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Authors: Gagliardi, Alessandra, Preatoni, Damiano, Volponi, Stefano, Martinoli, Adriano, and Fasola, Mauro

Source: *Ardea*, 109(3) : 583-591

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/arde.v109i2.a25>

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When gate crashers show up: does expansion of Great Cormorant *Phalacrocorax carbo* in north-western Italy affect breeding site selection in Grey Heron *Ardea cinerea*?

Alessandra Gagliardi^{1,2,*}, Damiano Preatoni¹, Stefano Volponi³,
Adriano Martinoli¹ & Mauro Fasola⁴



Gagliardi A., Preatoni D., Volponi S., Martinoli A. & Fasola M. 2021. When gate crashers show up: does expansion of Great Cormorant *Phalacrocorax carbo* in north-western Italy affect breeding site selection in Grey Heron *Ardea cinerea*? *Ardea* 109: 583–591. doi:10.5253/arde.v109i2.a25

Breeding Great Cormorants *Phalacrocorax carbo* have been rapidly increasing in Italy since the 1990s, and have settled their colonies in sites already used by other colonial waterbirds. We investigated the patterns of interference between Grey Herons *Ardea cinerea* and Great Cormorants, the two species most prone to competition due to their similar preference for nest sites. The analysis of long-term population trends in colonies with both species compared to colonies without Cormorants, showed that the number of Grey Heron nests gradually decreased following the settlement of Great Cormorants. The two species exhibited a gradual spatial segregation in nest location, both horizontally and vertically, within the same colony. In some heronries we found clear examples of interaction, but we also report cases where the interaction was less clear. Thus, although Great Cormorants might be competitively dominant over Grey Herons for nest site occupancy in many of their shared colonies, the spatial competition dynamics might also be influenced by factors affecting population dynamics in the wider environment. We envisage specific observations and focus on areas with an apparent abundance of trees suitable for nesting by both species.

Key words: Great Cormorant, Grey Heron, nesting site, interactions between species, population trend, spatial segregation, north-western Italy.

¹Università degli Studi dell'Insubria, Dipartimento di Scienze Teoriche e Applicate, Unità di Analisi e Gestione delle Risorse Ambientali - Guido Tosi Research Group, via Dunant 3, 21100 Varese;

²Istituto-Oikos, via Crescenzago 1, 20134 Milano;

³Istituto Superiore per la Ricerca e la Protezione Ambientale, via Cà Fornacetta 9, 40064 Ozzano dell'Emilia (Bologna);

⁴Università degli Studi di Pavia, Dipartimento Scienze Terra Ambiente, via Ferrata 1, 27100 Pavia;

*corresponding author (alessandra.gagliardi@uninsubria.it)



The mainland breeding population of Great Cormorants *Phalacrocorax carbo* in Italy has increased rapidly since the early 1990s. In 2012, when the last exhaustive count of breeding pairs at a national level was carried out, the number of occupied nests was estimated at around 4000 in 48 colonies mainly located in the north of the Peninsula and at the two major islands, Sardinia and Sicily (Volponi & CorMoNet.it. 2013). Most colonies are located in the north-western plain, including Lombardy, Piedmont and the western part of Emilia-Romagna, along the Po River and its tributaries

(27 colonies in 2012 with 1561 nests, around 40% of the total for Italy), and in the wetlands along the Adriatic coast, in the eastern part of Emilia-Romagna, in Veneto and Friuli-Venezia Giulia (14 colonies in 2012 with 2147 nests, 55% of the Italian total). Most colonies in north-western Italy (77.5%) are located in protected areas (natural reserves, regional or natural parks, Natura 2000 network sites), free from disturbance, both directly (e.g. colony harassment) and indirectly (e.g. hunting activities, shooting at wintering birds).

Throughout north-western Italy (Lombardy and Piedmont), where counts of breeding pairs are carried out regularly every year, 30 out of 33 Great Cormorant breeding sites in 2015 were located in heronries, of which four were with Grey Herons *Ardea cinerea* only, and 26 with Grey Herons and one up to six other species of herons and egrets (Figure 1). Most of these colony sites had been used for several years or even for many decades by breeding Grey Herons and other colonial herons and egrets, whose populations have been monitored regularly since 1972 (Fasola *et al.* 2010, 2011). Seven species of herons and egrets are abundant in this region, owing to the presence of the largest surfaces of rice cultivation within Europe. Herons and egrets breed syntopically in a variety of sites, including small wetlands with alder *Alnus* spp. woods, bushy willows *Salix* spp. and Reed *Phragmites australis* beds, or dry mature woodlands, Black Locust *Robinia pseudo-acacia* groves, poplar *Populus* spp. plantations and suburban parks, in a landscape strongly urbanised and

exploited for agricultural activities (Fasola *et al.* 2011). Their nests are placed at elevations related to their body size (Fasola & Alieri 1992a) with apparently little or no competition. However, competition for suitable nesting sites within a colony is possible, in particular between Great Cormorants and Grey Herons. In fact, (1) the two species place their nest preferably in the upper part of the canopy, unlike the other waterbirds that prefer lower vegetation, (2) their breeding season peaks concomitantly from February to May, while the other species breed one to two months later, and (3) the availability of optimal sites, i.e. wetlands safe from human disturbance and predators, is limited (Fasola & Alieri 1992b).

We investigated whether the recent establishment of the Great Cormorant in north-western Italy triggered any competitive interference with Grey Herons at their traditional colony sites. In detail, we aimed to (1) check whether the long-term trends in the number of Grey Heron nests differed in the colonies with and



Figure 1. A mixed breeding colony with three Great Cormorant nests on the tree top in the centre of the picture and several nests of Grey Herons and Little Egrets *Egretta garzetta* at lower elevation (photo Alessandra Gagliardi, Brescia colony, 8 April 2013).

without Cormorants, predicting that breeding Cormorants would reduce the number of nesting Grey Herons, (2) measure the spatial overlap in nest distribution among species, predicting that the overlap on the horizontal plane would be smaller in colonies where Cormorants coexist with Herons for a longer period and (3) describe the vertical distribution of the nests of the two species, assessing the possible existence of interference.

METHODS

Trends in number of nests

Data from a long-term monitoring program (from 1972 to 2015) of the breeding colonial Ardeidae throughout north-western Italy (performed by the research group Garzaie Italia; see Fasola *et al.* 2011) and from nest counts of Great Cormorants in Italy (Volponi & CorMoNet.it. 2013) were used for a trend analysis, using the R environment (R Core Team 2015). The analysis was performed on the number of nests in all the heronries within the overlapping Great Cormorant's and Grey Heron's breeding range in north-western Italy (247 heronries with Grey Herons, and 30 colonies where Great Cormorants bred in syntopy with Grey Herons). The number of nests by species, site and year was used to plot the general trend for each species. Then the same dataset was divided into sites with or without breeding Cormorants in order to check whether the presence of Cormorants affected the population of Grey Herons in the communal colonies. Two yearly time series were extracted, one for Grey Herons and one for Great Cormorants, and a simple linear regression model accounting for time and a constant was applied to each one. From each linear model, the residuals were extracted and then used to calculate a pairwise correlation coefficient. This procedure was selected since it is the simplest detrending (i.e. 'pre-whitening') technique that could eliminate spurious correlations (Yule 1926) depending just on the time index in non-stationary time series (Yaffee & McGee 2000, Shumway & Stoffer 2011).

Moving from a distribution range scale (corresponding to the two species overlapping breeding range) to the single colony scale, we analysed a selection of nine heronries with enough repetitive counts, sufficient to analyse the patterns in numbers. Long-term data on the number of nests of Grey Herons and Great Cormorants allowed the analysis of the dynamics of the two species.

Spatial pattern analysis: horizontal overlap

We collected field data to explore the effects of Great Cormorant establishment on the spatial distribution of the Grey Heron nests in ten colonies in north-western Italy, between early April and late July of the 2013 and 2014 breeding seasons (Figure 2). These colonies differed in the year of settlement by Cormorants (Table 1), thus we used them as samples at different stages of a possible dynamic interaction between Great Cormorants and Grey Herons.

At each colony, all trees with nests were located and mapped using a code-only GPS receiver, with WAAS-EGNOS differential correction enabled (Garmin Dakota 20), accounting for an average horizontal dilution of precision (HDOP) of 6–8 m. Every occupied nest on each tree was identified as belonging to Great Cormorant, Grey Heron or another species of Ardeidae, by spotting either nestlings or adults, or when these were not present, by nest shape and size. Great Cormorants build nests with a more globular and compact shape than Grey Herons do. The overlap between Great Cormorants and Grey Herons in each colony was estimated by producing around each occupied tree a 5-m buffer (the mean foliage projection of the trees used by the breeding birds) and by calculating for each site the intersection between the buffers for each species, weighed by the total surface area of the colony (i.e. the sum of the surface area of the buffers for all the trees in the colony). This spatial analysis was carried out using the 'rgeos' R package (Bivand & Rundel 2015).

We investigated whether the overlap between the two species depended on the time of Great Cormorant settlement, the number of Grey Heron nests or the number of Great Cormorant nests in the colony, using a quasi-binomial Generalized Linear Model (GLM) in R (Long 1997, Baum 2008). The proportion of overlap was the dependent variable and years since Cormorant establishment, number of Cormorants and number of Grey Herons were the independent variables.

Spatial pattern analysis: vertical nest distribution

The vertical distribution of the two species' nests was investigated using a random sample of at least 30 trees per colony. Nest and tree height were measured using a hypsometer (Blume Leiss BL 6). We used a GLM with nest height as dependent variable and explored the effects of species, tree height, the species by tree height interaction, year since Cormorant settlement and the total number of nests of either species (colony size).

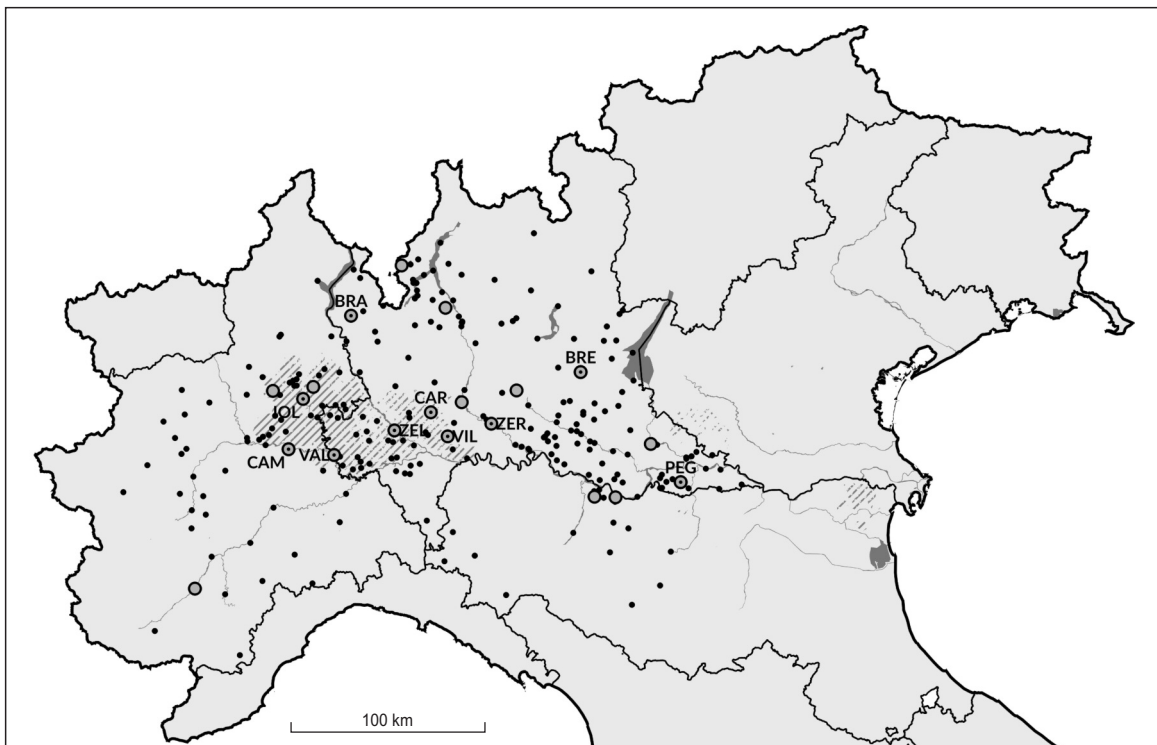


Figure 2. Colonies (black dots) of Grey Herons or of the other six species of Ardeidae in the study area in north-western Italy, Piedmont Lombardy and western Emilia. Larger grey dots indicate the colonies with both Cormorants and Grey Herons. Larger grey dots with a black dot inside indicate the sample of ten colonies studied for horizontal and vertical overlap of nesting sites of both species. BRA: Brabbia, BRE: Brescia, CAM: Camino, CAR: Carpiano, IOL: Oldenico, PEG: Pegognaga, VAL: Valmacca, VIL: Villanterio, ZEL: Zelata, ZER: Zerbaglia. Major waterbodies (lakes and rivers) are indicated in dark grey and rice paddy areas are dashed.

RESULTS

Horizontal overlap in mixed colonies

Spatial overlap between Cormorant and Grey Heron nest sites was high in some colonies of recent Cormorant settlement (e.g. 61% at Brescia where Cormorants first bred in 2011), while lower overlap was recorded for some colonies where Cormorants had been present for a longer time (Table 1). At the Zerbaglia colony, where Cormorants bred since 2005, the overlap was 20%, and at the Brabbia colony there was no overlap between the two species, due to the gradual shift of the Grey Herons since the first settlement of Cormorants in 2004. Excluding the two colonies where Cormorants settled more than 20 years ago (Camino and Oldenico), there was an inverse correlation between time elapsed since Cormorant settlement and spatial overlap between the two species (Figure 3). The two colonies mentioned above were excluded from the analysis, since no data were available for the initial phases of the Cormorant settlement. Furthermore, both colonies are located in

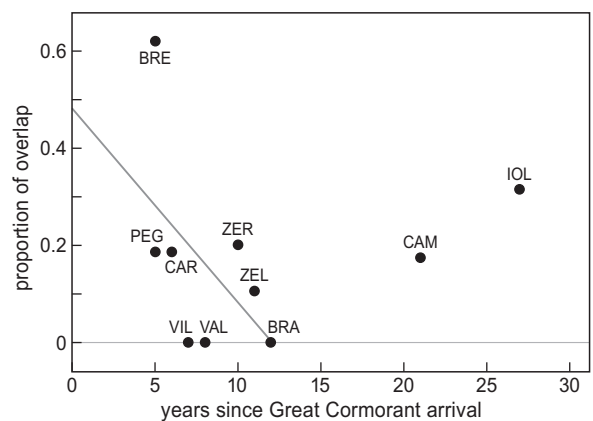


Figure 3. Proportion of overlap between Grey Heron and Great Cormorant nesting areas in colonies with different Great Cormorant arrival times. The grey line indicates the general trend of decreasing overlap through time. See Figure 2 for colony acronyms and location. See text and Table 1 for details. The old colonies IOL and CAM were excluded from analysis (see text).

rather small suitable habitat patches: both the scarce availability of alternative nesting areas and the longer coexistence of both species could have resulted in different overlap and space partitioning dynamics. The proportion of overlap was inversely related to the number of years elapsed since Cormorant appearance ($\beta_{\text{YearSince}} = -0.216 \pm 0.045$, $t = -4.76$, $P = 0.009$) and to the number of Cormorant nests ($\beta_{N_PhaCar} = -0.138 \pm 0.024$, $t = -5.66$, $P = 0.005$). In contrast, the number of Grey Heron nests had a positive effect in slowing down the effect of Cormorant settlement ($\beta_{N_ArdCin} = 0.015 \pm 0.003$, $t = 5.46$, $P = 0.006$). Of the three factors considered, time since Cormorant settlement had the strongest effect.

Vertical nest distribution in mixed colonies

Nest height and tree height were significantly correlated (species pooled, Pearson $r = 0.90$, $df = 969$, $P < 0.0001$). Great Cormorants tended to place their nests at higher elevations than syntopic Grey Herons and on higher trees (average nest height $\pm$ SE for Great Cormorants: 12.75 ± 0.22 m, for Grey Herons: 10.59 ± 0.32 m; Figure 4). Great Cormorant nests were at significantly higher elevations than Heron nests ($\beta = 1.462 \pm 0.421$, $t = 3.477$, $P < 0.0005$). The effect of tree height was significant ($\beta = 0.923 \pm 0.018$, $t = 50.878$, $P < 0.0001$), as well as the negative effect of Great Cormorants on Grey Heron nest height ($\beta = -0.208 \pm 0.0255$, $t = -8.146$, $P < 0.0001$). Significant but less strong relationships were found with time since Cormorant's appearance ($\beta = 0.032 \pm 0.0125$, $t = 2.603$, $P = 0.009$), and with the number of nests per

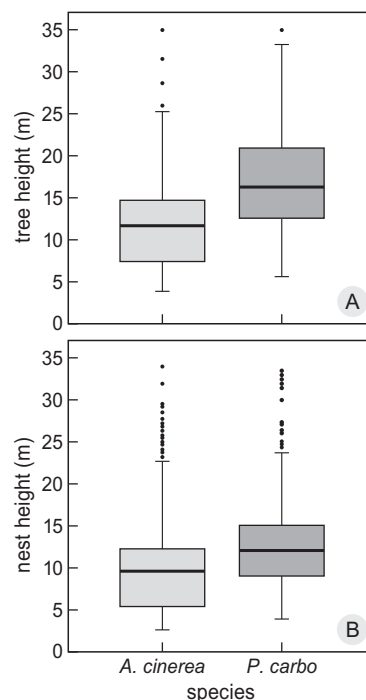


Figure 4. (A) Average tree height and (B) nesting height for Grey Heron and Great Cormorant. The horizontal line inside the 'box' represents (A) the median tree or (B) nest height, the box upper and lower limits indicate the first and third quartiles (i.e. 25th and 75th percentiles) and the vertical 'whiskers' extend up and down no further than 1.5 times the interquartile distance (measured between the first and third quartiles as defined above). Data beyond the end of the whiskers are plotted individually. See McGill et al. (1978) for details on this kind of plot.

Table 1. Colonies where spatial nesting patterns were studied. The number of nests (in brackets) for the Oldenico colony refers to 2014, and for Zerbaglia colony to 2011, as counts did not take place in the appropriate years.

Colony name	Coordinates (degrees WGS84)	Year of settlement by Great Cormorants	Number of Grey Heron nests in the year of settlement by Great Cormorants	Number of Great Cormorant nests in the year of settlement	Number of Grey Heron nests in 2015	Number of Great Cormorant nests in 2015
Oldenico	45°3870'N, 8°3979'E	1989	156	1	92	(93)
Camino	45°1519'N, 8°3044'E	1995	272	2	20	130
Brabbia	45°7762'N, 8°7132'E	2004	81	4	118	232
Zelata	45°2416'N, 9°0026'E	2005	627	60	92	149
Zerbaglia	45°2712'N, 9°6425'E	2006	(165)	(57)	183	275
Valmacca	45°1263'N, 8°6047'E	2008	104	31	31	39
Villanterio	45°2134'N, 9°3537'E	2009	19	10	48	15
Carpiano	45°3259'N, 9°2433'E	2010	44	2	38	42
Brescia	45°5070'N, 10°2377'E	2011	192	1	277	62
Pegognaga	44°9850'N, 10°8840'E	2011	36	2	42	45

colony, calculated as sum of Grey Heron and Great Cormorant nests in 2015 ($\beta = -0.005 \pm 0.0007$, $t = -6.953$, $P < 0.0001$).

Is it possible to scale up the findings of the mixed colonies to the population trends?

The trend analysis (Figure 5) revealed a constant increase in the total number of Great Cormorant nests since 1990, and a particularly marked increase after 2005. Grey Herons also showed a considerable increase within this same region and throughout the whole of north-western Italy, especially from 1985 to 1995. This increase was stimulated by diminishing human-induced mortality and by climatic factors (Fasola *et al.* 2010). Recently, the Grey Heron population levelled off and then started to decrease slightly, probably due to diminished suitability of the rice paddies, which have gradually lost their importance as foraging habitat because they are increasingly cultivated without permanent irrigation (Ranghetti *et al.* 2018, unpubl. results of the Garzaie-Italia research group). A detailed breakdown of the Grey Heron/Great Cormorant dynamics for nine of the ten studied heronries is shown in Figure 6. The trend of the Grey Herons in the colonies without Cormorants diverged from that in the colonies with Cormorants since 1995, i.e. five years after Cormorant settlement. Grey Herons in colonies with Great Cormorants decreased particularly after 2004, when Cormorants started to increase markedly (Figure 5). The concomitant shift in the Grey Heron trend with the increase in the number of Great Cormorants is confirmed by the detrended cross-correlation analysis of time series data, which indicates a significant, inverse proportionality between the residuals of the two time series ($r = -0.59$, $df = 25$, $P = 0.001$). Overall, our results indicate that a single Great Cormorant breeding pair causes a decrease in the Grey Heron population of 1.1 ± 0.3 breeding pairs per year of Great Cormorant presence.

Patterns and trends in single colonies

Detailed trends in the nine colonies of Figure 6 show a high variability among colonies for both species. At two colonies, Camino (CAM) and Zelata (ZEL), the number of Grey Heron nests markedly declined in parallel with the Great Cormorant increase, confirming the observed overall inverse numerical trend between the two species. However, in the Zelata colony, Grey Herons apparently crashed strongly after 2000, just before Cormorant settlement. In Palude Brabbia (BRA) the increase in both species after the crash of Grey Herons in mid-2000s appears to contradict the interference

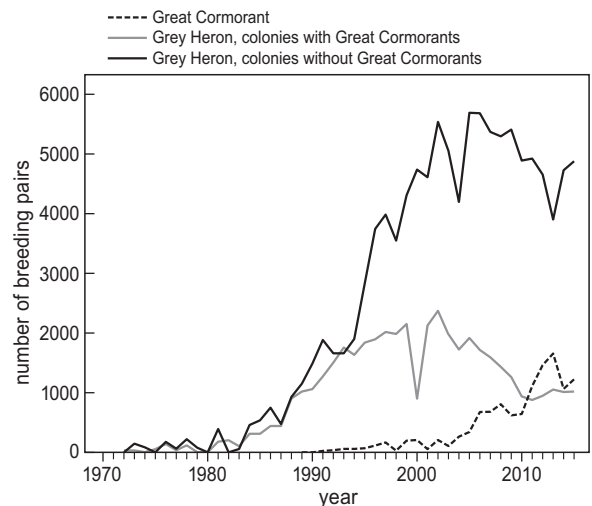


Figure 5. Number of nests of Grey Herons and of Great Cormorants from 1972 to 2015 in their overlapping breeding range. In the colonies where the Great Cormorant appeared, Grey Herons showed a decreasing trend, concomitant with the increase of the Cormorants, while Grey Herons fluctuated but did not decrease in the colonies where the Great Cormorant never settled.

hypothesis. However, the simultaneous increase was also paralleled by the gradual shift of the heronry (about 1 km) outside the traditionally occupied area after the settlement of Cormorants. Conversely, the number of Grey Heron nests in Valmacca (VAL) declined gradually since 1995, while Great Cormorants arrived only later, in 2008. At the Oldenico colony (IOL), Grey Herons numbers sharply declined from 2008 onwards, after Great Cormorants had been breeding there for more than 15 years. However, Cormorants were not accurately censused in the years when Grey Heron numbers crashed. In three colonies, Carpiano (CAR), Villanterio (VIL) and Pegognaga (PEG), both Grey Herons and Great Cormorants settled recently and in small numbers.

DISCUSSION

The arrival of a larger, dominant species may force inferior competitors to shift their niche so as to relax asymmetrical competition (Morse 1974, Persson 1985). The interactions of the heavier Great Cormorant and the lighter Grey Heron at their communal breeding colonies could be an example of such asymmetrical competition. Our study suggests that the settlement of breeding Great Cormorants could affect the Grey Heron's nest site choice and population trends. In our study colonies, Grey Herons responded to the increasing

settlement of Great Cormorants by progressively placing their nests at apparently sub-optimal elevations thus reducing the vertical overlap with Cormorant's nests, as well as by shifting to trees not used by Cormorants and by moving to marginal areas of the colony thus reducing the horizontal overlap. At the level of the entire breeding range, the increase in the number of breeding Great Cormorants was followed by a gradual decrease in Grey Heron nests.

However, a clear inverse relationship between the trends of the two species was found only for three colonies. That such a relationship was not found in the other six colonies might be due to the difficulty of disentangling the effect of competition for nesting space from all other factors affecting population trends at the level of the colony. At each site, the effect of Cormorant settlement on breeding Grey Herons acts in conjunction with the differing environmental context of the colony, regarding food availability, legal protection,

human pressure, availability of alternative colony sites, etc. In some parts of our study area for instance, large changes in the availability of prey for Grey Herons have occurred since 2000 in relation to new rice cultivation practices (Fasola & Cardarelli 2015), and these changes may have caused different population trends in these areas compared to areas without rice fields. Therefore, the fact that some of our study colonies do not fit within the general pattern of asymmetrical competition between Cormorants and Grey Herons may also be due to other environmental factors, not taken into account here, affecting the trend in numbers rather than conditions of a particular colony and the position of other species competing for nesting space.

We do not have detailed cues about the mechanisms that are involved in the asymmetrical competition between the two breeding species. In general, in our study area and elsewhere, both Grey Herons and Great Cormorants use the colony site as a winter roost

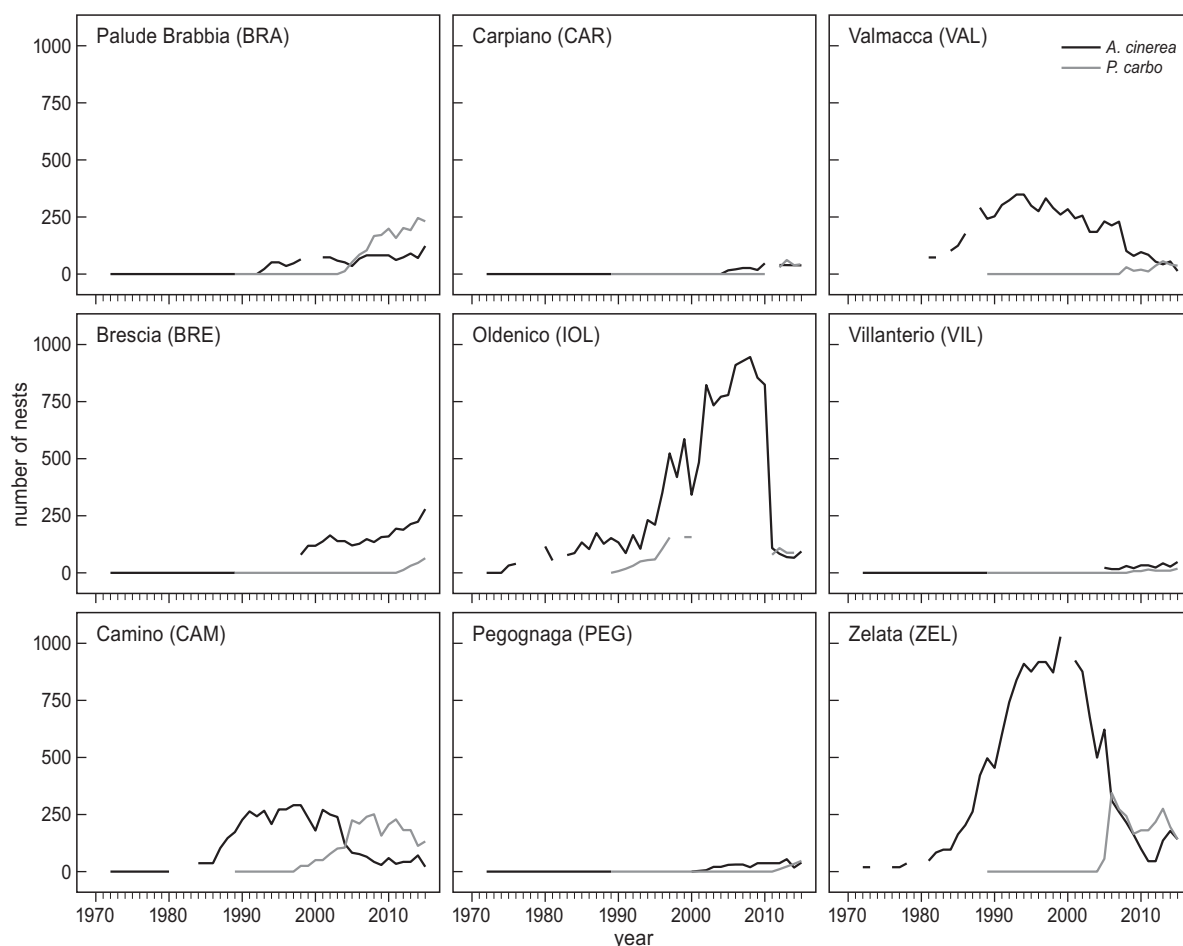


Figure 6. Long-term series of number of nests of Grey Herons (black lines) and of Great Cormorants (grey lines) from 1972 to 2015 in nine selected heronries (see Figure 2 and Table 1) where the Great Cormorant appeared.

and start breeding by mid-January. It is thus possible that competition between the two species for the best nesting places occurs already in winter, well before nest construction. Great Cormorants are more abundant in winter and aggregate in denser groups than Grey Herons. Roosting Great Cormorants tend to occupy the highest position on trees, and the Grey Herons sharing a roost with Cormorants are rarely seen on tree branches densely occupied by Cormorants. These observations support the suggestion that exclusion of co-occurring Grey Herons from the optimal nesting trees starts well before nesting.

Intriguingly, our results suggest that the interference between Cormorants and Herons occurs despite an apparent abundance of suitable trees at several colonies where nests cover only a small fraction of the woodland patch. At two of our study colonies, where Cormorants had settled since more than 20 years before (Camino and Oldenico; Figure 3), we recorded only a partial horizontal segregation between the two species. This might have been due to the limited size of the woodlands hosting these colonies, which might have prevented Grey Herons from completely avoiding the trees used by Cormorants. Instead of giving up the colony the Herons squeezed themselves into the narrow space left by the dominant Cormorants.

The spatial segregation between the two species occurs also in other regions of Italy where they breed together, such as the Po Delta in north-eastern Italy. Great Cormorants and Grey Herons colonised the Delta between the late 1980s and the mid-1990s (Volponi & Emiliani 1991, Volponi 1999, Mezzavilla & Scarton 2002). Their colonies were established in a variety of freshwater and brackish habitats (Fasola *et al.* 2007, Mezzavilla & Scarton 2002, Costa *et al.* 2009). Both species showed high adaptability and they placed their nests on different substrates, reed beds, willow bushes, high trees, and the Great Cormorant even on artificial structures. However, in north-eastern Italy the segregation among colonial waterbirds for nest sites seems to be steered by vegetation structure. Grey Herons and all other six species of colonial Ardeidae traditionally breed in bushes dominated by Common Sallow *Salix cinerea*, European Elder *Sambucus nigra*, Desert False Indigo *Amorpha fruticosa* or in reed beds dominated by *Phragmites australis*, while Great Cormorants breed almost exclusively on trees. Thus, in five out of six sites shared by the two species in north-eastern Italy, competition for nest sites does not occur. In the only site where the two species breed in trees (Valle Dindona, Po Delta), five to 15 nests of Grey Herons were built either on the lowest and external branch of large white poplar

trees or on isolated smaller white *Salix* trees located at the periphery of the colony. There, the rapid increase in Great cormorant numbers, from 10 nests in 2009 to 380 in 2014, led to the split of the Cormorant colony with the occupation of a new site located 7 km away where in 2016 about a hundred Great Cormorants nested on isolated poplar trees and in a row of tamarix *Tamerix* sp. During the same period, Grey Herons moved from the traditional site to a newly established mixed heronry – without Great Cormorants – located just 1.5 km apart. The numbers of Grey Herons rapidly increased in the new location exceeding any previous record (from 6–10 nests in 2016 to 61–65 in 2017). Such observations support the finding that Great Cormorants may influence the presence and the number of Grey Herons where nesting in syntopy.

The Great Cormorants breeding in Italy are still only a small fraction of the European population (less than 2%). The overall Italian population seems to be well under the carrying capacity, and has been rapidly increasing during the last few years (Volponi & CorMoNet.it 2013). In order to understand the complex interactions between Great Cormorants and Grey Herons, further studies will be necessary on their use of nesting space inside the colonies, on their nest success, as well as on their population trends in relation to the environmental changes outside colony sites.

ACKNOWLEDGEMENTS

The authors would like to thank all contributors to the long-term monitoring programs, the Cormorant Colony Count and the Garzaie Italia research groups. This project was supported by the Italian Ministry of Education, University and Research (PRIN 2010–2011, 20108 TZKHC). Counts of the Great Cormorant colonies in Italy were coordinated by ISPRA within the ‘Cormorant counts in the Western Palearctic’ project organised by the IUCN-WI Cormorant Research Group as part of the CORMAN initiative promoted by the EU DG Environment.

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SAMENVATTING

Sinds de jaren negentig is de Aalscholver *Phalacrocorax carbo* in Italië sterk in aantal toegenomen. In dezelfde tijd heeft de soort zich gevestigd in kolonies waar al andere soorten watervogels nestelden. Wij hebben in kolonies waar Aalscholvers samen broeden met Blauwe Reigers *Ardea cinerea* (twee soorten die wat betreft nestplaatskeuze en broedhabitat veel overeenkomst vertonen), de interacties tussen de twee soorten onderzocht. In gemengde kolonies bleken Blauwe Reigers in aantal achteruit te gaan nadat Aalscholvers zich in de kolonie hadden gevestigd. In gemengde kolonies waren de twee soorten wat betreft nestplaatskeuze, zowel horizontaal als verticaal, ruimtelijk gescheiden. De horizontale scheiding nam met de tijd en het aantal Aalscholvers in de kolonie toe. Bij grote aantallen broedende Blauwe Reigers was het effect minder snel te merken. Aalscholvers broedden in hogere bomen en hoger in de boom dan Blauwe Reigers. In sommige kolonies vonden wij duidelijke gevallen van interactie tussen de twee soorten, maar in andere kolonies was dat minder duidelijk. Ofschoon Aalscholvers dus dominant zijn over Blauwe Reigers met betrekking tot nestplaatskeuze, zijn er waarschijnlijk ook andere factoren die op de ruimtelijke scheiding van invloed zijn.