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Factors influencing species composition and nest abundance of heron colonies

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Heron and egret colonies are widely distributed in the Greek wetlands. Among the seven colonially breeding heron species with 6097 nests in 44 colonies in 2009, Grey Heron (*Ardea cinerea*) was the most widespread and Little Egret (*Egretta garzetta*) the most numerous. Twenty-five factors were for the first time co-evaluated in order to detect possible influences on the heron colonies species composition and species nest abundance. We used direct (detrended correspondence analysis), indirect (canonical correspondence analysis) gradient analysis and Kendall's tau correlation. At least, seven significant factors were detected which explained 43.14% of the total variability regarding species composition of heron colonies. Eight more factors influence, positively or negatively, nest abundance of certain heron species. The analysis revealed that a diverse feeding habitat, especially with freshwater marshes, mostly in protected areas could potentially host a mixed colony, including Squacco Heron (*Ardeola ralloides*), Little Egret and non-Ardeidae species. Woods and reed beds within rice fields are potential heron colony sites, especially for Black-crowned Night Heron (*Nycticorax nycticorax*). Trees are the main nesting habitat for Grey Heron while reed beds for Purple Heron (*Ardea purpurea*) and Squacco Heron. The presence of Ardeidae and non-Ardeidae species in a colony influences the nesting of Squacco and the Black-crowned Night Heron. The maintenance of wood patches near wetlands, the creation of freshwater marshes and the protection of these around the existing colonies as well as the establishment of a buffer protection zone around certain colonies, are the proposed conservation actions for the protection of heron colonies.

Key words: Ardeidae, heron colonies, egrets, herons.

INTRODUCTION

Heron and egret colonies are widely distributed in Greece. They can be found in a variety of habitats and landscapes from remote wetlands to wetlands close to cities, towns or villages, in agricultural land and even in villages. In 33 colonies that were recorded in Greece during the first national heron colony survey in 2003, at least 5589 nests of seven heron species were counted. These species were: Little Egret (*Egretta garzetta*), Black-crowned Night Heron (*Nycticorax nycticorax)*, Grey Heron (*Ardea cinerea*), Squacco Heron (*Ardeola ralloides*), Purple Heron (*Ardea purpurea*), Great Egret (*Ardea alba*) and Cattle Egret (*Bubulcus ibis*) (Yfantis & Kazantzidis, 2004).

The establishment either of a colony in an area or of a species into a colony, as well as its nest abundance, depends on a series of factors. Besides vegetation

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structure and the extent and quality of feeding habitats surrounding the colony site, social factors, such as interspecies associations and disturbance, especially from human activity around the colonies, also play an important role (Krebs, 1978; Burger, 1981; Gibbs *et al*., 1987; Fasola & Alieri, 1992a,b; Hafner & Fasola, 1992; Baxter, 1994; Perennou *et al*., 1996; Gibbs & Kinkel, 1997; Kushlan & Hafner, 2000; Kelly *et al*., 2008).

The wetlands in Greece have been exploited by man since ancient times and have been modified according to human needs (crop and animal farming, urban and industrial development, fishing, tourism, etc.). More than two thirds of the wetlands were drained in the 20th century, most of which were converted into agricultural land (Athanassiou, 1990; Handrinos, 1992). Only recently, the attitude towards wetlands has changed, and in certain cases, conservation actions have been implemented (e.g. restoration of former lakes, coastal lagoons etc., see Zalidis *et al*., 2002). However, the deterioration of wetlands is still a serious threat and is reflected by three heron species being included in the threat categories of the Red Data Book for the Threatened Animals of Greece due to their declining breeding population (Legakis & Maragou, 2009). These are the Purple Heron (Endangered), the Squacco Heron (Vulnerable) and the Black-crowned Night Heron (Near threatened). It is worth noting that the threat category of these species has been revised since the previous evaluation was carried out before 20 years (Karandeinos, 1992). Although herons and egrets are among the most studied bird species in Greece, research on the relation of their colonies to the wetlands is limited (Kazantzidis, 2007).

The objectives of the present study were to determine the factors that influence the species composition of heron colonies in Greece and the pattern of species nest abundance within colony sites. Specifically, we, for the first time, jointly examined the potential effects of a series of environmental factors on each species separately and on the species nest abundance within colony sites. The aim of the present research is to generate key information needed in a conservation management plan for heron colonies and wetlands that host heron colonies in Greece.

MATERIALS AND METHODS

Inventory of colonies

The heron colonies in Greece were surveyed in May 2009, during the second national heron colony survey. When a colony was located, the type of vegetation where the nests were situated, the predominant tree or bush species and the number of the nests for each heron species were recorded, as well as any other species nesting in the colony.

Nest count

The nest count involved active nests only. Nest abundance of each species was recorded during the chick rearing period of most of the nesting pairs (late May, Kazantzidis *et al*., 1997). In four colonies, we made a second visit (until mid-June) specifically for counting the nests of Squacco Heron, which starts nesting later in relation to other heron species. In most cases, we counted the nests outside the colony, either from the ground or from boat, using binoculars and/or telescopes. In those cases where the colony was inaccessible (four colonies), we estimated the number of nests by tallying the birds departing for the feeding grounds; starting before dawn, we observed the birds for approximately one hour (Fasola *et al*., 2011). We assumed that two birds correspond to one nest. In four cases of large, mixed colonies, we counted all the nests after entering the colonies in the morning (6-9 am).

Factors affecting species composition and nest abundance of colonies

Twenty-five factors (variables) grouped into five categories were investigated in 43 heron colonies (Tables 1 and 2). We examined each factor within a 5-km radius around each colony site using Google Earth Pro satellite images and/or aerial photographs. In the cases where image resolution was insufficient, we made local visits in order to define the habitat type and/or edge. A 5-km radius was applied, since the vast majority of Little Egrets, Black-crowned Night, Squacco and Purple Herons were recorded foraging within this range in almost all the wetlands, although there were also a few cases involving Grey Heron colonies along rivers where the birds were recorded foraging at further distances (unpublished data).

The category "Feeding habitat" refers to the feeding or foraging habitat types larger than 0.1 km^2 (and irrigation or draining canals that were wider than three meters) that were potentially important for herons. Besides the expanse of sea around the colonies, the factor "Sea" also includes salt marshes which are present in 12 out of 15 cases with the factor "Sea" (Table 1). Salt marshes had a mean extent of approximately 2% of the surface of the factor "Sea" where they co-

TABLE 1. Characteristics of each factor of the categories “Feeding habitat”, “Interspecies association”, “Disturbance” and “Non-feeding habitat” at a 5-km radius around the heron colonies in Greece, in 2009. N: the number of colonies where the relevant characteristic was recorded

Category	Factor	Mean ± SD (min. – max., N)
Feeding habitat	i) Sea (km^2)	9.24 ± 17.78 (2.58 – 67.25, 15)
	ii) Lake (km^2)	8.20 ± 12.66 (1.10 – 43.94, 18)
	iii) Freshwater marsh (km^2)	2.88 ± 4.98 (0.30 – 28.30, 23)
	iv) River bed (km^2)	0.44 ± 0.77 (0.20 – 3.34, 19)
	v) Rice fields (km^2)	3.50 ± 10.24 (1.70 – 52.22, 7)
	vi) Sea coast (km)	5.74 ± 9.56 (3.20 – 30.80, 15)
	vii) Lake shore (km)	7.85 ± 10.38 (2.30 – 32.66, 20)
	viii) River (km)	9.33 ± 8.11 (4.40 – 28.39, 31)
	ix) Canal (km)	5.67 ± 8.01 (0.90 – 27.21, 22)
	x) Distance to nearest potential feeding area (km)	0.54 ± 0.96 (0.00 – 3.62, 43)
	xi) Feeding habitat diversity (number of habitats)	2.42 ± 1.16 (1 – 5, 43)
Interspecies association	i) Distance to nearest colony site (km)	20.88 ± 39.68 (0.75 – 258.18, 43)
	ii) Heron richness (number of heron species nesting in each colony)	2 ± 1.32 (1 – 6, 44)
	iii) Great Cormorant (number of nesting pairs)	918.0 ± 1780.2 (2 – 4490, 6)
	iv) Other species (number of nesting pairs of non-Ardeidae species)	
	Pygmy Cormorant	385.8 ± 624.5 (2 – 1555, 8)
	Spoonbill	37.8 ± 31.9 (6 – 95, 6)
	Glossy Ibis	16.7 ± 16.8 (4 – 43, 7)
Disturbance	i) Distance to nearest village (km)	1.65 ± 1.86 (0.00 – 8.25, 43)
	ii) Distance to nearest paved road (km)	1.04 ± 1.47 (0.1 – 8.00, 43)
Non-Feeding habitat	i) Fields (km^2)	29.92 ± 24.05 (0.30 – 71.17, 40)
	ii) Village (km^2)	4.55 ± 7.35 (0.10 – 34.39, 42)
	iii) Forest-shrubs (km^2)	10.58 ± 16.85 (0.12 – 61.15, 27)
	iv) Other non-feeding habitats (km^2)	9.25 ± 16.70 (0.12 – 63.95, 33)

exist. However, they can only rarely be clearly delineated and measured in order to be presented as a separate feeding habitat. "Sea coast" was considered as the length of the coast line excluding the coast line at salt marshes. We also took into consideration the feeding habitat diversity, as expressed by the number of different feeding habitat types within a 5-km radius around each colony.

In the category "Interspecies association" we considered the number of Ardeidae species nesting in the same colony as the factor "Heron richness". The factor "Great Cormorant" was put in a separate category due to the fact that this species nests at the highest sites of the colony, starts breeding much earlier than any of the other species and is the most abundant of the non-Ardeidae species in almost all cases where they coexist (Table 1).

The category "Nesting habitat" refers to the prevailing vegetation type where the colony was situated (Table 2). "Bush" was considered as the vegetation usually up to three meters height, with no main trunk and dense branches that sprout from the ground level. "Tree" was considered as the vegetation with more than three meters height, with a main trunk and usually with no understorey.

The category "Disturbance" refers to the potential disturbance that may be caused to herons by the nearest paved road, the boundaries of the nearest village, and any other human installment (e.g. factory, industrial zone, airport etc.), to the edge of the colony site (Table 1). Additionally, we considered the protection status of the area where the colony was situated –whether it was a Special Protection Area (SPA) or not– taking into account that in Greece, disturbance for wildlife is relatively higher in the denser paved-road network in non-protected areas along which there is more human activity in contrast to the areas with no roads (Votsi *et al*., 2012). A Special Protection Area (or SPA) is a site designated under the Birds Directive (2009/147/EC). These sites, together with Special Areas of Conservation (or SACs) form the Natura 2000 network which includes internationally important sites for threatened habitats and species. SPAs selection criteria includes the presence of a number of rare, threatened or vulnerable bird species listed in Annex I of the Birds Directive.

The final category "Non-feeding habitat" included the non-foraging areas and habitat types that are not suitable as foraging sites for egrets and herons, as factors (Table 1).

We measured the extent of each habitat, the length of the canals, and the distances to sites using Google Earth Pro polygons and rulers.

Statistical analysis

Two types of ordination were used to analyze heron colonies in relation to environmental gradients. A) Detrended correspondence analysis (DCA) in CANOCO 4.5 (ter Braak & Smilauer, 1998), an indirect ordination was used: a) to examine the relationships between species and environmental factors, and b) to detect the main gradients that arise from the pattern of heron species nest abundance. The detrending by segments option and species data were transformed [$\log_{10}(x + 1)$] and down-weighted for rare species. B) Based on the unimodal distribution (first DCA segment > 4), canonical correspondence analysis (CCA), a direct gradient ordination, was used to estimate important habitat factors that explain the observed variation in the heron species matrix. We used biplot scaling and a focus on inter-species distances. Although rare species would also be examined with gradient analysis, these species tend to obscure species composition because their weak occurrence introduces a large number of absences. These species may have an unduly large influence on the analysis (ter Braak & Smilauer, 1998) by creating an increase in the total inertia of the species data set or a distortion of the ordination. For these reasons, we omitted the Great and Cattle Egret, which were recorded at three and

TABLE 2. The number of nests and the number of colonies (in parenthesis) of each heron species nesting in three vegetation types in 2009, in Greece (GRHE; Grey Heron, LIEG; Little Egret, NIHE; Black-crowned Night Heron, SQHE; Squacco Heron, PUHE; Purple Heron, GREG; Great Egret, CAEG; Cattle Egret)

Category	Factor	Heron species						
		GRHE	LIEG	NIHE	SQHE	PUHE	GREG	CAEG
Nesting	i) Tree	1395 (24)	1149 (12)	641(11)	115 (5)	8 (2)	2 (1)	1 (1)
habitat	ii) Bush	47 (3)	712 (6)	403 (3)	115(2)	1 (1)	39 (1)	10 (1)
(vegetation)	iii) Reed bed	27 (2)	688 (3)	281 (3)	332 (3)	36 (8)	80 (1)	0

two colonies respectively, from the data set for the subsequent analysis. Tests of significance in CCA do not depend on parametric distributional assumptions (Palmer, 1993). Therefore, species data and factors were not transformed.

Separate CCAs were performed for each of the five categories (Feeding habitat, Interspecies association, Nesting habitat, Disturbance and Non-feeding habitat) to determine their level of variance for each heron species independently. In each CCA, the marginal and conditional effects of factors were examined using forward selection by Monte Carlo 1000 permutation tests, to assess the relative contribution of the factors for predicting species composition (ter Braak & Smilauer, 1998). As the main goal for the separate CCAs was to discover the most important factor in each category, partial CCAs using the other datasets as co-variables were not conducted. To maintain the recommended ratio 3:1 sample to variable, as is proposed for multivariate analyses (McGarigal *et al*., 2000), the factors that contributed significantly ($p < 0.05$) at the conditional effect (on the basis of maximum extra fit) to each sub-model were selected. These factors form the final list for the overall model, and using all the subset and intra-set correlations, we evaluated the relative contribution of selected factors in predicting heron colony species composition. We also examined variation inflation factors (VIFs) in the final set of variables (high VIFs > 10 are indicative of multi-collinearity among variables).

Additionally, we used Kendall's tau correlation (r_s) (Sheskin, 2004) to measure the correlation between the environmental factors (Tables 1 and 2) and the nest abundance of each of the five most prevalent species. Furthermore, χ^2 test was used to analyze the differences in the number of heron species in colonies with or without the presence of Squacco and Black-crowned Night Heron. ANOVA was used for testing the null hypothesis of the equality of the respective mean distance to nearest paved road and village in colonies in SPAs and non-SPAs. Data were transformed using $\log_{10}(x + 1)$, $\log_{10}$ or square root algorithms to meet normality distributions, where necessary.

RESULTS

The number of colonies and the nest abundance of the heron species

We recorded information for 49 heron colonies. For five of these, only the location coordinates were available. Based on our inventory of active nest sites, we recorded 6097 nests of six heron species in 44 colonies (Table 3).

Grey Heron was the most widespread species and Little Egret the most numerous followed by Black-crowned Night and Squacco Heron. Purple Heron formed small colonies with the lowest mean number of pairs. Great and Cattle Egret were the species with the fewer colonies (Table 3).

The vast majority of heron colonies (91.3%) were in the mainland Greece and only four on islands or islets very close to the mainland.

Main gradients of heron species composition patterns

The DCA revealed that the total inertia (variation in heron communities) was 1.4 and the length of the DCA was 7.8, indicating a unimodal response (SD > 4). The full environmental data set explains 71.07% of the observed variation in species matrix, indicating that the important factors associated with heron distribution in colonies have been measured.

Feeding habitat

The first CCA was related to feeding habitat characteristics and accounted for 33.28% of the total variability. Nine foraging habitats were recorded around heron colonies, in a mean potential foraging area of 24.25 ± 21.24 km^2 (N = 43, Table 1). The factors "Freshwater marsh", "Rice fields" and "Feeding habitat diversity" had significant conditional effects on colony species composition (Table 4). Freshwater marshes surrounded 23 colonies and covered 22.2% of the total feeding area within a 5-km radius around colony

TABLE 3. The number of heron colonies and the number of nests of each species with the percentages (%) of the sum of species nest abundance (in parenthesis) recorded in 2009, in Greece

Species	Number of colonies (monospecifics)	Number of active nests (%)
Grey Heron	30 (15)	1484 (24.3)
Little Egret	21 (2)	2549 (41.8)
Black-crowned Night Heron	17	1325 (21.7)
Purple Heron	11 (5)	45 (0.8)
Squacco Heron	10	562 (9.2)
Great Egret	3	121 (2.0)
Cattle Egret	2	11 (0.2)
Total	44 (22)	6097 (100.0)

TABLE 4. Amount of variation explained by each model (Marginal and Conditional Effects; the significant factors to conditional level used for the overall model are denoted in bold)

	Marginal effect			Conditional effect		
	Lamda1[a]	*p*	F	LamdaA[b]	*p*	F
Feeding habitat						
Sea (km^2)	0.05	0.144	1.573	0.02	0.602	0.48
Lake (km^2)	0.01	0.738	0.432	0.01	0.644	0.47
Freshwater marsh (km^2)	0.15	0.002	5.002	0.15	**0.002**	**5.00**
River bed (km^2)	0.02	0.486	0.732	0.02	0.510	0.65
Rice fields (km^2)	0.07	0.092	2.023	0.08	**0.040**	**2.68**
Sea coast (km)	0.06	0.116	1.842	0.03	0.474	0.80
Lake shore (km)	0.02	0.65	0.573	0.04	0.188	1.61
River (km)	0.05	0.196	1.406	0.01	0.578	0.62
Canal (km)	0.10	0.03	3.317	0.01	0.942	0.17
Distance to nearest potential feeding habitat (km)	0.12	0.022	3.776	0.01	0.736	0.45
Feeding habitat diversity	0.08	0.086	2.396	0.09	**0.042**	**3.20**
Interspecies association						
Distance to nearest colony site	0.02	0.526	0.62	0.01	0.766	0.32
Heron richness (number of heron species in each colony)	0.22	0.002	7.52	0.08	**0.018**	**3.03**
Nesting of Great cormorant	0.06	0.146	1.72	0.04	0.202	1.51
Other species (nesting of non-Ardeidae species)	0.28	0.002	10.32	0.28	**0.002**	**10.32**
Nesting habitat (vegetation)						
Tree	0.22	0.002	7.76	0.22	**0.002**	**7.76**
Bush	0.07	0.106	2.013	0.04	0.216	1.45
Reed bed	0.15	0.008	4.801	–	–	–
Disturbance						
Distance to nearest village (km)	0.13	0.02	4.32	0.07	0.100	2.08
Distance to nearest paved road (km)	0.12	0.03	3.89	0.00	0.894	0.23
Protection status	0.14	0.004	4.69	0.14	**0.004**	**4.69**
Non-Feeding habitat						
Fields (km^2)	0.02	0.564	0.666	0.03	0.532	0.76
Village (km^2)	0.01	0.796	0.234	0.01	0.672	0.39
Forest - shrubs (km^2)	0.04	0.27	1.219	0.04	0.270	1.22
Other non feeding habitats (km^2)	0.02	0.592	0.557	0.07	0.092	2.19

[a] Variance explained by this factor if it is used as the only environmental variable
[b] Additional variance explained by this factor at the time it was included

sites. Little Egret and Squacco Heron showed a preference for colonies surrounded by freshwater marshes considering that the total nest abundance for each of these species was 69.75%. On the other hand, rice fields were an important feeding habitat mainly for Black-crowned Night Heron whose biggest colony (36.6% of its total nest abundance) was situated close to the most extensive rice field in the country. The factors "Feeding habitat diversity" and "Sea coast" (Fig. 1a) affected the Little Egret nest abundance positively. The factor "Distance to nearest potential feeding area" positively affected the Grey Heron nest abundance, as it appears that the greater the distance, the bigger the colony (Distance to nearest potential feeding habitat = 0.77 ± 1.1 km, r = –0.457, $p < 0.01$, Table 5). In contrast, Purple Heron nested exclusively in flooded sites (Distance to nearest potential feeding area = 0.0 km, r = –0.546, $p < 0.01$, Table 5).

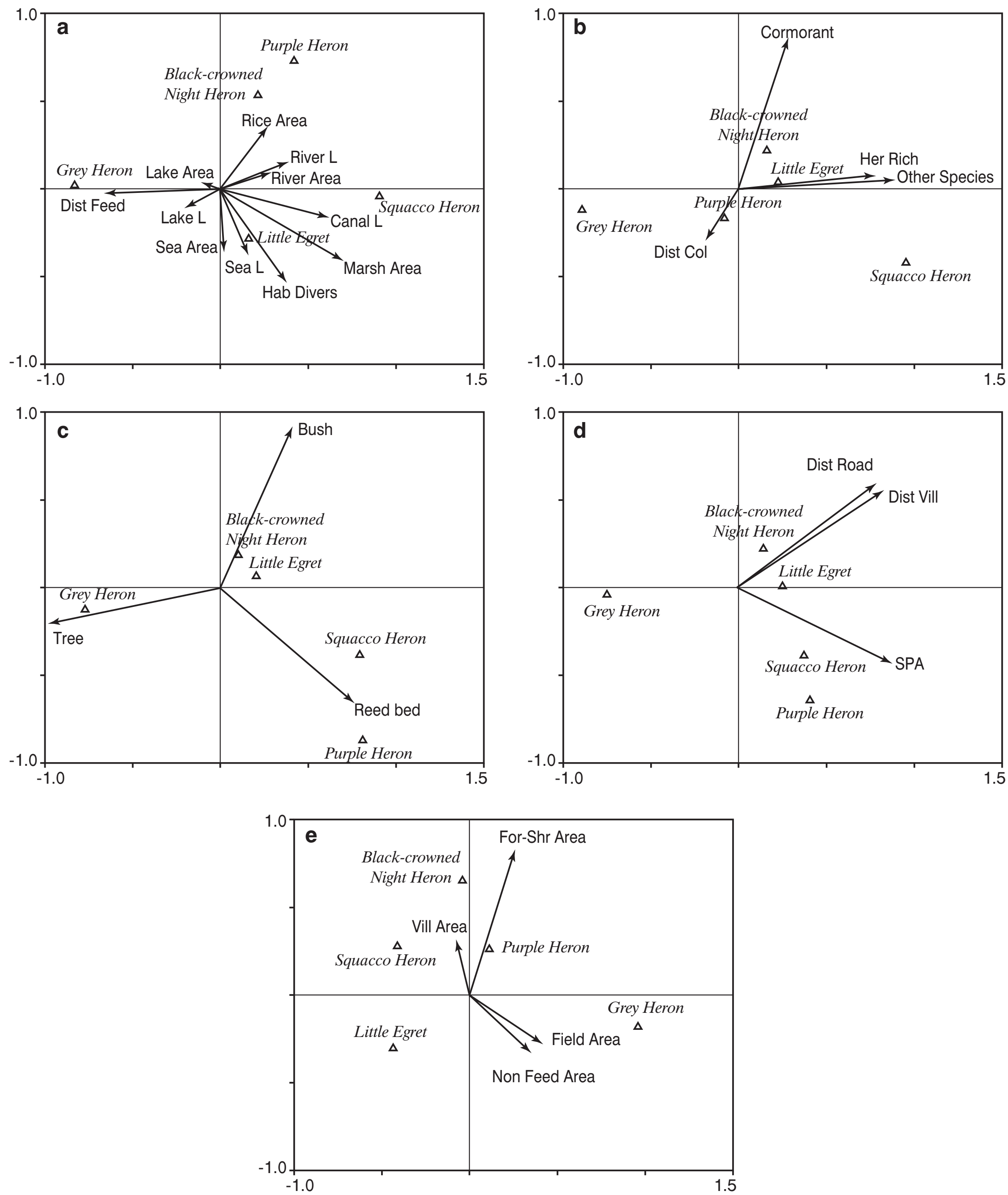

FIG. 1. Ordination diagram of Canonical Correspondence Analysis (CCA) of heron colonies in relation to categories: (a) Feeding habitat, (b) Interspecies association, (c) Nesting vegetation type, (d) Disturbance and (e) Non-Feeding habitat (for more details, see Materials & Methods). The length of arrows indicates the relative importance of the factor, while the proximity to the axes indicates their association to that axis. The projected location of each species point (triangle) along each arrow indicates the environmental preferences of that species (Palmer, 1993). The longer the arrow, the greater the correlation between the factor and the ordination axes and hence, the greater the influence of the factor in explaining the pattern of species variation (ter Braak & Smilauer, 1998). Factor names are abbreviated from their names given in Table 1. The abbreviations "L", "Area" and "Dist" next to the habitat type means "length", "extent" and "distance", respectively.

Interspecies association

The second CCA considers the "Interspecies association" which accounted for 29.07% of the total variability. The factors "Heron richness" and "Other species" (the number of heron and non-heron species in mixed colonies, respectively) were significant for heron colony species composition (Fig. 1b, Table 4). The factor "Other species" was found to be significant for Little Egret, Black-crowned Night and Squacco Heron nest abundance (r = 0.537, $p < 0.01$, r = 0.455, $p < 0.01$, and r = 0.579, $p < 0.01$, respectively, Table 5). Indeed, Squacco Heron was positively affected by the presence of other species, as it was only found nesting in mixed colonies and in most cases (eight out of 10) with other, non-Ardeidae species. The number of heron species in colonies where Squacco and Black-crowned Night Heron nested was higher than the mean (4.3 and 3.4 species per colony, $\chi^2_5 = 36.276$, $p < 0.001$ and $\chi^2_5 = 33.704$, $p < 0.001$, N = 43, for the two species, respectively). Black-crowned Night Heron nested only in mixed colonies, whereas there were only two monospecific Little Egret colonies with small nest abundance (60 pairs each or 4.7% of the total nest abundance). Additionally, the presence of Great Cormorant was also an important factor for Little Egret and Black-crowned Night Heron nest abundance (r = 0.337, $p < 0.05$ and r = 0.302, $p < 0.05$, respectively, Table 5). Similarly, Black-crowned Night Heron nested in five out of six colonies mixed with Great Cormorant (34.0% of the former's total nest abundance). On the other hand, Grey Heron colonies were negatively associated with the above mentioned factors (Fig. 1b). Half of the Grey Heron colonies with 46.6% of the total nest abundance were monospecific and seven (with a nest abundance of 30.9%) were with only one other species (Little Egret in four colonies and Black-crowned Night Heron in three). Only in three cases was the Grey Heron recorded nesting with the Great Cormorant, and this was in low numbers (103 nests or 6.9% of the Grey Heron nest abundance).

Nesting habitat

The category "Nesting habitat" contributed to 18.86% of the total inertia and the factors "Tree" and "Reed bed" had a significant marginal effect. Trees emerged as a strong factor for Grey Heron nesting sites and nest abundance (r = 0.483, $p < 0.05$, Fig. 1c, Table 4). Eighty percent of Grey Heron colonies (24) with 94.0% of the total nest abundance were in trees (mostly poplars – *Populus* spp., plane trees – *Platanus orientalis*, pine trees – *Pinus brutia* and *Pinus halepenrsis*). However, "Trees" were negatively associated with Purple Heron (r = –0.441, $p < 0.01$, Table 5). On the other

TABLE 5. Environmental factors, which positively or negatively influence heron species nest abundance (based on Kendall's tau correlation whose result appears in the text, abbreviations are the same as in Table 2)

Category	Factor	Positive	Negative
Feeding habitat	Distance to nearest potential feeding area	GRHE	PUHE
Interspecies association	Great Cormorant	LIEG NIHE	
	Other species	LIEG SQHE NIHE	
Nesting habitat (vegetation)	Tree	GRHE	PUHE
	Bush		GRHE
	Reed bed	PUHE	GRHE
Disturbance	Distance to nearest village	LIEG PUHE	GRHE
	Distance to nearest paved road	LIEG PUHE	GRHE
	Protection status		GRHE
Non-Feeding habitat	Fields	GRHE	
	Forest-shrubs	PUHE	

hand, reed beds (consisting of Wild reed *Phragmites australis*) were the preferred choice for Purple Heron ($r = 0.736$, $p < 0.01$, Table 5), as 81.8% of its colonies, with a nest abundance of 80.0%, was found in this type of vegetation. Generally, the two heron species avoided mutual nesting sites, although they were recorded nesting together in three cases, albeit in low numbers (10 pairs or 22.2% of the total Purple Heron nest abundance). "Reed bed" was a strong factor for Squacco Heron as well (Fig. 1c). Over half, i.e. 59.1%, of the total nest abundance of this species nested in reed beds (where 30.0% of the colonies were situated). Furthermore, there was a negative association between the factor "Reed bed" and Grey Heron ($r = -0.343$, $p < 0.01$) as well as "Bush" (in most cases consisting of Tamarisks *Tamarix* spp.) and Grey Heron ($r = -0.267$, $p < 0.05$, Table 5). Finally, both Little Egret and Black-crowned Night Heron presented no specific preference as they nested in all the types of vegetation.

Disturbance

The fourth separate CCA examined the effect of the potential disturbance and explained 15.20% of the total variability. Up to 85% of all cases fell within Axis 1, where each of the three factors in this category was found to have significant marginal effects ($p < 0.05$) (i.e., if each corresponding factor is the only one; Fig. 1d). "Protection status" out of these three was the only factor, which had a significant conditional partial effect (i.e., the additional variability explained by a given factor at the time it was included in the model; Table 4).

We recorded 25 colonies with 4216 active nests in SPAs, which accounts for 69.2% of the total heron nest abundance in Greece. The largest colonies were in SPAs and included the majority of nests of all the species, with the exception of the Grey Heron. Furthermore, all colonies established after 2003 (at least six) were in SPAs. The vast majority of Purple and Squacco Herons nested in SPAs (10 out of 11 colonies for the former with a nest abundance of 97.8% and seven out of 10 for the latter with a nest abundance of 97.9%). In non-SPAs, mostly monospecifc colonies were found (in total 13 out of 19). The Grey Heron presented a negative correlation with the "Protection status" factor ($r = -0.332$, $p < 0.05$, Fig. 1d, Table 5) as 16 out of the 30 colonies (64.3% of total nest abundance) were located in non-SPAs.

The factors "Distance to nearest paved road" and "Distance to nearest village" were positively correlated with Purple Heron ($r = 0.257$, $p < 0.05$ and $r = 0.317$, $p < 0.01$, respectively) and Little Egret nest abundance ($r = 0.309$, $p < 0.01$ and $r = 0.267$, $p < 0.05$, respectively, Table 5). In contrast, both these factors were negatively correlated with Grey Heron ($r = -0.273$, $p < 0.05$ and $r = -0.337$, $p < 0.01$, respectively) as Grey Heron colonies were closer to towns or roads than colonies of the other species. Generally, the colonies were established at greater distances from paved roads and villages in SPAs (1.49 ± 1.74 km and 2.29 ± 2.12 km, respectively) than in other areas (0.40 ± 0.58 km and 0.75 ± 0.81 km, respectively; $F_{1,42} = 6.593$, $p = 0.014$ and $F_{1,42} = 8.557$, $p = 0.006$, respectively).

Non-feeding habitat

The CCA related to "Non-feeding habitats" accounted for 10.64% of the total variability but none of the factors measured significantly explained the observed heron colony structure (Table 4). In comparison to all the other heron species, Grey Heron appear to choose a more agricultural landscape (Fig. 1e), being positively associated with the area covered by agricultural fields ($r = 0.272$, $p < 0.05$). Furthermore, Purple Heron was positively associated with the area of forest-shrubs ($r = 0.284$, $p < 0.05$) denoting that the colonies of this species were located in areas far from human activity.

Combined model colony features

Using only the significant factors (e.g. Freshwater marsh, Rice fields, Feeding habitat diversity, Heron richness, Other species, Trees and Protection status) the overall findings explained 43.14% of the total variability and were thus highly significant ($p < 0.001$; Table 6). Axis 1 presents 69.20% of species variance (Fig. 2). No multicollinearity was detected in the seven selected factors and, thus, canonical coefficients and intraset correlations can both be used to assess the relative contribution of factors to the prediction of heron colony species composition (Table 6).

Axis 1 (Fig. 2) correlates positively with those cases (colonies) where the nesting vegetation is "Tree". However, a negative correlation was found in colonies in SPAs, which were associated with a greater number of feeding habitats, more extensive freshwater marshes, and a greater number of nesting species. The Grey Heron chose to nest in trees, away from the other species, such as the Squacco Heron and Little Egret which are more sensitive to human presence.

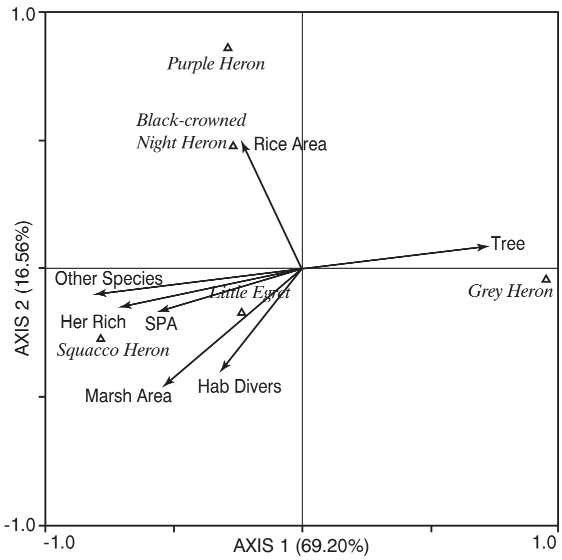

FIG. 2. Canonical correspondence analysis ordination diagram showing axes 1 and 2 of the overall model of heron colonies (for further explanations and abbreviations, see Fig. 1).

Axis 2 (Fig. 2) on the one hand, is positively correlated with the factor "Rice field" and on the other, negatively correlated with the factors "Feeding habitat diversity" and "Freshwater marsh". The factors "Heron richness", "Other species" and "Protection status" have an intermediate canonical coefficient. Therefore, Axis 2 shows a clear separation between the species that are mainly associated with heterogeneous habitats and freshwater marshes, as are the Squacco Heron and the Little Egret, and those found in rice fields, such as the Black-crowned Night Heron. On the other hand, in Axis 2, the Purple Heron appears on its own apart from the other species.

DISCUSSION

A series of distinct factors appear to affect species composition and species nest abundance of heron colonies. These are related to the feeding and nesting habitat structure, human intervention, and the presence of other species in the colonies. Each factor influences each of the heron species differently.

The feeding habitats are among the most important factors, which affect heron colonies. They have been the subject of numerous studies in the Mediterranean and elsewhere, as their characteristics (extent, quality, diversity, etc.) affect not only the diversity of heron species but also the size of the colonies (Fasola & Alieri, 1992b; Hafner & Fasola, 1992; Farinha & Leitão, 1996). According to our results, freshwater marshes are of high importance to heron colonies species composition. Their value to maintain heron species is widely recognized as research carried out in

TABLE 6. Summary of DCA, CCA of the overall model and intraset correlations of the selected factors (in order of their relative contribution in influencing species composition of heron colonies in Greece)

DCA	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.615	0.182	0.040	0.007	1.400
Cumulative percentage of variance of species data	43.9	56.9	59.8	60.3	
CCA overall model					
Eigenvalues	0.418	0.100	0.053	0.033	
Cumulative percentage variance of species data	29.8	37.0	40.8	43.1	
Sum of all canonical eigenvalues (0.604)					
	Intraset correlations				
	Axis 1	Axis 2	Axis 3	Axis 4	
Other species (nesting of non-Ardeidae species)	–0.8146	–0.1016	–0.2445	–0.0910	
Tree	0.7264	0.0852	0.0169	–0.2311	
Heron richness (number of heron species in each colony	–0.7149	–0.1681	–0.0920	–0.1165	
Freshwater marsh (km^2)	–0.5484	–0.4611	–0.2696	0.2161	
Protection status	–0.5761	–0.1595	0.0973	0.2470	
Feeding habitat diversity	–0.3265	–0.4098	0.5479	–0.0050	
Rice fields (km^2)	–0.2431	0.5036	0.4614	–0.3673	

30 colonies around the Mediterranean basin showed that the expanse and quality of the freshwater habitat were the main factors that determine the size and diversity of breeding heron populations (Fasola, 1986; Hafner & Fasola, 1992; Hoffmann *et al*., 1996). Likewise, rice fields are the most significant man-made foraging habitat for nesting ardeids worldwide, especially during the breeding season, due to the variety, density and size of prey organisms, as well as the suitability of water depth and substrate (Fasola *et al*., 1996; Fasola & Ruiz, 1996; Maeda, 2001; Czech & Parsons, 2002; Kazantzidis & Goutner, 2008; Longoni, 2010). Especially in Europe, following the loss of many natural freshwater habitats that have been converted to rice fields, herons are now heavily dependent on the continuation of rice cultivation. According to our study, there is at least one heron colony in the vicinity of each of the six areas where rice is cultivated in Greece. Worth noting are the four heron colonies that are located around the most extensive rice fields at the deltas of the Axios and Aliakmon rivers (central Macedonia), where approximately 70% of the total rice production of Greece takes place (Athanassiou, 1990). Rice fields are especially important for Black-crowned Night Heron, which tend to set up colonies close by, using them extensively as feeding sites. Similarly, in Italy, there was a much higher density of Black-crowned Night Heron than any other heron species in rice fields (Fasola, 1986; Hafner & Fasola, 1992).

The diversity of the feeding habitats around the heron colonies in the Mediterranean is a key factor in heron species diversity (Fasola & Barbieri, 1978; Hafner & Fasola, 1992). The present study indicates that the nesting distribution of Little Egret and Squacco Heron were particularly positively associated with greater feeding habitat diversity around the colonies. These two species were recorded breeding mostly in deltaic ecosystems where the variety of feeding habitats is greater in relation to other wetland types, since they include both freshwater and coastal habitats. Each heron species tends to have specific feeding habitat requirements. However, some, like the Little Egret, are generalist, and when available they exploit all three types of habitat (freshwater marshes, sea coastal habitats and rice fields), showing an apparent preference for the first two (Kazantzidis & Goutner, 1996 and present study). On the other hand, the Squacco Heron is specialist, only making use of freshwater marshes, as also documented in other Mediterranean wetlands (Hafner & Fasola, 1992). Lastly, agricultural land (fields), under certain conditions, serves as a feeding area of Grey Heron and this explains the positive influence of fields in Grey Herons nest abundance. Similar findings were recorded in Spain where the structural homogeneity of agricultural land following the construction of an extensive irrigation plan led to an increase in Grey Heron population (Parejo & Sánchez-Gúzman, 1999).

Squacco Herons and most of Little Egrets and Black-crowned Night Herons in our inventory always nested in colonies with other, ardeid or non-ardeid, species. Probably, the time of nesting plays a crucial role in attracting other pairs (whether conspecific or not) to the colony and early nesting species may attract others to nest in the vicinity. Squacco Heron starts nesting very late in relation to other species (it has been noted to start breeding even as late as May – Papakostas, 2002). On the other hand, Great Cormorants, a species that in our results as a factor appears to be significant for the Little Egret and Black-crowned Night Heron nest abundance, is an early breeder (they start nesting from early March – Liordos, 2004). So, probably, Great Cormorants 'attract' certain species of herons to nest close to them where the vegetation structure is suitable for the nests to be located. The Grey Heron is also an early breeder, but is only rarely found breeding in mixed colonies. Usually, it breeds solitarily in areas surrounded by non-diverse habitats, which are not suitable as foraging habitats for other heron species.

Nesting habitat is a crucial factor for herons to breed in a wetland, however, the lack of available nesting sites as a consequence of land reclamation is a common problem throughout the Mediterranean (Fasola & Alieri, 1992b). The most striking feature in heron colonies in Greece, according to our results, is that they show a clear separation as regards the nesting substrate (expressed by the type of vegetation). Hence, on the one hand, there are colonies in trees (in small forests, wood patches or in single trees) mainly occupied by Grey Herons and on the other, there are colonies in reed beds, mainly occupied by Purple and Squacco Herons. Similar segregations were recorded in Italy (Fasola & Alieri, 1992a), France (Moser, 1984; Barbraud *et al*., 2002), Ukraine (Schogolev, 1996) and Israel (Ashkenazi & Yom-Tov, 1997). As far as Little Egret and Black-crowned Night Heron are concerned, they are able to adapt to a variety of nesting vegetation types that greatly overlap. Elsewhere, both species were also recorded nesting in a variety of vegetation types, such as trees (Fasola &

Alieri, 1992a,b), bushes (Kushlan & Hafner, 2000) and reeds (Ashkenazi & Yom-Tov, 1997). This most likely is on account of their similar body size (Fasola & Alieri, 1992a; Kushlan & Hafner, 2000).

The "Protection status" of a site is an important factor, since most heron colonies in Greece were in SPAs where, among other things (e.g. habitat extent and quality), nesting sites are potentially safer due to less disturbance from human activity. It is estimated that herons were influenced by SPAs status because: a) all recently established colonies were located in SPAs and, b) only eight colonies are known to have been established in areas before their declaration as SPAs (1997) and two of them were chosen as SPAs based on criteria other than the existence of heron colonies (herons were not among the trigger species). The rest eleven colonies are unknown whether they have been established before or after the declaration of the relevant areas as SPAs.

Likewise, disturbance (indicated by the distance of a colony from the nearest road and village) negatively affected the nest abundance of colonies with Little Egrets and Purple Herons. Heron colonies in other countries have also been located largely in undisturbed areas with characteristics such as low road density (Watts & Bradshaw, 1994; Gibbs & Kinkel, 1997). The Grey Heron, which is a species that is much more tolerant to human presence, establishes its colonies mostly in non-SPAs where agriculture predominates. Similar results were recorded in France where the distribution of Grey Heron colonies was related to the hydrographic network (Boisteau & Marion, 2007); while in Poland, human disturbance was of negligible importance to the breeding success of the species (Jakubas, 2005).

The extent of forest-shrub area around Purple Heron colonies indicates the value of this habitat type for the establishment of its colonies for this species. This is also confirmed from the positive association of Purple Heron nest abundance with the factors "Distance to nearest village" and "Distance to nearest paved road'.

Taking into consideration the findings of the present research, we propose that wood patches (especially those with poplars, plane and pine trees) that are within a 5-km radius from a wetland should be maintained, as they are potential nesting sites for herons. Additionally, feeding habitats and particularly freshwater marshes should be maintained within a 5-km radius around the existing colonies with at least one threatened species. The creation of appropriate freshwater foraging habitats in the framework of wetland restoration projects might also play a key role in the establishment of heron colonies in the vicinity. Finally, a buffer zone of at least a 0.5-km radius around colonies (especially with Purple Heron) should be established, where the construction of roads should not be allowed and any human activity should take into consideration the maintenance of the heron colony.

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