ibérica. III Censo Nacional y I Censo Ibérico coordinado, 1999. Madrid: SEO/BirdLife

Del Moral, J. C., Molina, B. (eds.) (2018): El buitre leonado en España, población reproductora en 2018 y método de censo. Madrid: SEO/BirdLife.

Demerdzhiev, D., Hristov, H., Dobrev, D., Angelov, I., Kurtev, M. (2014): Long-term Population Status, Breeding Parameters and Limiting Factors of the Griffon Vulture *(Gyps fulvus* Hablizl, 1783) Population in the Eastern Rhodopes, Bulgaria. Acta Zoologica Bulgarica 66: 373-384.

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 Conserv.Int. pp. 1-16. DOI: https://doi.org/10.1017/S0959270921000198.

Döltmayr, G. (2003). Iz ornitološke beležnice: Griffon Vulture *Gyps fulvus*. Acrocephalus 24 (116): 37

Fergusson-Lees J., Christie D.A. (2001): Raptors of the world: A field guide. London: Helm.

Fernandez, C., Azkona, P., Donázar, J. (1998): A Density-dependent effects on productivity in the Griffon Vulture *Gyps fulvus* - the role of interference and habitat heterogeneity. Ibis 140: 64-69.

Genero, F. (2017): Movements and home range of the Eurasian Griffon Vulture (*Gyps fulvus*) in the eastern Alps and Adriatic region, in relation to food availability. PhD Thesis. University of Udine. Udine.

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.

Houston, D.C. (1989): Factors influencing the timing of breeding in African Vultures. pp. 203-210 In. Meyburg, B-U., Chancellor, R.D. (eds.): Raptors in the Modern World. WWGBP, Berlin.

Iezekiel, S., Bakaloudis, D.E., Vlachos, C. (2004): The status and conservation of Griffon Vulture *Gyps fulvus* in Cyprus. pp. 67-74 In: Chancellor, R.D., Meyburg, B-U. (eds.): Raptors Worldwide. Budapest: WWGBP/MME.

Johnson J. A., Lerner H. R., Rasmussen P. C., Mindell D. P. (2006): Systematics within *Gyps vultures:* a clade at risk. BMC Evolutionary Biology 6:1-12.

Kapelj, S., Modrić, M. (2017): Monitoring of Griffon Vulture *Gyps fulvus* population of Kvarner area in 2017. Larus 52: 74-75.

Krebs, J. R. (1974): Colonial Nesting and Social Feeding as Strategies for Exploiting Food Resources in the Great Blue Heron *(Ardea herodias).* Behaviour 51(1/2): 99-134.

Krvavica, M., Vrdoljak, M., Kegalj, A. (2021): Number of sheep and production of sheep meat in the world and in Croatia. (Broj ovaca i proizvodnja ovčjeg mesa u svijetu i u Hrvatskoj). In Croatian with English Summary. Meso 14: 491-495

Leconte, M. (1985): Present status of the Griffon vulture on the northern slopes of the western Pyrenees. pp. 117-127 In: NEWTON, I., CHANCELLOR, R.D. (eds.): Conservation Studies In Raptors. ICBP Technical Publication No.5. Paton Press, Norwich.

Le Gouar, P., Rigal, F., Boisselier-Dubayce, M-C., Samadi, S., Arthur, C., Choisy, J-P., Hatzofe, O., Henriquet, S., Lecuyer, P., Tessier, C., Sušić, G., Sarrazin, F. (2006): Genetics of restored population of Griffon vulture *Gyps fulvus* in Europe and in France. pp. 116-126 In: Houston, D.C., Piper, S.E. (eds.): Conservation and Management of Vulture Populations, Natural History Museum & WWF Greece.

Le Gouar P., Rigal F., Boisselier-Dubayle M.C., Sarrazin F., Arthur C., Choisy J.P., Hatzofe O., Henriquet S., LÉcuyer P., Tessier C., Susic G. & Samadi S. (2008): Genetic variation in a network of natural and reintroduced populations of Griffon vulture (*Gyps fulvus*) in Europe. Conservation Genetics 9: 349-359.

López-López, P., Garcia-Ripolles, C. & Verdejo, J. (2004): Population status and reproductive performance of Eurasian Griffons (*Gyps fulvus*) in Eastern Spain. Journal of Raptor Research 38: 350-6.

Lukač, G., Stipčević, M., Haupt, R. (2003): Recent observation on the Griffon Vulture *(Gyps fulvus)* in the Paklenica National Park (Croatia). Acrocephalus 24 (117): 51-9.

Lukač, G. (2011): Atlas ptica Nacionalnog parka Paklenica. Javna ustanova Nacionalni park Paklenica. Starigrad-Paklenica.

Marinkovic, S., Orlandic, L., Mickovic, B., Karad, B. (2007): Census of vultures in Herzegovina. Vulture News 56: 15-26.

Marinkovic, S., Orlandic, L., Skoric, S., Karadzic, B. (2021): Nest-site preference of Griffon vulture (*Gyps fulvus*) in Herzegovina. Archives of Biological Sciences 64: 385-392.

Marinković, S., Hribšek, I., Tatalović, N., Skorić, S. (2020): A long-term population study of the Eurasian griffon *(Gyps fulvus)* in Serbia before and following the establishment of a supplementary feeding program, Ethology Ecology & Evolution, DOI: 10.1080/03949370.2020.1844302

Mateo-Tomas, P., Olea, 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.

Newton, I. (1979): Population Ecology of Raptors. Berkhamsted.T&AD Poyser.

Newton, I. (2013): Bird Populations. Collins New Naturalist Library, Book 124. London: HarperCollins Publishers.

Orta J. (1994): Eurasian Griffon. pp. 127-128 In: Del Hoyo J., Elliott, A., Sargatal, J. (eds.): Handbook of birds of the world. Vol. 2. New World vultures to guinea fowl. Barcelona: Lynx Edicions.

Parra, J., Telleria, J. (2004): The increase of the Spanish population of Griffon Vulture *Gyps fulvus* during 1989-1999: effects of food and nest site availability. Bird Conservation International 14: 33-41.

Payo-Payo, A., Genovart, M., Sanz-Aguilar, A., Greño, J.L., García-Tarrasón, M., Bertolero, Piccardo, A.J., Oro, D. (2017): Colonisation in social species: The importance of breeding experience for dispersal in overcoming information barriers. Sci. Rep. 7:42866 DOI: 10.1038/srep42866

Pennycuick C.J. (1972): The soaring flight of vultures. Sci. Amer. 229:102-109.

Pennycuick, C., Pennycuick, S. (2015): Birds Never Get Lost. Leicestershire: Matador.

Perco, F., Toso, S., Sušić, G., Apollonio, M. (1983): Initial data for a study on the status, distribution and ecology of the Griffon vulture, *Gyps fulvus fulvus* (Hablizl, 1783) in the Kvarner Archipelago. Larus 33-35: 99-134.

Piper, S.E. (2004) Proposed global Population-monitoring Scheme for the Cape Griffon *Gyps coprotheres*. pp. 83-92 In: Chancellor, R. D., Meyburg, B.-U. (eds.): Raptors Worldwide. Budapest: WWGBP/MME.

Rebrović, M.J. (2017): Griffon vultures and the inhabitants of the island of Cres. Etnološka istraživanja 22: 61-74.

Robertson, A.S. (1984): Aspects of the population dynamics of Cape Vultures in the Cape Province. Ostrich 55: 196-206.

Sarrazin, F., Bagnolini, C., Pinna, J.L., Danchin, E. (1996): Breeding biology during establishment of a reintroduced Griffon vulture *Gyps fulvus* population. Ibis 138: 315-325.

Schwammer, H.M. (1988): Nest site preference, census and status of the griffon vulture *Gyps fulvus fulvus* (Hablizl 1783) in the Kvarner Archipelago (Jugoslavia). Verhandlungen der Deutschen Zoologischen Gesellschaft 81: 329-330.

Scott, H.A. (1997): The status and breeding performance of Cape Vultures *Gyps coprotheres* at the Potberg and Little Karoo colonies, Western Cape, South Africa: 1991-1995. Vulture News 36: 2-16.

Statistički Ljetopis (2005). Republika Hrvatska, Državni zavod za statistiku. Statistički ljetopis (dzs.hr). Opened on October 12th, 2021.

Sušić, G. (1985): Ecological conditions for the range and dispersion of the Griffon Vulture *Gyps fulvus fulvus* (Hablizl 1783) in the Kvarner Archipelago. (Ekološka uvjetovanost rasprostranjenosti i veličine populacije bjeloglavih supova, *Gyps fulvus fulvus* (Hablizl 1783) na Kvarnerskim otocima). M.Sc thesis (Magistarski rad). University in Zagreb (Sveučilište u Zagrebu). Zagreb. In Croatian.

Sušić, G. (1994): Wing-marking of Eurasian Griffons *Gyps fulvu*s in Croatia - Evaluation and Initial Results. pp. 373-380 In: Meyburg, B.-U., Chancellor, R.D. (eds.): Raptor Conservation Today. WWGBP/The Pica Press.

Sušić, G. (2000): Regular Long-distance Migration of Eurasian Griffon *Gyps fulvus.* pp. 225-230 In: Chancellor, R.D., Meyburg, B.-U. (eds.): Raptors at Risk. WWGBP/Hancock House.

Sušić, G. (2002): The Eurasian Griffon in Croatia. pp.66-89 In: Sušić, G., Grbac, I. Do You Want Reality or Myth or Reality? The Story of Eurasian Griffon. The Croatian Natural History Museum, Zagreb.

Sušić, G. (2004): The Situation of the Griffon vulture in Croatia. pp. 32-36 In: Slotta - Bachmayr, L., Bogel, R., Camina Cardenal A. (eds.): The Eurasian Griffon Vulture *(Gyps fulvus)* in Europe and Mediterranean. Status report and Action Plan. East European / Mediterranean Griffon Vulture Working Group, Salzburg.

Sušić, G. (2013a): Griffon Vulture, *Gyps fulvus* Hablizl, 1783. pp. 145-147 In: Tutiš, V., Kralj, J., Radović, D., Ćiković, D., Barišić, S. (eds.): Red Data Book of Birds of

Croatia. Ministry of Environmental and Nature Protection, State Institute for Nature Protection, Zagreb.

Sušić, G. (2013b). Bjeloglavi sup, *Gyps fulvus*, Eurasian Griffon. pp 70-72 In: Kralj, J., Barišić, S., Tutiš, V., ČIković, D. (eds.): Croatian Bird Migration Atlas. HAZU, Zagreb.

Sušić, G. (2020): Institute of Ornithology CASA and NGO Grifon - 39 years together in research and conservation of Eurasian Griffons in Croatia. pp. 36-55 In: TOME, D. (ed.): Griffon vulture *(Gyps fulvus):* Alpe - Adria subpopulation. Presentations and discussions from the Workshop held on 27.11. 2019 in NR **Škocjanski** zatok, Koper.

Sušić, G., Kruchten, C. (2017): Children of the Storm. Griffon Vulture in the Kvarner Bay. Der Falke 64: 22-27.

Sušić, G., Radek, V. (2013): Vulture status and conservation in Croatia. pp. 16-19 In: ANDEVSKI, J. (ed.): Vulture Conservation in the Balkan Peninsula and Adjacent Regions. 10 years of research and conservation. Vulture Conservation Foundation (VCF).

Terrasse M. (2006): Long term reintroduction projects of Griffon *Gyps fulvus* and Black vultures *Aegypius monachus* in France. pp 98-107 In: Houston, D.C., Piper S.E. (eds.): Proceedings of the International Conference on Conservation and Management of Vulture Populations. Thessaloniki. Natural History Museum of Crete and WWF-Hellas.

Verdoorn, G.H., Becker, I. (1992): Cape griffons of the Megaliesberg: 1991 census of nestlings and firs breeding record at Nooitgedacht since 1964. Vulture News 27: 19-25.

Wittenberger, J.F., Hunt, G.L. (1985): The adaptive significance of coloniality in birds. pp.1-78 In: Farner, D.S., King, J.R., Parkes, K.C. (eds.): Avian biology. Vol. 8. New York: Academic Press.

Whittington-Jones, C., Wolter, K., West, S. (2011): Monitoring of Cape *Vulture (Gyps coprotheres)* breeding colonies in the Megaliesberg, South Africa: 2007-2009. Vulture News 60: 6-12.

Xirouchakis S. (2010): Breeding biology and reproductive performance of Griffon Vultures *Gyps fulvus* on the island of Crete (Greece). Bird Study 57:213-235.

Xirouchakis S.M., Andreou, G. (2009): Foraging behaviour and flight characteristics of Eurasian griffons *Gyps fulvus* in the island of Crete, Greece. Wildlife Biology 15: 37-52.

Xirouchakis M.S., Mylonas, M. (2005a): Status and structure of the Griffon vulture *(Gyps fulvus)* population in Crete. European Journal of Wildlife Research 51: 223-231.

Xirouchakis M. S., Mylonas, M. (2005b): Selection of breeding cliffs by Griffon Vultures *Gyps fulvus* in Crete (Greece). Acta ornithologica 40: 155-161.

Yoshino, M. (1976): Local Wind Bora. University of Tokyo Press, Tokyo.

Zuberogoitia, I., Alvarez, K., Olano, M., Rodriguez, A., Arrambarri, R. (2009): Avian scavenger populations in the Basque Country: status, distribution and breeding parameters. pp. 49-58 In: Donázar, J.A., Margalida, A., Campion, D. (eds): Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspectiva of conservation biology. Sociedad de Ciencias Aranzadi. Munibe Suplemento - Gehigarria 29.

Zuberogoitia, I., Castillo, I., Zabala, J., Iraeta, A., Azkona, A. (2011): Population trends of diurnal forest raptors in Biscay. pp. 70-80 In: Zuberogoitia, I., Martinez, J.E. (eds): Ecology and Conservation of European Forest-dwelling Raptors: Bilbao: Diputacion Foral de Bizkaia.

Zuberogoitia, I., Martínez, J.E., González-Oreja, J.A., PÉrez De Ana, J.M., Zabala, J. (2019): Factors affecting population regulation of a colonial vulture. Ibis 161: 878-889.

SAŽETAK

Populacija bjeloglavog supa u Hrvatskoj značajno se smanjila tijekom prve polovice 20. stoljeća, ne samo brojnošću, već i brojem gnijezdećih područja i veličini gnijezdećeg areala. U ovom radu prikazani su rezultati koji se odnose na populacijski trend i reprodukcijske parametre, uključujući pomicanje kolonija, na temelju 40-godišnjeg istraživanja (1981 – 2021). Populacija se smanjila s 110-150 parova u 10 kolonija 1981. na 75 parova u 6 kolonija 1999. Kasnije se povećala sa 75 na 141-150 parova u 6 kolonija u 2013, da bi zatim pala na 100-tinjak parova 2019. godine. Nakon otvaranja hranilišta na Cresu i Učki, populacija ponovno lagano raste. Povećanje od 13% u 2000. moglo bi djelomično ili u potpunosti biti posljedica prebacivanje grupe gnijezdećih parova s Paklenice na Kvarner. Godine 2021. na pet otoka: Cresu, Plavniku, Krku, Prviću i Pagu gnijezdilo se ukupno oko 120 parova. Gustoća naseljenosti procijenjena je na 32,5 odraslih jedinki/100 km^2, 15 teritorijalnih parova/100 km^2 i 13,75 gnijezdećih parova na 100 km^2. Detaljna istraživanja populacije provedena su tijekom 15 godina kako bi se dokumentirala popunjenost kolonija, zasićenost litica, te pomicanje gnijezda između i unutar kolonija. Za razdoblje od 10 godina izračunati su reprodukcijski parametri: uspješnost gniježđenja (Bs = 0,60 ± 0,059) i produktivnost (Pd = 0,55 ± 0,054). Zauzetost gnijezda bila je vrlo niska (između 9,83% i 22,6%; M = 15,05%), što znači da kapacitet okoliša kod kvarnerskih supova nije bio određen dostupnošću litica za gnijezda, već su ga determinirali dostupnost hrane i gustoćom uvjetovani socijalni mehanizmi, kao i da je populacija još uvijek daleko od razine zasićenosti. Šest kvarnerskih "kolonija" u stvarnosti nisu zasebne kolonije (prema aktualnoj definiciji kolonije) nego su jedna metakolonija s mnogo gnijezdećih grupa (klastera) na istom ili različitim otocima, godišnje pulsirajući s brojem aktivnih gnijezda na liticama i redovito se prebacujući s litice na liticu (pa i između različitih otoka) i natrag. Postojeća definicija kolonije kod bjeloglavog supa nije zadovoljavajuća i potrebna su dodatna istraživanja kako bi se utvrdili razlozi pulsiranja broja parova u pojedinim grupama gnijezda, posebno „okidača“ koji ih pokreće.