BREEDING COLONIES, POPULATION GROWTH AND BREEDING SUCCESS OF THE DALMATIAN PELICAN *PELECANUS CRISPUS* IN GREECE: A COUNTRY-WIDE PERSPECTIVE, 1967-2021

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Abstract

Greece holds the third largest breeding population of Dalmatian pelican in the world. We present data about the establishment and growth, breeding performance and conservation status for all current six colonies of the species in Greece for the last 40 years. Colony surveys were carried out with various methods, adapted to the particularities of each wetland and availability of resources, and targeted estimating the number of Apparently Occupied Nests and numbers of near-fledged young via direct counting, either during on-site visits or from vantage points, and recently, counts on photos taken by drones flown one or more times during breeding. Main features of wetlands and colonies are described. The overall breeding population in Greece grew from ca 100 nests in two colonies in 1967 to over 2,000 nests in six colonies in 2021, exhibiting an annual growth rate of 7.9%. Younger colonies show high annual growth rates clearly attributed to immigration, while older colonies have growth rates less than 10%. Natural factors at a local and regional scale, as well as anthropogenic factors, that could have contributed separately or in combination to an increase in Dalmatian pelicans in Greece during the last 40 years, are discussed.

Key Words: *Dalmatian pelican, breeding, colonies, population trends, breeding success, Greece, long-term data series, seabirds, waterbirds, colony growth*

Introduction

The value of long-term ecological studies has been repeatedly acknowledged (Strayer et al. 1986; Cody & Smallwood 1996; Collins 2001; Magurran et al. 2010). They have substantially improved our understanding of the life history strategies of animals. Through such studies we try to detect changes in size and other population parameters and correlate them with environmental events and variables. We also try to document the consequences of stochastic events (such as mass mortality, disease, predation, flood, drought, etc) upon the year-to-year variation in productivity and survival, as well as to collect evidence for density-dependent processes in population regulation (Wooler et al. 1992). Some patterns of fluctuation in bird populations can only be detected by long-term studies (Newton 1998). Such studies are also needed in order to understand complex system dynamics, all of which may result from natural and anthropogenic causes (Franklin 1989). Long-term datasets are also useful for providing guidance in conservation management, assessing the efficiency of conservation policies and informing public policy decisions (Collins 2001; Magurran et al. 2010; Reif 2013).

Particularly for seabirds and waterbirds, long-term studies are not only crucial for their conservation, but the past decades have shown that there is also a need for spatial integration in their management, which must be expanded to a landscape scale, at the level of many square kilometres. Equally important is the integration of population dynamics with habitats, such as the identification of "source" and "sink" populations, for example (Erwin 2002). Aggregated results from many different study plots can clearly give a more representative picture of regional dynamics than studies at a single study site (Newton 1998).

The Dalmatian pelican (hereafter DP) *Pelecanus crispus* Bruch 1832, although principally a freshwater species, is listed among seabirds due to its taxonomic position in the Pelecanidae and many of its life history traits, which it shares with real marine birds (Schreiber & Burger 2002). It has a Eurasian distribution, from Montenegro in the west, to China in the East, whilst its global population trend is increasing after a decline that reached its lowest in the mid-20th century (Crivelli & Schreiber 1984). Its global conservation status was downgraded from "Vulnerable" to "Near Threatened" in 2017 (BirdLife International 2021). After Kazakhstan and Russia, Greece is the third most important country for this species in the world, as it hosts 20-25% of the global population (Catsadorakis & Portolou 2018) and is the species' stronghold in the Black Sea-Mediterranean flyway.

Up to the late 1970s, little was known about the status, populations and ecology of this species outside the former Soviet Union. In 1977, the French Research Centre Tour du Valat launched a long-term project (entitled: "International Pelican Research and Conservation Program", IPRCP), led by A. J. Crivelli for over 30 years, aiming to explore the ecology and ensure the conservation of the DP. A network of local partners in several countries was gradually built in the 1980s, with more intensive work carried out in Prespa and in Amvrakikos and, later, other wetlands of Greece.

After the 1990s, knowledge and understanding of the species' needs improved, legal protection was enhanced and, combined with environmental changes and conservation measures in various countries, resulted in a population expansion and the formation of new colonies. Research and conservation work carried out in Greece played a crucial role in the regional population recovery, principally due to the spectacular increase of the Prespa colony (Doxa et al. 2010; 2012a; 2012b; Deinet et al. 2013; Catsadorakis 2015; Barboutis et al. 2021). The DP is one of the few bird species in Greece for which quite detailed population and breeding performance data have existed for many years, but which have remained unpublished so far (but see Crivelli 1983; 1987; Crivelli et al. 1991; Hatzilacou 1992; Crivelli et al. 2000). Conditions, however, have changed radically in the last 20 years, not least with the appearance of new colonies. In this paper, we present up-to-date data about the establishment, growth, breeding performance and conservation status of all six colonies of the species in Greece over the last 40 years. We also discuss the local and regional natural factors that may have affected growth, either in individual colonies or in groups of colonies, as well as human effects on the colonies. These data will offer insightful conclusions for management and conservation everywhere across the species range, and particularly for other neighbouring populations in Albania, Bulgaria, Romania and Turkey, as the species is highly management-dependent (Grace et al. (2021)). Furthermore, they can be useful for the envisioned re-introductions of the species in several northern and central European countries and the British Isles (Kurstjens et al. 2021; Crees et al. 2022).

Study Areas

The two adjoining Prespa lakes (Fig. 1a, Table 1) are situated in a closed mountain basin. Mikri Prespa Lake is eutrophic and c. 47 km^2 in area, with a maximum depth of 8.4m. Megali Prespa Lake is mesotrophic, c. 250 km^2 and has a maximum depth of c. 50m. Both lakes are cyprinid dominated, with the more abundant species being *Alburnus belvica* and *Rutilus prespensis*. Lake Cheimaditis (Fig. 1b, Table 1) is one of four hydraulically connected lakes, in a joint catchment of 2,145 km^2. Reedbeds consisting mainly of *Typha* spp. and *Schoenoplectus lacustris* and less of *Phragmites australis* cover less than 20% of the lake surface. Average depth is less than one metre. The most abundant fish species are *Lepomis gibbosus*, *Alburnus thessalicus* and *Carassius gibelio,* (Petriki 2015).

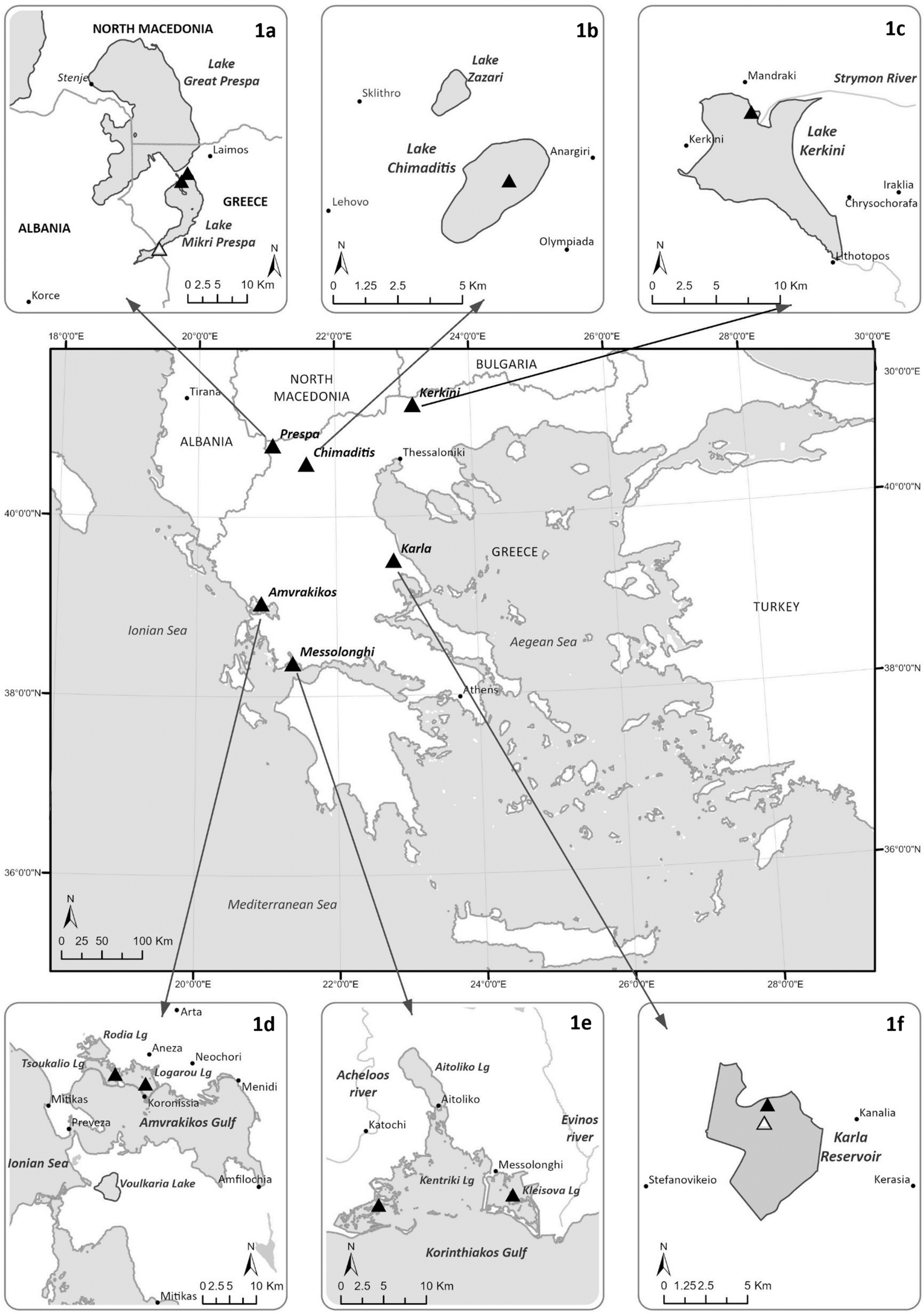

Figure 1: The locations of Dalmatian pelican colonies in Greece. Full triangles denote active colonies, open triangles denote former colonies. 1a: Prespa lakes, 1b: Lake Cheimaditis , 1c: Lake Kerkini, 1d: Amvrakikos wetlands, 1e: Messolonghi wetlands, 1f: Karla Reservoir.

In its present form, Lake Kerkini (Fig. 1c, Table 1) is a reservoir on the river Strymon, created by damming the river in 1982 for irrigation and flood control purposes. Its area of open water fluctuates from 5,000 to 7,300 ha according to the water level, which varies seasonally between 31 and 35.50 m asl. It is one of the most important waterbird breeding and wintering sites in Greece (Handrinos et al. 2015) and is also its most productive inland freshwater body (Tatarakis 1995; Petriki & Bobori 2009). *Carrasius gibelio* and *Cyprinus carpio* are fished in high quantities. Amvrakikos (Fig. 1d, Table 1) is a closed gulf (470 km^2), separated from the Ionian Sea by a narrow mouth, and has a maximum depth of 65 m and a seabed covered by mud or sand (Tsolakos et al. 2020). Two rivers discharge into the gulf, which includes 14 lagoons covering ca 86 km^2 (Katselis et al. 2013). Most of the lagoons are operated as natural fish farms, i.e., parallel to the traditional use there is restocking with gilthead sea bream *Sparus aurata* and European sea bass *Dicentrarchus labrax*.

Messolonghi (Fig. 1e, Table 1) consists of a double delta, lagoons and salt and freshwater marshes, coastal spits with dunes and salt pans (Pergantis & Handrinos 1992; Zalidis & Mantzavelas 1994). Th maximum depth of most lagoons is 1.5 m and the main lagoons are the Kentriki (11,2 km^2), Aitoliko (14 km^2) and Kleisova (3 km^2). Fisheries exploitation relies on the seasonal migration of fish from the open sea to the lagoons and the summer-to-winter offshore fish migration (Hotos & Katselis 2011)**.** Karla Reservoir (Fig. 1f, Table 1) was built in the early 2000s in a part of a drained lake and started filling with water in 2009. The mean water depth is 1.5 m. Extensive cyanobacterial blooms took place there between 2010 and 2018 (Oikonomou et al. 2012; Gkelis et al. 2017; Papadimitriou et al. 2018). More detailed data about each colony and its history are included in Table S1.

Methods

From 1967 to1982 all available data on colony sizes at Amvrakikos and Prespa were collected from a wide variety of published and unpublished sources and are of limited accuracy, mostly collected in one visit to the colony. The number of Apparently Occupied Nests (AON) was counted on the spot, but the estimates of numbers of breeding pairs were often just an approximation. These data (presented in Table S2) are useful in giving just a rough measure of the breeding population size in that period and were not treated further in this paper.

After 1982 the census of the colonies was carried out with a variety of methods, adapted to the particularities of each wetland and availability of resources. Nonetheless, all methods aimed at estimating the number of AON and fledged young produced. The primary concern was to keep researcher disturbance to a minimum.

At Prespa, between 1983 and 2000 colonies were censused from vantage points with telescopes and visits were paid every 7-15 days, which eventually became sparser as the colony grew and disturbance multiplied. After 2000 colony visits stopped and nest survey was only carried out from vantage points, while number of young fledged was impossible to census. Drones were used to photograph colonies monthly (February-July) and count AON nests and young on photos after 2014. The number of AON at Kerkini was assessed by observers circling the platforms in boats, taking photos from several angles. In 2013 a birdwatching tower was built close to the platforms from which observation was made with telescopes, while drone photos were also used after 2017. Surveying at Cheimaditis was carried out monthly (March-July) by taking aerial photos of the colony with a drone and counting AON and near-fledged young on photos. At Karla, until 2014, the number of AON was estimated annually through observations from vantage points and one visit to the colony near the end of the brooding period. After 2014 drone photos were taken monthly. At Amvrakikos, colonies were approached carefully by boat early in the breeding season and the number of AON was estimated from several spots around the islands, while a few, well-timed visits were made at later stages to count near-fledged young.

At Messolonghi, in early spring, colonies were approached carefully on boats twice and the number of AON was estimated from several spots around the islands, while two visits were paid at later stages of the breeding cycle to count near-fledged young. After 2019 only drone photos were used for both estimation of colony size and breeding success.

In this paper, when two groups of nests lie more than 3kms apart, are arbitrarily considered as two discrete colonies (cf. Coulson 2002). However, for practical reasons, we refer to “Site X colony” for all colonies lying within a specific wetland, even though in the text we clarify that there is more than one colony at this site. Discrete groups of nest-clumps within a colony are termed “sub-colonies” (e.g., two islets with nests situated a few metres apart), whilst the “breeding unit” is used *sensu* Crivelli (1987) and Crivelli et al. (1998), i.e. equivalent to the term “colony” used by Knopf (1979) and Johnston (2016): a spatially rather discrete group of contiguous nests, within which birds breed more or less synchronously.

Annual growth rate of colonies was calculated from the formula:

$$\frac{\frac{V_{final}-V_{initial}}{V_{initial}} X\,100}{N}$$

Where: V_{final} = population size of the last year, $V_{initial}$ = population size of the initial year and N = number of annual cycles that lapsed between initial year and final year.

Table 1: Main attributes of the wetlands hosting pelican colonies in Greece

	PRESPA	KERKINI	KARLA	CHIMADITIS	AMVRAKIKOS	MESSOLONGHI
Names of waterbodies included	Lake Mikri (Lesser) Prespa & Lake Megali (Great) Prespa	Kerkini Reservoir and parts of River Strymon	Karla Reservoir and smaller reservoirs	Lake Cheimaditis	Tsoukalio lg., Logarou lg., Rodia lg., Tsopeli lg, Lake Voulkaria, etc.	Kleisova lg, Kleisova lg, Kentriki lg, Aitoliko lg., River Evinos, etc
Max. surface area of water bodies (km²)	307	73	38	11	170	160
Catchment area (km²)-watershed	1,395	>17,000	1,171	103	>4,200	>630
Wetland types included	Freshwater lakes, ponds, wet reedbeds	Dam lake and inner river delta	Shallow reservoir	Freshwater lake, wet reedbeds	Coastal lagoons and wetland complex: saltwater lagoons, brackish water lagoons, freshwater lakes, and streams, reedbeds	Coastal lagoons and wetland complex: saltwater lagoons, brackish water lagoons, freshwater lakes, and streams, reedbeds
Altitude (average, m asl)	840	35	46	591	0	0
Climate type	Cfb-Temperate	Cfa -Humid Subtropical	Csa-Hot summers Mediterranean	Cfb-Temperate	Csa-Hot summers Mediterranean	Csa-Hot summers Mediterranean
Salinity	Freshwater	Freshwater	Freshwater	Freshwater	Saline-brackish-fresh	Saline-brackish-fresh
Principal human activities	Agriculture, livestock rearing, fishing, tourism	Agriculture, livestock rearing, fishing, nature tourism	Livestock rearing, agriculture	Livestock rearing	Fishing, fish-farming, agriculture, livestock rearing, hunting, tourism	Agriculture, fishing, fish-farming, livestock rearing, hunting, tourism
Main practices affecting pelicans & pelican habitats	None	Water level management, some disturbance by fishers and visitors in boats	Hydrological manipulations	Some disturbance by fishers	Disturbance by fishers, hunters, poachers	Disturbance by fishers, hunters, poachers
Hydrology & water quality issues	Lowering water levels due to climate change and abstraction, ongoing eutrophication	Quick water level increase by 5-6 m in spring, high sedimentation rates	Nutrient-laden waters, no renewal, cyanotoxin events	Water abstraction for power plant cooling	Decreasing sedimentation, eutrophication, less freshwater to lagoons	Decreasing sediments, less freshwater to lagoons
Legislative/Protection Status	National Park, Ramsar wetland, SCI, SPA	National Park, Ramsar wetland, SCI, SPA	SCI, SPA, Ecodevelopment area	SCI, SPA	National Park, Ramsar wetland, SCI, SPA	National Park, Ramsar wetland, SCI, SPA

Throughout the text the "Eastern population group" refers to the colonies at Prespa, Kerkini, Karla and Cheimaditis, while the "Western population group" refers to the colonies at Messolonghi and Amvrakikos. Based on ringing data, the exchanges -cf. gene flow- between these two groups are very limited. It has been supposed that this is due to the role of the Pindus mountain range (A.J. Crivelli, unpublished data, Catsadorakis 2016) as a physical barrier to movements.

Results

Breeding population trends and breeding success per colony

In Prespa two periods of severe drought (2001-02 and 2007-08), when pelican breeding numbers were supressed due to shortage of nesting places, were followed by spectacular increases in the next breeding period (Fig. 3). Nest numbers rose from 114 in 1983 (Crivelli 1987) and levelled off at around 1,226-1,585 during 2017-2021, showing a c. 6.8% annual growth (Fig. 3). In the last ten years BS has been 0.78 ± 0.20 (SD) fledged young/AON, n=7), but has significantly declined compared to figures for the 1980s and 1990s (1.15 ± 0.20, n=15) (t=-3.53, df=20, p=0.002). (Periods compared are 1984-1998 and 2014-2021). The decline indicates density dependence effects.

The annual growth of the Kerkini colony was c. 16.4% (n=19 years) (Fig. 3) but varied greatly according to the final year used for calculation (16.4%-25% for the last five years) and number of nests, which varies according to the available surface, which in turn is based on management decisions. The Kerkini colony shows the highest average BS of all the colonies in Greece, with 1.11±0.21 fledged young/AON (n=9), and the least variability.

Catsadorakis (2019) discussed the establishment and growth of the DP colony in the Karla Reservoir, which started with one pair in 2011 and reached 445 AON in 2017 (Fig.3), showing an annual growth of 176.4%. This colony shows the lowest BS of all colonies in Greece, equal to 0.69±0.21 fledged young/AON (n=8).

In Lake Cheimaditis DPs nest on 4-6 reed rhizome "islands" (Fig. 2.3, Table 2), like those at Lake Mikri Prespa. Within five years (2017-2021) the colony showed an annual growth rate of c.18% but it has been irregularly affected by human disturbance. The BS in the last five years has been 0.75±0.31 fledged young/AON.

From 1987 to 2010 the breeding population at Amvrakikos quadrupled, although in some years BS was heavily affected by human disturbance (Table 2) and for the period 1985-2010 it was 0.87 ± 0.16 (SD), (range 0.58-1.16, n=26; D. Hatzilacou & AJ Crivelli, presented at the 1st Meeting of Pelican specialists, Pyli, Prespa, Greece, 1-2 May 2012). In the last eleven years, the birds have still bred on Tsoukalio and Logarou lagoons, and the BS has been similar to the previous period, though still irregularly affected by disturbance (range 0.30-1.26, mean 0.91 ± 0.32 (SD), n=7). The annual growth rate of the colony at Messolonghi has been around 34% for 11 years (2011-2021). The BS of the colony is 0.88 ± 0.30 (SD), (range 0.57-1.37, n=9), (see Table S3).

Among colonies, Kerkini shows the highest and least varying mean BS (Fig. 4), which is significantly higher than that of Prespa, Cheimaditis and Karla (Mann -Whitney pairwise test 0.017, 0.045 and 0.003 respectively) and is also higher, but not significantly, than that of Amvrakikos and Messolonghi (Mann -Whitney pairwise test 0.223 and 0.133 respectively).

Regional and overall breeding population in Greece

According to all available data (Catsadorakis 2019, Bounas et al. 2022) the Eastern population group (1,820-1,930 AON in the last five years) exhibits a high degree of interconnectedness in terms of origin of breeders and immigration, as well as because many birds spend large parts of their annual cycle in two or more of them (Efrat et al. 2018, Georgopoulou et al. 2023). The annual growth rate of the whole Eastern population group is ca 7.7% (1983-2021), (Fig.5A).

The Western population group (200-400 AON in the last five years) currently consists of two colony-sites and four colonies (2 at Amvrakikos and 2 at Messolonghi). Its overall annual growth rate is ca 9.6 % (1983-2021, n=38) and, while Amvrakikos seems to have levelled off, Messolonghi, a more recent colony, continues to increase (Fig.5B).

The average total number of DP nests in Greece for the period 1967-1977 was 110 (range 70-155 AON) and continuously increased subsequently, with an annual growth rate of ca 7.9% (n=38 years, 1983-2021) (Fig. 5C).

Discussion

Data quality

Despite probable variability owing to different census methods and different observers, census results can be used for an overall analysis such as in this paper. This claim can be justified by the fact that: a. the adopted methods were based on common guidelines developed by the IPRCP in the 1980s (Crivelli 1987); b. the objectives of study did not change to a degree that undermined the value of the survey (Magurran et al. 2010); c. the straightforward nature of the surveyed objects (number of AON during the breeding period) and d. the same experienced researcher trained all other observers in all methods.

The shift in census methodology, basically the introduction of drone use, might be a source of bias mainly for the Prespa population, for which vantage-point surveys in the period 2000-2013 might have slightly underestimated

Figure 2: Aerial and ground images of the pelican colonies in Greece: (1) Prespa, natural islets, (2) Prespa, close up of the mixed colony; (3) Cheimaditis; (4) Karla, the old nesting island; (5) Karla, the current artificial island; (6) Karla, aspect of the boulder island with nesting pelicans; (7) Kerkini, the artificial island; (8) Kerkini, the wooden raised platform; (9) Amvrakikos natural islands; (10 &12) Messolonghi, natural islands; (11) Messolonghi, sub-colony on old disused road. Photo credits: 1,3,4,7/ O. Alexandrou-SPP Archive, 2/ F. Marquez-The Living Med, 5/ D. Michalakis-N.E.C.C.A., 6/ R. Papadopoulou, 8/ Th. Naziridis-N.E.C.C.A. 9/ S. Konstas-N.E.C.C.A., 10-12/ I. Kasvikis-N.E.C.C.A.

total population size, due to varying visibility between sub-colonies. Differences were minimised due to the experience of the principal observer, who has been the same over the years. A similar shift also took place at Karla and Messolonghi, but colony sizes in these locations are small and discrepancies between results obtained by the two methods are thus also considered to be very small.

Population growth and trends

Prespa: Besides the intrinsic growth potential of the Prespa population, growth might have been affected by a spatial expansion of the nesting area, which was made possible in 1990 due to management measures, as well as the stochastic formation of two very large nesting islands, which might have enhanced social stimulation through higher breeding densities (Catsadorakis & Crivelli 2001). In the last ten years, population growth seems to have levelled off, egg and chick mortality has increased, and breeding success declined, something commonly observed in colonies at a similar stage (Newton 1998). Laying initiation has advanced (Doxa et al. 2012a) and is still advancing (G. Catsadorakis & O. Alexandrou, unpublished data), late winter-early spring adverse weather events affect BS negatively and re-laying seems to have been a common phenomenon during the last 8 years. In years of extreme drought many nesting islands become accessible by land, limiting available nesting habitat, so the breeding population declines. At the other extreme, in very wet years parts of nesting islands are flooded and become unavailable to pelicans (Catsadorakis et al. 1996). Furthermore, the Prespa lakes are the highest-lying large lakes in the Balkans and although they also offer an abundance of fish, these are not available to the birds in January to March. The water level of Lake Megali Prespa, the main feeding ground for pelicans, has suffered a 9 m drop and this might have changed the availability of fish. In the last 30 years, due to the dramatic advancement of laying (Doxa et al. 2012a), many DPs start breeding when it seems no prey is available in these lakes. A mismatch is thus created due to the inverse relationship between laying initiation date and food availability, which may be the main reason for the failure of early breeders. In the past, DP nesting early in Prespa had to visit the lower-lying Lake Kastoria to feed (Crivelli 1987; Hatzilacou 1992), but in recent years they have been obliged to travel even farther to find food, as far as Lake Kerkini (Efrat et al. 2018; Georgopoulou et al. 2023) which lies ca 200 kms away.

Kerkini: The number of breeding pairs is limited by the space available on the artificial nesting platforms depending on management decisions. Shortage of nesting space was clearly demonstrated after increases in platform area (Figs 2.7, 2.8) led to increases in breeding pairs. Furthermore, hydrological manipulations determine water level during January-February when nest-building starts, and this in turn determines how many nests will be built on the artificial islet. If the area around it is not yet flooded, pelicans delay nest initiation and the final number of nests is low.

Karla: Initially increasing nest numbers dropped when rising water levels forced birds to abandon the first occupied site for a new, higher-lying colony island, but they have started to increase again. Thus, it makes no sense to discuss the growth rate of this colony separately. Furthermore, between 2016 and 2019, 247 DPs died in Karla, with the probable mortality attributed to cyanotoxins (Papadimitriou et al. 2018). The timing of deaths coincided with the shift in colony site, so no conclusions can be drawn from the confounding effect of these two variables on the population size, which nevertheless did not seem to directly affect the site's attractiveness for breeding.

Cheimaditis: Only five years of data are not enough to discuss the growth pattern of this newest of colonies to any great extent. In the last three years it seems there has been a stability in nest numbers, but the BS remains low, in some years due to disturbance by fishermen and in 2021 by H5N8-caused mortality (G. Catsadorakis & O. Alexandrou, unpublished data).

Amvrakikos: Because the two groups of nesting islands are c. 9 km apart, we can refer to the presence of two colonies in this site. Since the 1980s many nesting islands have eroded away, whilst the existing ones suffer from erosion associated with limited sediment inputs, rising lagoon water levels and wave action, noted by Crivelli (1987) and Hatzilacou (1993). Nesting islets are visible from all around and are easily accessible by boat. In the 1980s disturbance by fishermen, visitors, and fish- and wildfowl poachers was frequent, hence the Hellenic Ornithological Society carried out a volunteer guarding project (1985-1990, taking place for four months annually. During the IPRCP (1985 to 2009), the increase of the breeding population can be possibly associated with regular surveying of the colonies and successful sensitisation and awareness actions. However, the colonies suffered from disturbance in 2009 and 2010, which coincided with the termination of the IPRCP study (D. Hatzilacou, unpublished data). After 2016, patrolling by the national park management body improved, acceptance of pelicans by fishermen increased and disturbance declined, which may have allowed pelicans' breeding success to improve and numbers to increase, however this seems to have levelled off at around 150 pairs.

Messolonghi: The >30% annual growth rate of the Messolonghi colony is a strong indication that this new colony continues to receive immigrants from the Amvrakikos colonies. After the disturbance event of 2018, pelicans colonised more islands in the Kentriki lagoon, so that two separate colonies were formed 12 km apart. The breeding population is still on the increase and the Kentriki colony in particular seems to have a huge potential for increase.

Table 2: Basic descriptive features and attributes of the Dalmatian pelican colony sites in Greece

ATTRIBUTES	PRESPA	KERKINI	KARLA	CHEIMADITIS	AMVRAKIKOS	MESSOLONGHI
Date of colony establishment	<1936	2002	2011	ca 2015	mid-19th c.	1677-1940s/ 2011-
Number of frequently occupied discrete islands	>30	1--3	2	3--5	3--4	5--7
Number of discrete colonies (concentrations >3km apart)	1--2	1	1	1	2	2
Type of nesting islands /natural/artificial/other	Natural	Artificial	Artificial / Other	Natural	Natural	Natural/Other
Type of substrate of nesting islands	Reed rhizomes	Wooden platforms/ Rocks	Gravel/ Rocks	Reed rhizomes	Sandy	Sandy / Gravel
Vegetation cover/ plant species	Reeds & other aquatic macrophytes	None	Nitrophiles	Reeds & other aquatic macrophytes	Salicornia, Athrocnemum	Salicornia, Anthonomus / none
Western population group / Eastern population group	E	E	E	E	W	W
Type of water body	Lake	Dammed river/Reservoir	Reservoir	Lake	Lagoons	Lagoons
Purposeful disturbance occurrence*	Low	Low	Low	Some	High	Medium
Unintentional, side-effect disturbance occurrence	Low	Some	Low	Some	High	High
Colony island erosion	Some	Some	Some	Some	Medium	Medium
Suspected limitation by nesting space	High	High	Medium	Low	Low	Low
Suspected limitation in access to food	Low	Low	Some	Low	Medium	Medium
Suspected occurrence of competition for food	High	High	Some	Medium	Low	Low
Suspected/ indications for competition for nesting space	High	Low	Some	Some	Low	Low
Disturbance at feeding areas	Low	Some	Low	Some	Medium	Medium
Frequent mortality causes	N/A	N/A	Toxins	N/A	Collisions	Collisions
Maximum distance between most distant nests of same colony (m)	2,150	150	45	950	330	1,600
Area covered by Minimum Convex Polygon of all nesting islands, Km^2)	0.1/0.1	<0.1	<0.1	<0.1	<0.1	1
Strong water level fluctuation	Low	High	Medium	Low	Some	Some

*Threats according to Salafsky et al. 2008. Magnitude scale: Nil, Low, Some, Medium, High

Greece: There is a consensus in the ornithological literature that most seabird populations are regulated, usually in a density-dependent way, and that important regulatory factors are food, breeding space, parasites and predation (Croxall & Rothery 1991). After 35 years of work with DPs in Greece there are no indications that parasites and predation do substantially affect breeding performance and/or numbers of these birds anywhere.

As regards prey abundance and availability, in Greece there are neither fish stock estimations (but see Bounas et al. 2021 for Prespa) nor adequate understanding of fish movement patterns in these shallow wetlands in relation to season, water temperature and light. Shallow Mediterranean lakes suffer from rapid eutrophication and, as such, fish stocks in lakes in northern Greece, which are dominated by cyprinids, have increased everywhere (Beklioğlu et al. 2007), but prey abundance is not always a good measure of food-supply when other factors limit its accessibility (Newton 1991). Kerkini, being the most productive lake in the region, has a key role in the wetlands network used by pelicans in northern Greece. It is used as the last staging site for pelicans migrating to Prespa, Cheimaditis and Karal to breed and it hosts pelicans all year round in contrast to the other three sites of the Eastern population group.

The increase of DP might possibly be attributed to: a. increased survival rates through reduced mortality owing to the milder climate in wintering grounds due to climate change (cf. Barboutis et al. 2021); b. higher fish availability due to the sustained activity allowed by higher mean winter temperatures (cf. also Lack 1968), also due to climate change; c. lower disturbance due to enhanced patrolling in protected areas; d. higher numbers of sympatrically nesting great cormorants that allow higher feeding efficiency (cf. Giokas et al. 2020); and e. less persecution by fishermen as a result of the shrinking size of commercial inland fisheries, similar to the marked increase of many seabirds in the North Sea during the 20th c., which had also been attributed to the relaxation of human persecution (Cramp et al. 1974). A rapid increase is the norm in new colonies (Newton 1998), as has been the case with Karla, Cheimaditis and Messolonghi, due to high net immigration rates.

Formation of new colonies and patterns of human influence

The formation of new colonies is not a frequent phenomenon in seabirds (Coulson 2002). For at least 60 years (1940s-early 2000s) there were only two DP colonies in Greece. Starting from around 100 AON in the period 1967-1982, in 2002 (before the third colony at Kerkini appeared) the Greek breeding population had increased by c. 640%, but no new colonies were formed. In the next 20 years the population rose threefold and 4 new colonies were formed. This fact indicates that external factors were keeping pelican populations suppressed and when these factors relaxed or were lifted, populations exploded, but it is likely that the processes for the creation of new colonies set off when the two "parent" colonies reached their maximum capacity in spatial terms and recruits could not be accommodated within them. Whether seabirds are indeed limited by nesting space and whether there is competition over it are both notoriously difficult to prove (Coulson 2002; Hamer et al. 2002). In the case of DPs in Greece, the creation of new colonies was made possible after suitable artificial nesting structures were offered to pelicans (Kerkini in 2002) and when a new wetland emerged (Karla in 2009) with a semi-natural nesting island that was free of disturbance (Catsadorakis 2019). The "natural experiments" described above, combined with the large intra-colony differences in breeding success in Prespa, are possible indications of a shortage of high-quality nesting sites. The relaxation of pressure from fishermen may also have contributed to allowing the initiation of new colonies at Messolonghi and Cheimaditis.

Conservation

Until the 1980s the two colonies at Prespa and Amvrakikos suffered from disturbance, mainly by fishermen and secondarily by wildlife photographers. Besides Prespa, where effective conservation measures in the 1980s and 1990s allowed the population to increase, conservation measures had been improving slowly everywhere in Greece and possibly also in Turkey's main wintering wetlands.

The levelling-off which is observed in the two old colonies and the dynamic growth of the new colonies show that conservation measures should not be designed and decided for individual wetlands only but should consider the dynamic nature of the two population groups (meta-populations?). In the last twenty years a transitional phase has been observed with the creation of new colonies, but perhaps even more will be created soon, so monitoring of all pelican populations on an annual basis is required, as it will give quick and timely warnings for necessary measures.

During the 20th century many seabird species have increased greatly, in some places because of reduced human persecution and in others because human fishing activities have made their food more available (Newton 1998). The role of anthropogenic factors that strongly interact with natural factors, and are all assumed to have contributed to the pelican increase in Greece in the last 40 years, should not underemphasised: legal protection status for all pelican-hosting areas; increasingly effective protection and conservation measures in the field; public awareness campaigns; provision of artificial nesting structures; decrease of pollution; decline of disturbance and persecution due to relaxation of pressure by fishermen and decline of fisheries; appearance of new wetlands and alteration of wetlands due to human intervention.

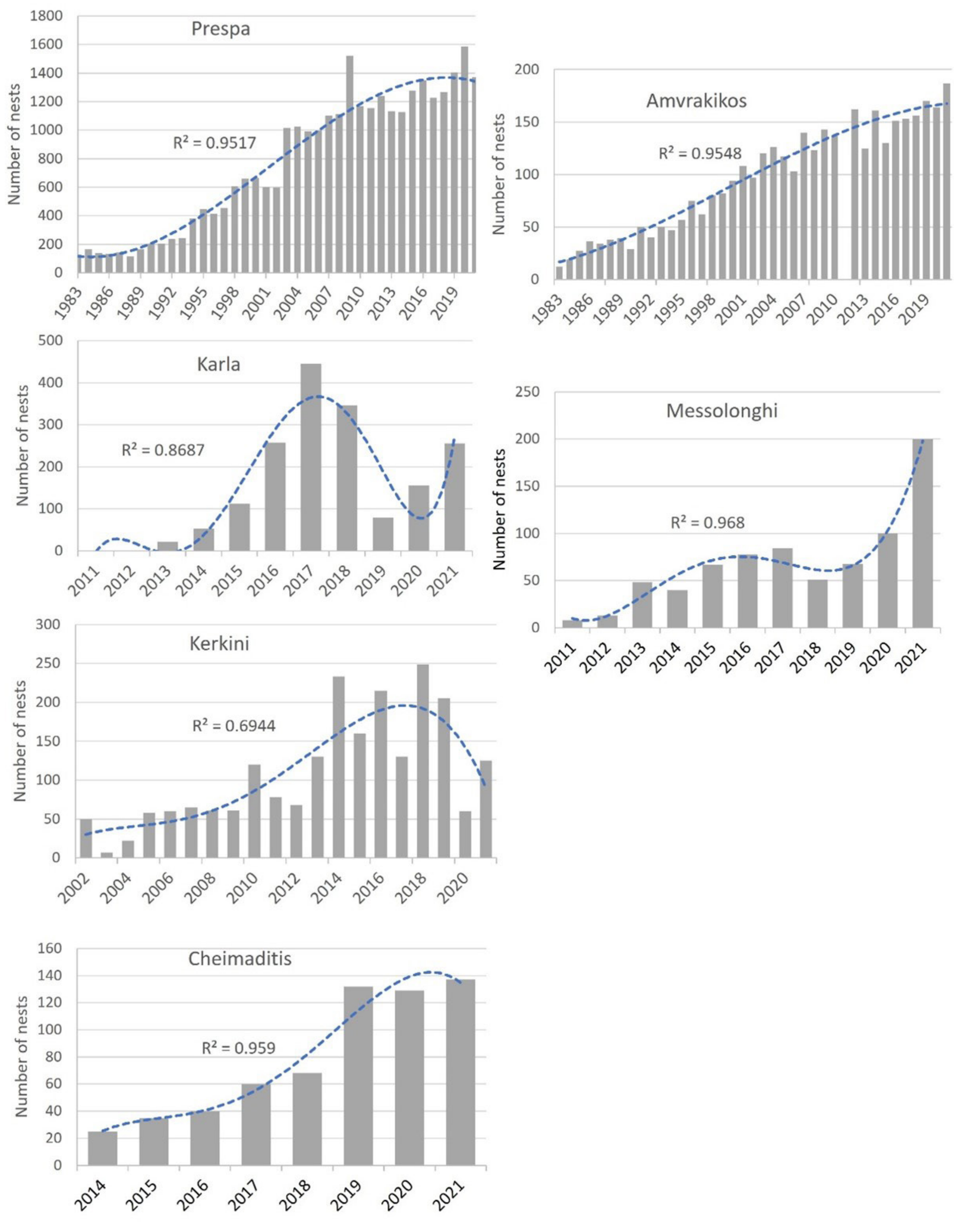

Figure 3: The growth of AON numbers in each of the six colonies of Greece (1983-2021). For the Prespa and Amvrakikos colonies a cubic polynomial regression curve is fitted and shown. For all other colonies a bi-quadratic polynomial regression line is shown. Note the differences in scale.

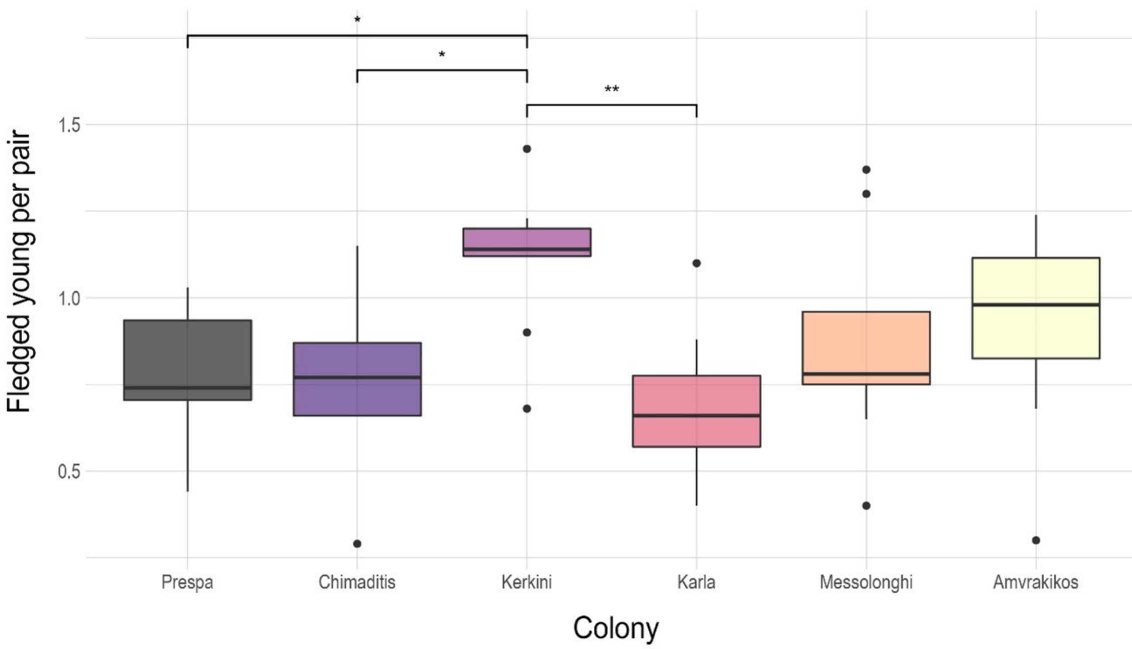

Figure 4: Boxplots showing the median (horizontal line) and interquartile range (box) of the breeding success (fledged young/pair) of Dalmatian pelican colonies in Greece, 2012-2021. *=p<0.05, **= p<0.01.

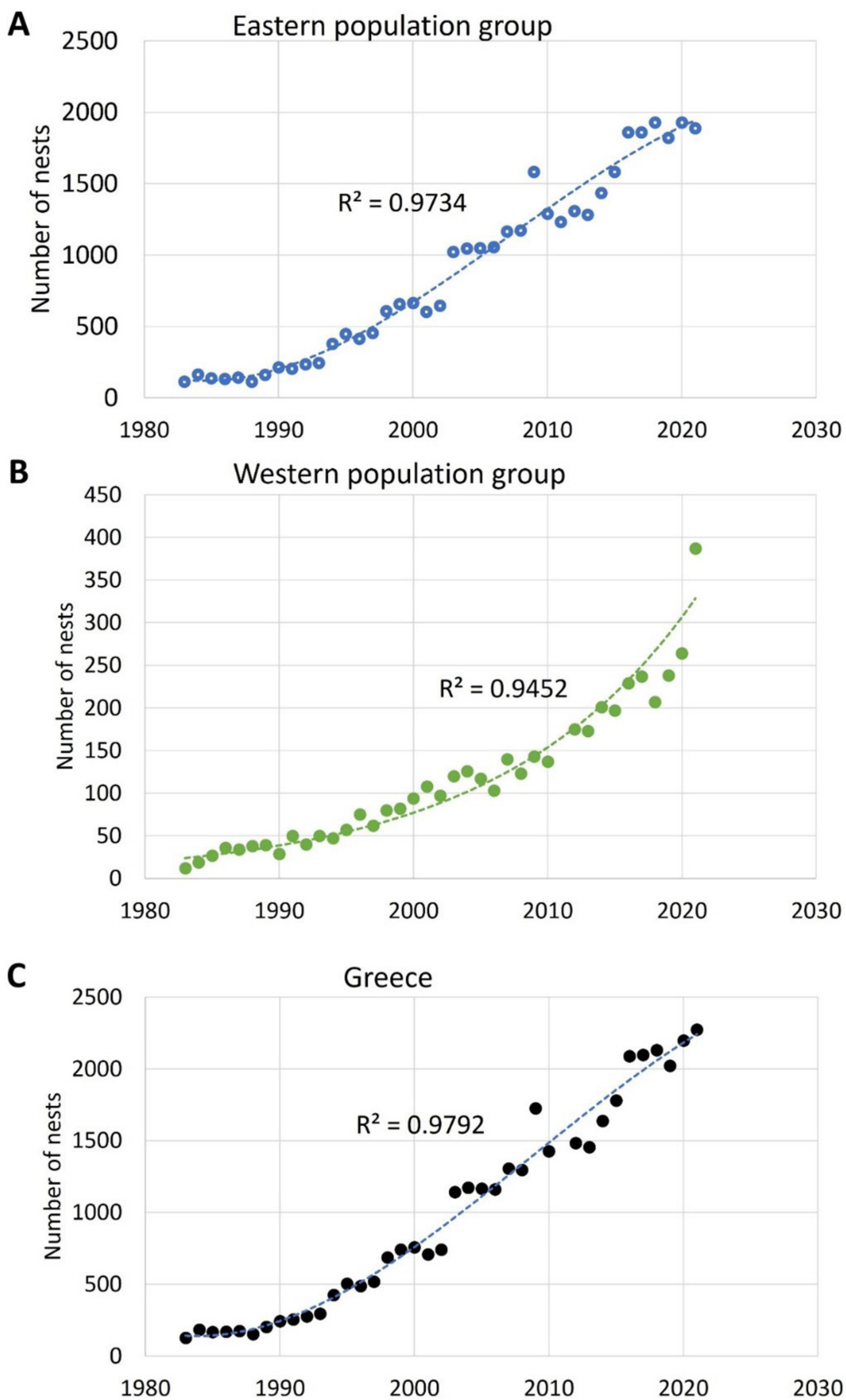

Figure 5: The evolution of total Dalmatian pelican breeding population sizes (estimated as AON) in Greece 1983-2021. A. The Eastern population group, B. The Western population group and C. The whole of Greece. A cubic polynomial regression curve is shown for each.

Disturbance-free nesting sites and reduced mortality causes should be secured. Monitoring population trends and especially BS in as standard a mode as possible is crucial for evaluating conservation measures. An assumed shortage of nesting space merits a closer examination to shed light to the exact importance of its impact upon DPs, as, not only are the physical attributes of the habitats involved but the social mechanisms too (cf. Coulson 2002). Further work should also be done to understand the patterns of use the DPs make of all wetlands for foraging and their feeding behaviour and efficiency.

Lastly, the movement corridors of these large soaring birds when moving between wetlands should be located and protected effectively, especially in view of the establishment of new wind parks on mountain slopes that are heavily used by commuting pelicans (Efrat et al. 2018; Georgopoulou et al. 2023).

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SUPPLEMENTARY MATERIAL

Table S1: The environment and history of pelican colonies in Greece

Lakes Mikri and Megali Prespa	The two mixed DP and great white pelican *Pelecanus onocrotalus* colonies, which lie ca 13.5 km apart were discovered in 1968 (Brosselin & Molinier 1968) and were: a. In the unused area in Lake Mikri Prespa, around the Greek-Albanian border, but which was abandoned in 1991; and b. In the inland Viro-1 pond, lying in the alluvial zone separating the two lakes. There are indications they had existed there since at least the early 20th c. (Handrinos & Catsadorakis 2020). For the period 1968-1982 there are scattered and incomplete estimations of AON for 11 of the 15 years (Crivelli 1980), ranging from 40 to 150 (average 89). A 3-year drought (1988-1990) excluded pelicans from their two traditional breeding grounds, which became accessible by terrestrial predators (Catsadorakis et al. 1996), but in 1990 they were finally forced to nest on artificial islands. Conservationists convinced local fishermen to "concede" a part of the open lake to pelicans for nesting (i.e. without approaching them during the breeding period). This allowed pelicans to use this new area at the NNW part of Mikri Prespa, which had been previously unavailable because of the daily presence of fishermen. The expansion allowed further increases in the nesting population.
Lake Cheimaditis	After the raising of dykes in 2012, water level fluctuates little, around 591.5 m asl. There are only a few fishermen in this cyprinid-dominated lake. It is a wetland long known to be used by both species of pelicans for staging, roosting and foraging, particularly during spring (Pyrovetsi 1990, Hatzilacou 1992, 1993, 1996). The colony in this lake was discovered in 2017 but may have initiated 1-3 years earlier and had remained undetected (Handrinos & Catsadorakis 2020).
Lake Kerkini	A reservoir created by damming the River Strymon in 1932 for irrigation and flood control purposes. In 1982 a bigger dam and higher dykes increased its storage capacity. Colonies of 11 large waterbird species lie in the riparian forest, mainly of willows *Salix* sp., which is flooded during the breeding period (Crivelli et al. 1995; Naziridis & Papageorgiou 1996). Although pelicans were abundant in Kerkini all year round since at least the 1980s, the dramatic increase of water level in spring precludes pelican nesting, as all natural islands are flooded. It was only in May 1990 that pelicans attempted to breed on a natural island (13-15 nests with eggs, Pyrovetsi 1997), as well as on flooded trees (2 nests, Crivelli & Naziridis, unpublished data). In subsequent years 5-15 nests were made almost annually but were flooded. In 2002 a small, raised platform was built but not used and 52 nests were made but were also flooded. The following summer (2003) the raised platform area was doubled and DP nested (7 nests) but could not rear any young to fledging, something which finally took place in 2004 (Crivelli & Naziridis unpublished data, Handrinos & Catsadorakis 2020) and continues to date.
Karla Reservoir	Karla was a natural, floodplain lake in Thessaly, but was drained in 1962 to provide arable land and minimise flood impacts. The reservoir receives water from the River Pinios (35 km straight-line distance NW of Karla) and surface runoff from the surrounding catchment (Sidiropoulos et al. 2012). Dathe & Profft (1939) and Geroudet (1962) mentioned the presence of both DP and GWP in the old Lake Karla but offered no evidence of breeding. Catsadorakis (2019) discussed the establishment and growth of the DP colony in the reservoir, which started with one pair in 2011 and reached 445 AON in 2017. However, in 2018 increasing water levels led to partial flooding of the nesting island, while in 2019 it became fully submerged and pelicans shifted to an artificial island (c. 85m X 55 m) constructed of rocks, specifically for waterbird nesting. The number of nests dropped to 82 but increased in the following years. The initial nesting island was a mound of unused gravel, part of an old dyke, that protruded above the water surface. Initially it had been entirely bare, but gradually aquatic macrophytes developed on the island's margins.
Amvrakikos Gulf	The Arachthos and Louros rivers discharge into the Amvrakikos gulf. Tsoukalio (28.3 km^2) and Logarou (35.0 km^2) are the largest lagoons. One or more DP colonies had existed in Amvrakikos since at least the mid-19th century (Crivelli 1980). In 1967 a colony was discovered in the Rodia lagoon but in the early 1970s it was exterminated by fishermen, to show up again in 1979, in Tsoukalio lagoon this time (Hatzilacou 1992). For the period 1967-1977 there are estimations of the breeding population only for 7 years and AON averaged c. 21 (range 15-35). From 1987 to date the birds have nested on both Tsoukalio and Logarou lagoons. Their nests lie on flat, sandy islets covered with halophytic vegetation of *Salicornia europaea* and *Arthrocnemum macrostachyum* (Hatzilacou 1993, D. Hatzilacou & AJ Crivelli, presented at the 1st Meeting of Pelican specialists, Pyli, Prespa, Greece, 1-2 May 2012, Iliadou et al. 2014).
Messolonghi wetlands	The Messolonghi wetland complex was formed at the mouths of the Acheloos and Evinos rivers. The abundant presence of pelicans in Messolonghi has been documented since 1675 (Spon & Wheler 1679) and later from various sources in the mid-19th century (Handrinos & Catsadorakis 2020), while they still bred there until the 1940s (Roussopoulos 2012). They resumed breeding in 2011 (Handrinos & Catsadorakis 2020). Some of their nesting islands are relics of dykes built in the mid-20th c. as part of works for improving the lagoon's productivity for fisheries. Other nesting islets are low and flat, formed of sand and seashells with halophytic vegetation of *Salicornia* and *Arthrocnemum*. Initially pelicans nested only on 4-5 islets in the Western Kleisova lagoon, but in 2018, after a serious disturbance, they expanded to natural islands in the Kentriki lagoon. The two concentrations are over 10km apart and they constitute two rather separate colonies. Pelicans started with 6-8 nests in 2011 (Roussopoulos 2012), but in 2021 they had exceeded 180 AON in 19 breeding units on 8 different islets. Despite regular patrolling, disturbance events by visitors and wildfowl-poachers are not averted. Disturbance is probably often also caused by fishermen, who attempt to scare away great cormorants.

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Table S2: Estimated apparently occupied Dalmatian pelican nests in the colonies of Greece 1967-2021

YEAR	Prespa	Kerkini	Karla	Cheimaditis	Amvrakikos	Messolonghi	GREECE
1967	no data				18--20		-
1968	70-120				no data		-
1969	70				19--20		c.90
1970	40-50				no data		-
1971	80-100				20		100-120
1972	100-120				no data		-
1973	80-100				no data		-
1974	no data				no data		-
1975	50-70				no data		-
1976	40-50				no data		-
1977	>120				no data		-
1978	>35				no data		-
1979	150				35		185
1980	no data				15		-
1981	no data				15		-
1982	no data				20		-
1983	114				12		126
1984	165				19		184
1985	139				27		166
1986	133				36		169
1987	143				31		174
1988	114				38		152
1989	163				39		202
1990	202	15-17			28		243
1991	205				50		255
1992	235				41		276
1993	245				50		295
1994	380				46		426
1995	447				56		503
1996	414				74		488
1997	455				63		518
1998	607				79		686
1999	659				82		741
2000	666				93		759
2001	602				106		708
2002	597	52			95		742
2003	1,016	7			120		1,143
2004	1,025	22			126		1,173
2005	991	58			116		1,165
2006	996	60			104		1,160
2007	1,102	65			140		1,307

2008	1,112	61			124		1,297
2009	1,522	61			143		1,726
2010	1,169	120			137		1,426
2011	1,155	78	1		N/A	8	N/A
2012	1241	68	1		162	13	1,485
2013	1,131	130	22		125	48	1,456
2014	1,125	233	53	25	161	40	1,637
2015	1,276	160	112	35	130	67	1,780
2016	1,349	215	257	40	151	78	2,090
2017	1,226	130	445	60	153	84	2,098
2018	1,266	249	346	68	151	51	2,131
2019	1,405	205	79	132	134	68	2,023
2020	1,585	60	155	129	168	100	2,197
2021	1,370	125	256	137	187	200	2,275

Data sources

Prespa: 1968-1979, Crivelli 1980 (modified according Hatzilacou 1993); 1983-1986: Pyrovetsi & Crivelli 1988;1987-1992: Catsadorakis et al. 1996; 1993-2000: Crivelli & Catsadorakis (unpublished data); 2001-2010: SPP & Crivelli (unpublished data); 2011-2021: SPP (unpublished data).

Amvrakikos: 1967-1979: Crivelli 1980; 1980-1989: Hatzilacou 1993;1990-2010: Crivelli & Hatzilacou (unpublished data); 2011-2021: N.E.C.C.A.

Kerkini: 1990: Pyrovetsi 1997; 2002-2015: Crivelli & Naziridis (unpublished data); 2016-2021: N.E.C.C.A.

Karla: 2011-2017: Catsadorakis 2018; 2018-2021: N.E.C.C.A. & SPP

Cheimaditis: 2017-2021: SPP (unpublished data)

Messolonghi: 2011: Roussopoulos 2012; 2012-2021: N.E.C.C.A.

Table S3: Estimated Dalmatian pelican Breeding Success (near-fledged young per Apparently Occupied Nest) in the colonies of Greece, 2012-2021. Data sources: Prespa and Cheimaditis: SPP; Karla: N.E.C.C.A. & SPP, Kerkini, Messolonghi and Amvrakikos: N.E.C.C.A.)

YEAR	PRESPA	CHEIMADITIS	KERKINI	KARLA	MESSOLONGHI	AMVRAKIKOS
2012	no data		no data	no data	no data	0.68
2013	no data		1.43	0.57	0.65	0.3
2014	0.92		1.14	0.88	0.4	1.24
2015	1.03		1.16	0.57	1.3	no data
2016	no data		1.12	no data	0.77	no data
2017	0.95	1.15	1.23	0.7	0.78	no data
2018	0.73	0.66	1.12	0.4	1.37	0.97
2019	0.74	0.87	1.2	1.1	0.96	0.98
2020	0.44	0.29	0.68	0.74	0.95	1.15
2021	0.68	0.77	0.9	0.62	0.75	1.08