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Reproductive performance of the great cormorant (*Phalacrocorax carbo sinensis*) in three Greek colonies

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Several breeding parameters of the great cormorant (*Phalacrocorax carbo sinensis*) were studied in Greece in 2001 and 2002 and were found to be generally higher at Lake Kerkini than in the other colonies. Fledging success (proportion of hatched eggs that led to fledged nestlings) was significantly higher at Lake Kerkini and in the Axios Delta in both years than at Lake Mikri Prespa in 2002. Mean fledgling production (the number of young fledged per initiated clutch) was significantly higher at Lake Kerkini than at Lake Mikri Prespa in 2002. The high fledgling production (2.15–2.75 fledglings on average in this study), the high food availability and the low initial population density allowed the total Greek breeding population to grow at a fast rate (19.0% per annum) in the 1990s. Given the scarcity of information on great cormorant nesting in Greece, basic breeding parameters are important for modelling population dynamics.

Keywords: great cormorant; clutch size; egg size; breeding success; population dynamics; Greece

Introduction

The great cormorant (*Phalacrocorax carbo sinensis* (Blumenbach, 1798)) is a widespread fish-eating waterbird (Cramp and Simmons 1977; Johnsgard 1993). Its populations, although stabilised recently, have been increasing since the 1970s throughout its European range (Debout et al. 1995; Van Eerden and Gregersen 1995; Handrinos and Akriotis 1997), mainly as a response to legal protection and an increase in fish productivity due to eutrophication of aquatic habitats (Russell et al. 1996). As a consequence, severe conflicts with angling and fisheries interests have risen in many countries (Russell et al. 1996; Cowx 2003). Therefore, much research on the diet of the great cormorant, energetics and the impact on fish populations has been conducted, especially during the last ten years (see Baccetti and Cherubini 1997; Cowx 2003 and Keller et al. 2003 for reviews). Management and control plans have been formulated and applied (Kirby et al. 1996; Bildsøe et al. 1998).

The breeding population of the great cormorant in northwest Europe increased rapidly during the 1970s and 1980s, before levelling off at c. 100,000 pairs in the mid-1990s, a more than 20-fold increase (Bregnballe 1996). In contrast, the Greek breeding population changed little from 550 pairs in 1971 (at two colonies: Lake Mikri Prespa and the Evros Delta) to 660 pairs in 1990 (at four colonies: Lake Mikri Prespa, Lake Kerkini and the Axios and Evros deltas; Handrinos and Akriotis 1997). Subsequently, and following the levelling off of the northwest European population, the Greek breeding population of the great cormorant increased rapidly to c. 4300

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pairs in 1999–2001 to *c.* 5300 pairs in 2002–2006 at six colonies (with the addition of two small colonies at Lake Kastoria and Lake Volvi), showing an eight-fold increase since 1990 (Kazantzidis and Naziridis 2003; Liordos and Goutner 2003; Kazantzidis S, Naziridis T, personal communication).

There has been a focus on population monitoring and dietary analysis studies following the population expansion. Furthermore, aspects of the breeding biology of the great cormorant have been studied throughout its European range (e.g. in France, Debout 1988; Netherlands, Van Eerden et al. 1991; Italy, Volponi 1999; Denmark, Bregnballe and Gregersen 2003; Poland, Kopciwicz et al. 2003; England and Wales, Newson et al. 2005). On the other hand, there has been only one study on the breeding biology of the great cormorant in Greece (Liordos and Goutner 2003) dealing with the bird's population, clutch and egg size. In this study, clutch size was recorded in order to know whether differences in fledgling production are likely to be the consequence of differences in the number of eggs laid or differences in partial egg or nestling loss (Newson and Bregnballe 2003). Egg size was estimated because larger eggs are laid by older, larger and more experienced females (Coulson et al. 1969, Sæther 1987), are of better quality and their offspring may have a higher probability of survival (Nisbet 1978, Galbraith 1988, Grant 1991). The aims of this paper are therefore: (1) to estimate several breeding parameters of the great cormorant in three major Greek colonies in 2001 and 2002; (2) to reveal patterns and identify sources of variation in reproductive performance; and (3) to link breeding success with great cormorant population dynamics in Greece.

Materials and methods

The study sites

The three great cormorant breeding colonies studied are located in northern Greece: at Lake Kerkini and Lake Mikri Prespa and in the Axios Delta (Figure 1). All of them are designated as Wetlands of International Importance under the Ramsar Convention.

The Axios Delta (40° 27'–40° 38' N, 22° 33'–22° 52' E) belongs to a large wetland complex covering a total of 69 km², situated near the city of Thessaloniki (Athanasidou 1990). The mixed colony included black-crowned night heron (*Nycticorax nycticorax* (L., 1758)), squacco heron (*Ardeola ralloides* (Scopoli, 1769)), spoonbill (*Platalea leucorodia* (L., 1758)) and little egret (*Egretta garzetta* (L., 1758)), and was located on an islet in a riverine forest of tamarisks (*Tamarix hampaena* (Boiss. & Heldr.)), common alders (*Alnus glutinosa* (L.)) and willows (*Salix* sp.) (Kazantzidis et al. 1997) and on the opposite bank of the river on tamarisks. The breeding population changed from *c.* 120 pairs in 1990 (Kazantzidis 1998) to *c.* 220–600 pairs in 1995–1998 (Kazantzidis S, unpublished data), and to *c.* 400 pairs in 1999–2000 (Liordos and Goutner 2003), before levelling off at *c.* 220–270 pairs in 2001–2006 (Liordos 2004; Kazantzidis S, personal communication). All nests were located on the islet until 2000 but the trees were rapidly degraded due to the birds' faeces and pairs breeding there were reduced to 160 and 120 in 2001 and 2002, respectively. Sixty and 100 pairs in 2001 and 2002, respectively, nested on the river bank opposite to the islet, whereas by 2006 the old colony was completely abandoned, with great cormorants now nesting on a new islet about 100 m north of



Figure 1. Map showing the location of the three study areas in Greece.

the old one (c. 50 pairs) and mainly on the river bank (c. 200 pairs; Kazantzidis S, personal communication).

Lake Kerkini ($41^{\circ} 12' N$, $23^{\circ} 9' E$), a semi-artificial seasonally flooded lake, with a surface varying from 55 to 75 km², is located near the Greek–Bulgarian border. Great cormorants nested over water mainly on willow hybrids (*Salix alba* (L.) \times *S. fragilis* (L.)) in a mixed uniform colony of 12 waterbird species, including the endangered pygmy cormorant (*Phalacrocorax pygmeus* (Pallas, 1773)) and spoonbill, situated at the northeast part of the lake (Naziridis and Papageorgiou 1996). The dense flooded forest provides high quality nesting habitat and the number of breeding pairs doubled from 500 in 1990 to 1125 in 1993, further increasing to 2000–2500 pairs in 1996–2001, climbing to 3500 pairs in 2002 (Kazantzidis and Naziridis

2003) and further increasing to 3850 pairs in 2006 (Naziridis T, personal communication).

Lake Mikri Prespa (40° 44' N, 21° 4' E) in the far northwestern Greece, along with Lake Megali Prespa, is situated at an altitude of 853.5 m asl. Of its surface (47 km²), 92% belongs to Greece and the rest to Albania. Great cormorants nested in three closely situated colonies: on Vidronissi and Agios Achileios islands, and the Vromolimni area islands. The two latter colonies were not studied on order to avoid disturbance to the endangered Dalmatian pelicans (*Pelecanus crispus* (L., 1758)) that nest there in association with great cormorants. The Vidronissi island colony was composed of a uniform stand of ancient juniper (*Juniperus foetidissima* (Willd.)) trees. The total breeding population evolved from 451 pairs in 1990 (Catsadorakis et al. 1996) to 799 pairs in 2005 (Society for the Protection of Prespa, unpublished data). The Vidronissi colony size was estimated at 106 pairs in 1990 (Catsadorakis et al. 1996), increasing and fluctuating between 470, 170, 220 and 440 pairs in 1999, 2000, 2001 and 2002, respectively (Liordos 2004). The following years the breeding population fluctuated little around 300–400 pairs, and consisted of 368 pairs in 2005 and 310 pairs in 2006 (Society for the Protection of Prespa, unpublished data). By 2000, the colony was highly degraded due to the birds' faeces, containing many dead but still standing trees.

Great cormorant tree nests are mostly situated on islands (Lake Mikri Prespa, Axios Delta) or over water (Lake Kerkini), isolated from both land predators and humans. The only potential threat was posed by aerial predators such as magpies (*Pica pica* (L., 1758)), hooded crows (*Corvus cornix* (L., 1758)), jackdaws (*Corvus monedula* (L., 1758)), and several gull species (*Larus* spp.) that were present in all colonies. The mainland colony established in 2001 in the Axios Delta is more exposed to disturbance, but the lack of intensive human activities and the height of tree nests (>10 m) suggest that predation risk is minimal. In all areas great cormorants readily took the most common fish species: gibel (*Carassius gibelio* (Bloch, 1782)) and black goby (*Gobius jazo* (L., 1758)) in the Axios Delta (Goutner et al. 1997; Liordos 2004); gibel, bleak (*Alburnus alburnus* (L., 1758)) and roach (*Rutilus rutilus* (L., 1758)) at Lake Kerkini (Kazantzidis and Naziridis 2003; Liordos 2004); and gibel, *Chalcalburnus belvica* (Karaman, 1924) and pumpkinseed (*Lepomis gibbosus* (L., 1758)) at Lake Mikri Prespa (Liordos 2004).

Fieldwork and reproductive parameters

The three colonies were studied during the breeding seasons in 2001 and 2002 (from April to mid-June). The following numbers of tree nests were studied: 50 and 55 in the Axios Delta, 60 and 55 at Lake Kerkini, 39 and 48 at Lake Mikri Prespa in 2001 and 2002, respectively.

Each nest was visited prior to egg-laying and individually marked. Multiple colony visits were made at regular time intervals (5–7 days) from egg-laying to fledging. Newly found nestlings were recorded as “one-week-old”. They were considered fledged at the age of 7–8 weeks, as fledging in the great cormorant occurs at about 56 days (Cramp and Simmons 1977). Visits were made early in the morning (7:00–9:00 am), before feeding, to reduce the possibility of food loss from nestlings by regurgitation (Hughes et al. 1998). Areas within a colony may differ in quality (Van Eerden et al. 1991; Bregnballe and Gregersen 2003; Krag 2003) and nests studied were chosen therefore from several subsections of each colony. Visits inside

the colony were as brief as possible and each nest was visited for less than 30 minutes, to reduce the probability of nest predation and mortality due to heat or cold. At the egg-laying, incubation, and early-nestling stages, nests were either approached with the aid of a 4-m long aluminum ladder or inspected from the ground using a mirror adjusted at the top of a pole. When nestlings are four weeks or older, disturbance could potentially force premature fledging. Observations were made therefore from a distance using a telescope, unless poor nest visibility rendered entrance to the colony necessary. Nests were situated on the upper branches of the trees and although some breeders were flushed from their nests when approaching and moving through a colony, they soon returned. Corvids and gulls were seen flying over the colonies and a few predated eggs and nestlings were found, but it is suggested that researcher-induced predation was minimal because visits were kept short and in most instances nests were not approached physically.

Clutch size was determined as the number of eggs present in a nest just before hatching. The maximum length and width of the eggs of 20 complete clutches from each colony in 2002 were measured to the nearest 0.01 mm, using digital callipers. Indices of breeding performance include: (1) nest success, the proportion of nests that hatched at least one egg; (2) hatching success, the proportion of laid eggs that hatched; (3) fledging success, the proportion of hatched eggs that led to fledged nestlings; (4) breeding success, the proportion of initiated clutches from which at least one chick fledged; (5) brood size at fledging, the number of nestlings fledged per nest from which at least one chick fledged; and (6) fledgling production, the number of young fledged per initiated clutch.

Statistical analysis

Egg volume was estimated using the equation of Hoyt (1979): $Volume = 0.51 \times (length) \times (width)^2$. All egg dimensions met the requirements of normality and homoscedasticity and were compared using one-way analysis of variance (ANOVA). When differences were statistically significant multiple pairwise comparisons were made with Tukey HSD tests.

Frequency distribution of clutch size, nest and breeding success are categorical variables and were tested by chi-square (χ^2) analysis of contingency tables. Yates correction for continuity was used in all 2×2 contingency tables for the calculation of χ^2 . All other variables deviated significantly from normality and were compared with Mann–Whitney U tests and Kruskal–Wallis (K-W) ANOVA.

The statistical methods proposed by Underwood (1997) and Zar (1999) were followed. All statistical analyses were performed using Statistica 6.0 software (StatSoft, Inc. 2001).

Results

Clutch size

Clutch size ranged from three to five eggs in all areas, except in the Axios Delta, where two two-egg clutches were found in 2002 (Figure 2). Most clutches contained four eggs (38.18–53.84%) followed by those with three eggs (27.08–41.82%). There were no significant differences in the frequency distribution of clutch sizes between years within colonies ($\chi^2_1 < 6.669$, $P > 0.310$) nor between colonies within years

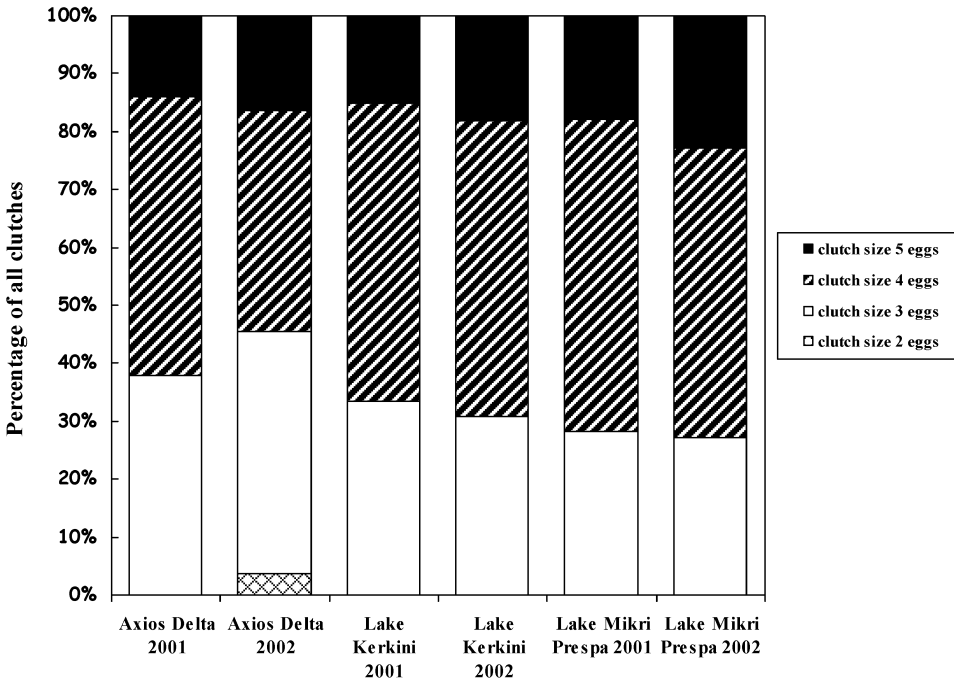


Figure 2. Clutch size distribution of the great cormorant in three Greek colonies in 2001 and 2002. See Table 1 for sample sizes.

($\chi^2_2 < 5.583$, $P > 0.061$). Mean clutch sizes were similar in all areas, though slightly larger at Lake Mikri Prespa than in the other two areas in both years (Table 1).

Egg dimensions

Egg dimensions were generally larger at Lake Kerkini than in the other colonies (Table 2). Mean egg length, width, and volume differed significantly between

Table 1. Differences in clutch size (mean \pm SE, n =number of nests examined) of the great cormorant between three Greek colonies, assessed by Kruskal–Wallis ANOVA ($k > 2$) and Mann–Whitney U test ($k = 2$).

Year	2001	2002	Year \times colony	
Colony				
Axios Delta	3.76 \pm 0.10 ($n=50$)	3.67 \pm 0.11 ($n=55$)	$U_1=1288.0$, $P=0.546$	
Lake Kerkini	3.82 \pm 0.09 ($n=60$)	3.87 \pm 0.09 ($n=55$)	$U_1=1581.0$, $P=0.671$	$H_5=5.062$, $P=0.408$
Lake Mikri Prespa	3.90 \pm 0.11 ($n=39$)	3.96 \pm 0.10 ($n=48$)	$U_1=894.0$, $P=0.694$	
	$H_2=0.941$, $P=0.625$	$H_2=3.903$, $P=0.142$		

Note: Year \times colony: the interaction between year and colony.

Table 2. Differences in egg length, width, volume and clutch volume (mean \pm SE, range in parentheses) of the great cormorant between three Greek colonies in 2002, assessed by one-way ANOVA.

Colony	Egg length (cm)	Egg width (cm)	Egg volume (cm ³)	Clutch volume (cm ³)
Axios Delta	6.17 \pm 0.04 (5.34–7.23)	3.88 \pm 0.03 (3.44–5.13)	47.48 \pm 8.97 (36.43–95.53)	170.92 \pm 1.06 (97.09–240.32)
Lake Kerkini	6.31 \pm 0.03 (5.70–6.95)	3.96 \pm 0.02 (3.55–4.28)	50.33 \pm 5.69 (36.36–61.76)	198.79 \pm 0.64 (143.35–279.49)
Lake Mikri Prespa	6.11 \pm 0.03 (5.42–6.76)	3.93 \pm 0.01 (3.75–4.12)	47.99 \pm 4.00 (36.01–56.18)	184.74 \pm 0.45 (129.89–244.91)
	$F_{2,225}=8.390$, $P=0.0003$	$F_{2,225}=3.900$, $P=0.022$	$F_{2,225}=4.220$, $P=0.016$	$F_{2,57}=2.728$, $P=0.074$

Note: Measurements of 20 full clutches from each colony and 72, 79, and 77 eggs from Axios Delta, Lake Kerkini and Lake Mikri Prespa respectively were taken. Bold type indicates results that were significant at the 0.05 level.

colonies in 2002. Post hoc comparisons showed that eggs were on average significantly longer at Lake Kerkini than in the Axios Delta (Tukey $P=0.017$) and at Lake Mikri Prespa (Tukey $P=0.0002$). They were also wider at Lake Kerkini than in the Axios Delta (Tukey $P=0.019$). Mean egg volume was larger at Lake Kerkini than in the Axios Delta (Tukey $P=0.023$). Mean clutch volume was also larger at Lake Kerkini, but the differences were not significant.

Breeding performance

Nest success ranged from 79.2% (Lake Mikri Prespa, 2002) to 89.1% (Lake Kerkini, 2002; Table 3). The chi-square tests did not reveal any significant differences between years nor between colonies.

Hatching success was higher at Lake Kerkini than in the other colonies in both years (Table 3). Spatio-temporal comparisons did not reveal any significant differences (with K-W ANOVA and Mann–Whitney U).

Fledging success was highest at Lake Kerkini in 2001 (91.0 \pm 2.1% SE) and lowest at Lake Mikri Prespa in 2002 (73.0 \pm 4.1%). There were no significant differences in fledging success between colonies within years (Table 3). But fledging success was significantly higher in 2001 than 2002 at both Lake Kerkini and Lake Mikri Prespa. The interaction between year and colony was also significant. In particular, pairwise Mann–Whitney U tests revealed that fledging success was higher at Lake Kerkini and in the Axios Delta in both years than at Lake Mikri Prespa in 2002 ($U_1 < 698.0$, $P < 0.047$).

The highest and lowest values for breeding success were found at Lake Mikri Prespa; 87.2% in 2001 and 70.8% in 2002. However, differences were not significant (chi-square tests, Table 3).

Mean brood sizes at fledging were largest at Lake Kerkini (mean 3.38 \pm 0.11 nestlings in 2001) and lowest in the Axios Delta in 2002 (mean 2.91 \pm 0.14 nestlings). The differences in mean brood size at fledging among colonies were significant in

Table 3. Differences in nest, hatching, fledging, and breeding success (mean \pm SE, n =number of nests examined) of the great cormorant between three Greek colonies, assessed by chi-square test using the Yates correction for continuity in 2×2 contingency tables and Kruskal–Wallis ANOVA ($k > 2$) and Mann–Whitney U test ($k = 2$).

Year	2001	2002	Year \times colony	
1. Nest success				
Axios Delta	0.840 ($n=50$)	0.818 ($n=55$)	$\chi^2_1=0.001$, $P=0.767$	$\chi^2_5=2.407$, $P=0.790$
Lake Kerkini	0.833 ($n=60$)	0.891 ($n=55$)	$\chi^2_1=0.386$, $P=0.373$	
Lake Mikri Prespa	0.872 ($n=39$)	0.792 ($n=48$)	$\chi^2_1=0.488$, $P=0.325$	
	$\chi^2_2=0.286$, $P=0.867$	$\chi^2_2=2.019$, $P=0.364$		
2. Hatching success				
Axios Delta	0.761 \pm 0.051 ($n=50$)	0.767 \pm 0.052 ($n=55$)	$U_1=1276.0$, $P=0.474$	$H_5=4.799$, $P=0.441$
Lake Kerkini	0.777 \pm 0.048 ($n=60$)	0.850 \pm 0.043 ($n=55$)	$U_1=1489.0$, $P=0.276$	
Lake Mikri Prespa	0.770 \pm 0.056 ($n=39$)	0.742 \pm 0.057 ($n=48$)	$U_1=933.0$, $P=0.977$	
	$H_2=0.939$, $P=0.625$	$H_2=2.785$, $P=0.248$		
3. Fledging success				
Axios Delta	0.867 \pm 0.025 ($n=42$)	0.845 \pm 0.027 ($n=45$)	$U_1=917.5$, $P=0.796$	$H_5=17.750$, $P=0.003$
Lake Kerkini	0.910 \pm 0.021 ($n=48$)	0.834 \pm 0.032 ($n=48$)	$U_1=913.0$, $P=0.037$	
Lake Mikri Prespa	0.880 \pm 0.030 ($n=34$)	0.730 \pm 0.041 ($n=38$)	$U_1=425.0$, $P=0.007$	
	$H_2=4.102$, $P=0.129$	$H_2=5.788$, $P=0.056$		
4. Breeding success				
Axios Delta	0.840 ($n=50$)	0.818 ($n=55$)	$\chi^2_1=0.001$, $P=0.767$	$\chi^2_5=5.312$, $P=0.379$
Lake Kerkini	0.800 ($n=60$)	0.855 ($n=55$)	$\chi^2_1=0.275$, $P=0.441$	
Lake Mikri Prespa	0.872 ($n=39$)	0.708 ($n=48$)	$\chi^2_1=2.478$, $P=0.066$	
	$\chi^2_2=0.905$, $P=0.636$	$\chi^2_2=3.616$, $P=0.164$		

Note: Year \times colony: the interaction between year and colony. Bold type indicates results that were significant at the 0.05 level.

2001 (Table 4). In particular, significantly more nestlings fledged at Lake Kerkini than in the Axios Delta ($U_1=705.0$, $P=0.014$).

Mean fledgling production was largest at Lake Kerkini (mean 2.75 ± 0.20 nestlings in 2002, 2.70 ± 0.20 in 2001) and lowest at Lake Mikri Prespa in 2002 (mean 2.15 ± 0.22 nestlings). The differences in mean fledgling production among colonies were significant in 2002 (Table 4). In particular, significantly more nestlings per initiated clutch fledged at Lake Kerkini than Lake Mikri Prespa ($U_1=1012.5$, $P=0.038$).

Discussion

This is the first detailed study of the breeding biology of the great cormorant in Greece. The other known study (Liordos and Goutner 2003) reported only clutch and egg size. Multiple colony visits, as in this study, allow for the identification of nest failures, and consequently, for the production of good estimates of reproductive output per nest that are suitable for population modelling, and for between years and between colonies comparisons (Newson and Bregnballe 2003).

The mode of clutch size was four (mostly) and three eggs. Clutch sizes recorded in the three studied colonies were within the range of three–four (a maximum of six) eggs given by Cramp and Simmons (1977). Mean clutch size did not vary significantly between the studied colonies and was also similar with that recorded in 1999 in the same areas (3.8 eggs at Lake Kerkini and in the Axios Delta, 3.95 eggs at Lake Mikri Prespa; Liordos and Goutner 2003). Mean clutch sizes recorded in other European colonies range from 2.6 to 4.1 eggs (Røv 1984; Debout 1988; Volponi and Emiliani 1997; Kopciewicz et al. 2003). The similarities found in mean clutch sizes between the studied colonies suggest that the differences in overall productivity are the result of differential loss of eggs and nestlings. Between 15.0% and 25.8% of the eggs produced were lost at the incubation stage at the three colonies. In contrast, 9.0–16.6% of the nestlings produced were lost before fledging, with the exception of Lake Mikri Prespa in 2002 (loss of 27.0% of the nestlings). The same trend was observed by Volponi (1999) and Newson et al. (2005) and may suggest greater vulnerability of nests at the incubation stage.

Mean egg volume was estimated as $47\text{--}50\text{ cm}^3$, similar to but somewhat larger than that reported by Boudewijn and Dirksen (1995) for several Dutch colonies ($44\text{--}49\text{ cm}^3$). Older and larger birds lay larger eggs (Coulson et al. 1969; Sæther 1987), which may produce offspring with higher probability of survival (Nisbet 1978; Galbraith 1988; Grant 1991). Eggs were significantly larger at Lake Kerkini than in the other colonies. The same trend was observed in 1999 by Liordos and Goutner (2003). Our results suggest that the Lake Kerkini population consists of older birds than the other two Greek populations. Bregnballe (2006) found that age is positively correlated with reproductive performance in the great cormorant. However, as other factors may have also been responsible for egg size variation, detailed studies on age of adults are needed. Difference in the mean clutch volume was not detected although mean egg volume was significantly larger at Lake Kerkini than the Axios Delta because clutch volume also depends on clutch size and within-clutch egg size variation (Welty 1975).

Mean fledgling production has been found to vary greatly between and within colonies in other European countries. It has been estimated at between 0.25 and 3.2

Table 4. Differences in brood size at fledging and fledgling production (mean \pm SE, n=number of nests examined) of the great cormorant between three Greek colonies, assessed by Kruskal–Wallis ANOVA ($k>2$) and Mann–Whitney U test ($k=2$).

Year	2001	2002	Year \times colony	
1. Brood size at fledging				
Axios Delta	2.95 \pm 0.13 ($n=42$)	2.91 \pm 0.14 ($n=45$)	$U_1=917.0$, $P=0.812$	$H_5=9.099$, $P=0.105$
Lake Kerkini	3.38 \pm 0.11 ($n=48$)	3.21 \pm 0.15 ($n=47$)	$U_1=1021.0$, $P=0.426$	
Lake Mikri Prespa	3.03 \pm 0.18 ($n=34$)	3.03 \pm 0.16 ($n=34$)	$U_1=572.5.0$, $P=0.946$	
	$H_2=6.557$, $P=0.038$	$H_2=2.108$, $P=0.349$		
2. Fledgling production				
Axios Delta	2.48 \pm 0.19 ($n=50$)	2.38 \pm 0.19 ($n=55$)	$U_1=1309.0$, $P=0.660$	$H_5=7.503$, $P=0.186$
Lake Kerkini	2.70 \pm 0.20 ($n=60$)	2.75 \pm 0.20 ($n=55$)	$U_1=1634.5$, $P=0.928$	
Lake Mikri Prespa	2.64 \pm 0.23 ($n=39$)	2.15 \pm 0.22 ($n=48$)	$U_1=762.5$, $P=0.129$	
	$H_2=2.001$, $P=0.368$	$H_2=6.152$, $P=0.046$		

Note: Year \times colony: the interaction between year and colony. Bold type indicates results that were significant at the 0.05 level.

nestlings (Van Eerden et al. 1991; Swann 1992; Lindell et al. 1995; Grieco et al. 1997; Veldkamp 1997; Volponi and Emiliani 1997; Kopciwicz et al. 2003; Krag 2003; Van Eerden and Van Rijn 2003; Newson et al. 2005). Variation in food availability has been identified as the main cause of variation in productivity (Van Eerden and Voslamber 1995; Newson et al. 2005). Mean fledgling production estimated in this study fell within the range reported by other researchers in Europe but, in contrast, present results showed little variation between colonies and years in the reproductive parameters measured. Between 2.15 and 2.75 fledglings per initiated clutch were produced on average, with differences being significant only between Lake Kerkini and Lake Mikri Prespa in 2002.

Breeding success was not limited by availability and abundance of prey in the present study, as evidenced by high fledgling production. Great cormorants forage in saline, brackish and freshwater habitats, taking advantage of the high diversity of the Axios Delta (Zalidis and Mantzavelas 1994; our observations). Despite great cormorant depredation, the fish biomass was found to be stable at Lake Kerkini (Kazantzidis and Naziridis 2003) and increased slightly at Lake Mikri Prespa (Crivelli et al. 1997) during the 1990s, due mainly to increased eutrophication of the lakes and the introduction of exotic species such as the highly adaptable pumpkinseed (Crivelli et al. 1997; Kazantzidis and Naziridis 2003). As far as predation is concerned, from observations during and after the visits within the colonies, it was judged that researcher-induced and overall predation rate was low and did not affect greatly the reproductive performance of the great cormorant.

The Lake Kerkini colony provides numerous densely arranged trees suitable for nesting that have not yet been affected by bird faeces. In contrast, the Lake Mikri Prespa and Axios Delta colonies have become more open because the nesting trees have deteriorated severely due to the birds' faeces, that kills tree foliage and branches, and ultimately the whole tree (Ishida 1996), thus exposing eggs and nestlings to bad weather conditions and the risk of predation. All studied colonies are located in northern Greece and climatic conditions do not vary greatly between them. However, extreme local events do occur, as at Lake Mikri Prespa late in the breeding season of 2002, when strong winds and heavy rainfall swept the already degraded and vulnerable colony causing the destruction of several tree nests, including four study nests, and resulting in greater loss at the nestling stage in 2002 than in 2001 (15.0%), and subsequently to lower productivity that year, compared with 2001 and the other colonies. Van Eerden et al. (1991), Kopciwicz et al. (2003), and Krag (2003) also observed that great cormorant colonies with declining nest density suffer lower breeding success.

The measured indices of breeding performance were generally higher at Lake Kerkini than at Lake Mikri Prespa and in the Axios Delta both in 2001 and 2002. Overall, the cormorants at Lake Kerkini had a higher fledgling production per initiated clutch than the cormorants in the other two colonies. Among the factors discussed above, the higher habitat quality of the colony site at Lake Kerkini contributed mostly to the better performance of the breeders at Lake Kerkini.

The Axios Delta breeding population increased by 12.8% per annum from 1990 to 2000. It then decreased by 45.0% in the following year and remained stable thereafter. The Vidronissi colony size increased by 12.6% per annum from 1990 to 2002, subsequently fluctuating but slightly decreasing by 2006. The overall Lake Mikri Prespa breeding population increased by 8.0% per annum from 1990 to 1998,

stabilising thereafter. The Lake Kerkini breeding population showed a seven-fold increase, with a growth rate of 17.6% per annum from 1990 to 2002, further increasing by 2.4% per annum by 2006. The total breeding population in Greece followed a model of increase similar to that of Lake Kerkini, increasing by 19.0% per annum from 1990 to 2002, but tended to stabilise, though slightly increasing, thereafter. Frederiksen et al. (2001) constructed a predictive population model and found that growth rates of 22.0% can be reached with an average fledgling production of 2.3 young per pair and survival probabilities as observed in the Danish colony of Vorskø. The high fledgling production found in our study suggests that similar growth rates could be sustained by Greek populations. However, the substantially lower than predicted rates of increase, followed by decrease and stabilisation, observed in the Axios Delta and at Lake Mikri Prespa colonies are mainly due to the destruction of suitable nesting habitat due to the birds' faeces, a density-dependent regulation of breeding population size. In contrast, the availability of high quality nesting habitat and the high fledgling production allowed for a high rate of population increase at Lake Kerkini. The subsequent lowering of growth rates could have been caused by saturation of high quality nesting habitat and/or reduced food availability due to population increase, both density-dependent regulating mechanisms, that may indicate the ecosystem is approaching carrying capacity. Overall, high food availability due to eutrophication of lakes and low initial population density, combined with high reproductive success, are considered the most probable causes of the high population growth rate sustained by Greek great cormorants in the 1990s. The subsequent small increase is probably due to the reasons discussed above, suggesting that the breeding population of the great cormorant will remain stable and/or decrease in the next years, unless new colonies are established. During population expansion, new colonies are established mainly by the immigration of first-time breeders from old and densely inhabited colonies, which thus act as "mother colonies" (Van Eerden and Gregersen 1995; Hénaux et al. 2007). The colonisation of new empty colonies has several advantages for first-time breeders, such as the easier acquisition of a territory and mating than in denser colonies (Potts et al. 1980), and easier access to partially exploited or unexploited foraging areas (Hénaux et al. 2007). A new colony of *c.* 80 pairs was established at Lake Volvi in 2004 (Kazantzidis S, personal communication), situated *c.* 65 km south of Lake Kerkini and east of the Axios Delta. This is an indication of further expansion of the breeding population and may have resulted from the immigration of breeders from either colony, because of the high nest density at Lake Kerkini and the degradation of nesting habitat in the Axios Delta.

Greek great cormorants breed in favourable environments of high food availability, as evidenced by high fledgling production. This has sustained high population growth rates during the 1990s. Nesting habitat degradation and/or saturation do not seem to greatly affect breeding success, but are thought to act as density-dependent regulating mechanisms responsible for the stabilising trend of the breeding population in the 2000s. However, several other factors concerning individuals, populations, the environment and their interactions may also operate simultaneously and proximate and ultimate causes affecting reproductive performance and population dynamics of the great cormorant in Greece may be difficult to determine.

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