

Breeding biology of the Little Egret (*Egretta garzetta*) in southwestern Spain

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The breeding biology of the Little Egret was studied during two seasons in three inland mixed heronries in the south west of Spain in relation to nest height and density. In addition, we compared the reproductive parameters with those found by other authors in the western Palearctic. The reproductive success did not differ between years whereas the median laying date did. Although comparison between our population and others is difficult because of differences in methodology, we observed that the less productive and earlier breeding Little Egrets in the Palearctic were in Extremadura. Neither nest height nor the total number of nests nor the number of Little Egret nests influenced the reproduction, pointing towards the non-existence of density-dependent effects on the reproduction of this species in Extremadura.



1. Introduction

The Little Egret *Egretta garzetta* is a medium-sized heron, widespread across the Palearctic region (Tucker & Heath 1994), with a patchy breeding distribution in the Mediterranean region (Cramp & Simmons 1977, Hafner *et al.* 1987). According to migration movements analysed by Voisin (1985, 1991), Little Egrets from the different breeding areas in southern Europe are part of a metapopulation system (Kazantzidis *et al.* 1996) that has been studied by numerous authors in relation to laying phenology (Hafner 1980, Prósper & Hafner 1996), clutch size (Fasola & Barbieri 1975, Hafner 1980, Voisin 1991, Fasola & Pettiti 1993, Prósper & Hafner 1996), eggs size (Schönwetter 1967), breeding success (Fasola &

Barbieri 1975, Voisin 1976, Hafner 1980, Hafner *et al.* 1986, Fasola & Pettiti 1993, Prósper & Hafner 1996), foraging behavior (Cézilly *et al.* 1990, Kersten *et al.* 1991, Hafner *et al.* 1993) and population dynamics (Hafner *et al.* 1998). However, the factors affecting the breeding success of the species have not been identified (see, however, Kazantzidis *et al.* 1996) despite their importance for conservation. The aim of this study was to analyse the breeding biology of Little Egrets in the south-west of Spain and provide information for the southern location in this metapopulation system. We investigated local and yearly variations in breeding performance and their relations with location of nests (height and density). Finally we compared the breeding biology of this species through its breeding range in the Western Palearctic.

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2. Study area and methods

The study was carried out in three mixed colonies of Extremadura (SW of Spain): Montijo (38°55'N, 6°23'W), Badajoz (38°53'N, 6°58'W) and Morante (39°03'N, 6°41'E). The Montijo colony was established at the end of the 1960s (Fernández-Cruz 1975), the Morante colony in 1984 (Fernández-Cruz unpublished data) and the Badajoz colony in 1994 (Parejo *et al.* 1997). The Badajoz and Montijo colonies were included in a highly transformed habitat (for more details see Parejo & Sánchez 1999), while the Morante colony was in a traditional area with holm-oak dehesas and pasturelands. The two former colonies were separated by 53 km and both were on islands on the Guadiana river covered with *Tamarix* sp., *Phragmites* sp., *Populus* sp. and *Eucalyptus* sp. Both colonies contained Cattle Egrets (*Bubulcus ibis*), Little Egrets and Black-crowned Night-herons (*Nycticorax nycticorax*). The Morante colony was 30.9 km from the Badajoz colony and 15.2 km from Montijo. The trees found in the Morante colony were mainly *Fraxinus* sp. and *Quercus rotundifolia*, and only Cattle and Little Egrets nested there. All the colonies were located in the mesomediterranean climate area (Rivas-Martínez 1987), with a mean annual temperature of 17°C and 600 mm of mean rainfall.

Fieldwork was carried out during the 1996 and 1997 breeding seasons (March–August). Before the birds arrived, we installed in the colonies wooden stakes of known height to use them as references of distance. We made large-scale photographs of the colony sites at the time nests were being constructed, to facilitate individual identification and monitoring (Parejo *et al.* 1999). This method allowed us to determine real distances and so obtain the height of nests by means of their location in photographs. We visited the colonies weekly and observed them from the same place where we had taken the photographs. Nests were controlled an average of 6.76 (± 2.32 SD; $n = 68$) times. We only considered nests with hatchlings from the first time that we observed chicks in them (based on the experience of observers and the descriptions of Cramp and Simmons [1977]). The date of laying for each nest was then estimated by subtracting the mean incubation period of the spe-

cies (Voisin 1991) from the observed hatching dates, taking into account the interval between the laying of two consecutive eggs of the species (2 days, Voisin 1991). We therefore monitored only successful nests, i. e. where at least one chick hatched. We recorded as estimators of the reproductive success: a) the number of hatchlings per successful nest (brood size per successful nest); b) the number of nestlings up to an age between 20 and 25 days per successful nest (at about 30 days chicks are able to fly (Hafner *et al.* 1994) and the whole brood is not necessarily being fed on the same tree (Kazantzidis *et al.* 1996), which makes difficult to locate chicks in colonies); c) the nestling mortality rate up to the age 20–25 days as the percentage of the total number of chicks hatched per successful nest that did not survive up to this age, assuming that a chick died when it was not in the nest the last day that we observed their family group.

We sectioned the large-scale photographs from bottom to top into areas of 2×2 m where. Where Little Egret nests were observed, we counted the total number of nests and the number of Little Egret nests to estimate the total nest density by sample plot and the Little Egret nest density by sample plot. Nest density in each plot was first recorded at the time the first pair in the plot reproduced and was again recorded after a period of 60 days (corresponding to the completion of breeding activities until the young of all species matured, according to Voisin 1991). Thus, we eliminated the possibility of variations in breeding density affecting one pair due to the late arrival of pairs in plots.

The number of birds breeding in each colony was controlled during the two breeding seasons by direct counting of nests.

For statistical methods the significance level was set at $P < 0.05$. The values are expressed as $\bar{x} \pm SD$ and sample sizes are given in parentheses. Two-way ANOVAs were used to compare mean values among localities and seasons (F), but previously we had to transform data because samples did not conform to the approximate normality assumption (Zar 1996). The Spearman correlation coefficient (r_s) was used to analyse the relation between variables. To test the fitting of nest distribution to the availability of vegetation, we used the χ^2 test. Because of the low number of

Little Egret nests in the lowest and highest height classes in some colonies (see below) we had to pool classes to apply this test. We applied the Yates correction when we obtained one degree of freedom.

We used partial correlations on data previously transformed according to Zar (1996) to examine independently the effect of mean laying date, mean nest height and mean density of nests in each sample plot on mean reproductive rates of Little Egrets by plot in all colonies. When dependent variables were the mean number of nestlings up to age 20–25 days per successful nest per plot or the mean nestling mortality rate up to this age per plot, we included the mean brood size per successful nest per plot as an independent variable.

We applied the sequential Bonferroni test to correct for the probability of a type-I error when we used two or more tests (that cannot be pooled) to test a common null hypothesis, and rejection of the null hypothesis was possible when only some of the tests were found to be individually significant (Rice 1989).

3. Results

3.1. Reproduction

In 1996 and 1997 the number of Little Egrets breeding in Badajoz were 60 and 95, respectively, while in Montijo 30 pairs bred in both years and 20 in Morante in the same years (Table 1).

During the two studied years the onset of egg laying ranged from 14 March to 2 May. There were significant differences in median laying dates between seasons ($F_{1,69} = 16.6$, $P < 0.0167$) but not between colonies ($F_{2,69} = 2.7$, $P = 0.08$). The yearly variation in this parameter did not vary in relation to localities ($F_{2,69} = 1.0$, $P = 0.37$). In all colonies, reproduction was earlier in 1997 (Table 1).

Neither the mean brood size per nest, nor the number of nestlings up to age 20–25 days per nest, or the mean nestling mortality rate varied between localities ($F_{2,62} = 0.3$, $P = 0.7$; $F_{2,62} = 1.0$, $P = 0.4$; $F_{2,62} = 0.8$, $P = 0.4$, respectively) or seasons ($F_{1,62} = 0.2$, $P = 0.6$; $F_{1,62} = 0.1$, $P = 0.8$; $F_{1,62} = 0.5$, $P = 0.5$, respectively). Similarly, yearly variation in these parameters was not affected by locality ($F_{2,62} = 0.7$, $P = 0.4$; $F_{2,62} = 0.9$, $P = 0.4$; $F_{2,62} = 0.1$, $P =$

0.9, respectively).

In Badajoz the brood size ranged from one to five chicks, while it ranged from two to four in Montijo and from one to three in Morante. The mean brood size, mean number of nestlings up to the considered age and mean nestling mortality rate for each locality (data for 1996 and 1997 pooled) are shown in Table 1.

3.2. Nest height and density

The mean nest height of Little Egrets varied only in relation to localities ($F_{2,82} = 13.9$, $P < 0.0167$), while it was not affected by years ($F_{1,82} = 0.7$, $P = 0.4$) and the intercolony variation did not vary in relation to years ($F_{2,82} = 0.3$, $P = 0.7$). In all colonies Little Egret nests were located in relation to the available vegetation (Table 2).

There were no significant differences between years ($F_{1,82} = 0.4$, $P = 0.5$) in nest density of Little Egrets by plot, whereas the reverse was true between localities ($F_{2,82} = 6.4$, $P < 0.05$). There was no variation in nest density between years ($F_{2,82} = 0.7$, $P = 0.5$). The mean nest density for all species by sample plot with Little Egret nests did not differ between years ($F_{1,82} = 0.6$, $P = 0.5$), whereas it differed between localities ($F_{2,82} = 8.8$, $P < 0.025$). Again, there was no significant variation in nest density per sample plot in relation to years ($F_{2,82} = 2.5$, $P = 0.1$).

3.3. Factors affecting the breeding performance of Little Egrets

There were no significant relationships between the brood size per nest and laying date, nest height, nest density of Little Egrets/sample plot or total nest density/sample plot with Little Egrets (Table 3). The number of nestlings up to age 20–25 days per nest was not related to laying date, nest height, nest density of Little Egrets/sample plot or total nest density/sample plot with Little Egrets. Brood size per nest was the only predictor that significantly affected the number of nestlings, with an increase in the number of nestlings up to age 20–25 days when brood size was higher (Table 3). The nestling mortality rate was not affected by any of the factors studied (Table 3).

Table 1. Basic breeding data of the Little Egret in the study area. The first day is considered to be the first of January. When a parameter did not differ between seasons we showed the pooled data for each locality.

Variables	Colonies								
	Badajoz			Montijo			Morante		
	1996	1997	Pooled data	1996	1997	Pooled data	1996	1997	Pooled data
Little Egret pairs	60	95		30	30		20	20	
Night Heron pairs	43	62		14	2		0	0	
Cattle Egret pairs	750	1000		750	700		525	550	
Nest height (x ± SD) (n)	3.7 ± 0.9 (17)	3.7 ± 1.4 (29)		2.3 ± 1.3 (12)	1.8 ± 1.0 (15)		3.7 ± 1.4 (8)	3.3 ± 1.4 (7)	
Nest density of Little Egret/ sample plot (x ± SD) (n)	1.8 ± 0.8 (13)	1.6 ± 1.0 (25)		1.3 ± 0.5 (12)	1.3 ± 0.5 (13)		1.0 ± 0.0 (8)	1.3 ± 0.5 (6)	
Total nest density/sample plot with Little Egrets (x ± SD) (n)	10.4 ± 4.7 (13)	9.5 ± 4.8 (25)		6.0 ± 3.4 (12)	5.4 ± 3.1 (13)		5.9 ± 2.0 (8)	9.7 ± 2.3 (6)	
Brood size/nest (x ± SD) (n)	2.6 ± 0.5 (10)	2.5 ± 1.1 (23)	2.5 ± 1.0 (33)	2.2 ± 0.4 (10)	2.7 ± 0.8 (11)	2.5 ± 0.7 (21)	2.4 ± 0.5 (7)	2.3 ± 0.7 (7)	2.4 ± 0.6 (14)
Nestlings up to 20–25 days/ nest (x ± SD) (n)	2.5 ± 0.7 (10)	2.2 ± 1.1 (23)	2.3 ± 1.0 (33)	2.1 ± 0.6 (10)	2.4 ± 0.9 (11)	2.3 ± 0.7 (21)	1.9 ± 0.4 (7)	2.0 ± 0.9 (7)	1.9 ± 0.7 (14)
Nestling mortality rate up to 20–25 days(%) (x ± SD) (n)	5.0 ± 15.8 (10)	13.5 ± 31.6 (23)	10.9 ± 27.8 (33)	5.0 ± 15.8 (10)	11.4 ± 20.5 (11)	8.3 ± 18.3 (21)	19.0 ± 26.2 (7)	19.0 ± 34.9 (7)	19.0 ± 31.2 (14)
Onset of egg-laying	2 May	14 March		26 April	26 March		18 April	27 March	
Laying date (x ± SD) (n)	142.5 ± 13.9 (15)	95.5 ± 36.9 (29)		129.5 ± 27.5 (6)	91.5 ± 11.6 (12)		124.0 ± 8.6 (7)	93.0 ± 19.2 (6)	

4. Discussion

4.1. Reproduction

The onset of egg laying and the median laying dates observed in the present study showed that some of the earliest breeding Little Egrets in the Western Palearctic are in Southwestern Spain (see revision in Prósper & Hafner 1996). Earlier reproduction in southern areas has been shown for other bird species, and has been interpreted as being due to the earlier onset of spring and production of food that occurs in these latitudes, which influences insectivorous (Järvinen 1989) and piscivorous birds (Kazantzidis *et al.* 1996). In the study area the earlier reproduction of Little

Egrets occurred in the year with higher winter temperatures and minor winter rainfall (18.7°C and 1.5 mm in 1997 versus 14.8°C and 2.8 mm in 1996). However, only data for two seasons are available in this study and a long time series would be needed to accurately check this point. The earlier reproduction in 1997 did not bring about an increase in reproductive rates although we could expect it taking into account the longer available period in this year for re-nesting attempts and replacement clutches. However, the study of only successful pairs did not allow us to fully estimate the advantages of breeding earlier.

Although the obtained breeding values overestimate the breeding performance of Little Egrets (we did not go into colonies to mark nests or eggs

Table 2. Values of χ^2 tests for comparison between number of Little Egret nests observed and expected in each height class of each colony. After the application of the sequential Bonferroni test there are no significant results.

Heights	Badajoz				Morante				Montijo			
	1996		1997		1996		1997		1996		1997	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
0–2 m	1	13.4	7	11.3	1	5.33	1	7.3	14	13.9	18	13.8
>2–4 m	25	13.4	19	11.3	8	5.33	11	7.3	13	13.9	11	13.8
>4–6 m	20	13.4	15	11.3	7	5.33	10	7.3	2	1.22	0	1.34
>6–8 m	1	6.85	1	8.2			0	0.18				
Test	$\chi^2 = 0.00$, df = 1, P = 1		$\chi^2 = 7.5$, df = 2, P = 0,02		$\chi^2 = 0.13$, df = 1, P = 0,71		$\chi^2 = 0.38$, df = 1, P = 0,53		$\chi^2 = 0.07$, df = 1, P = 0,79		$\chi^2 = 0.63$, df = 1, P = 0,43	

Table 3. Results of the partial correlations between the reproductive rates of Little Egrets and the independent factors analysed. The values of r (partial correlation coefficient) and P (level of significance) are given for each independent variable. Factors individually significant after the application of the sequential Bonferroni test are in bold type.

Independent variables	Dependent variables					
	Mean no. of hatchlings/nest		Mean no. of nestlings up to 20–25 days/nest		Mean nestling mortality rate up to 20–25 days/nest	
	r	P	r	P	r	P
Mean nest height/parcel	0.001	0.996	-0.18	0.27	0.22	0.17
Mean laying date/parcel	-0.14	0.38	0.21	0.19	-0.25	0.12
Density of Little Egrets/parcel	-0.02	0.90	-0.20	0.21	0.31	>0.025
Total density/parcel	0.18	0.25	0.16	0.33	-0.09	0.58
Mean no. of hatchlings/nest	-	-	0.72	<0.0167	-0.11	0.49

and consequently did not affect survivorship of young (Maddock & Baxter 1991, Baxter 1994), we found the lowest values of the Little Egret reproductive parameters in comparison with other localities in the Western Palearctic (Table 4) with the exception of the mean values given by Hafner *et al.* (1986) for the Camargue in 1984, which was a year characterised by extremely low food availability.

4.2. Nest height and density

Little Egret nest height was different between colonies but did not vary between years in the same colony. Since Little Egrets, as well as other heron species, use locally available vegetation as nest resources (Voisin 1991, Perennou *et al.* 1996), the differences observed seem to be due to differences between vegetation height in each locality. However, we would expect the nesting of the species in a middle height within the available range, as the vertical stratification pattern related to body size reported in mixed heronries predicts (Fasola & Alieri 1992, Parejo *et al.* 1999).

Differences between colonies in the number of nests of Little Egrets and the total number of nests by plot could be due to differences in the vegetation of colonies, as has been shown in other ardeids colonies (Kazantzidis *et al.* 1997).

4.3. Factors affecting the breeding performance of Little Egrets

The studied range of nest height did not have any effect on mean reproductive success, though other authors have shown the advantages of nesting high in the heronry vegetation (Fasola & Alieri 1992, Burger 1982). Similarly, the number of Little Egret nests or the total number of nests did not affect any of the parameters estimating the reproductive success of the species. This circumstance points out the non-existence of density-dependent effects on this species' reproductive performance, as happens in other colonial birds (Jehl 1994). However, to accurately assess density-dependent effects, experimental studies would be necessary to detect those effects that are not immediate or direct (Butler 1994). On the other hand, the studied range of other factors commonly thought to influence breeding success as laying dates do not seem to affect the reproductive performance of the species in Extremadura. Other factors such as predation, parasites, food availability or interspecific competition could be implied, though we can eliminate some of them such as food availability in the surroundings of colonies because we did not obtain different reproductive values for localities or seasons.

Table 4. Mean number of nestlings per nest up to different ages of the Little Egret through the western Palearctic.

Location	Latitude	Source	No. of nestlings per nest (n)	Up to age (days)	No. per.	Nest/egg marking
France	43°	Hafner <i>et al.</i> (1986)	2.7 ± 0.5 (149)	15–20	Successful nest	Yes
France	43°	Kazantzidis <i>et al.</i> (1996)	3.3 ± 0.8 (233)	20–25	Successful nest	Yes
Greece	40°	Kazantzidis <i>et al.</i> (1996)	3.0 ± 0.9 (214)	20–25	Successful nest	Yes
Valencia, Spain	39°	Prósper & Hafner (1996)	3.1 ± 0.1 to 3.8 ± 0.1 (211)	40–50	Successful nest	Yes
Extremadura, Spain	38°	This study	2.2 ± 0.9 (68)	20–25	Successful nest	No

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Selostus: Silkkihaikaran pesimäbiologiasta Lounais-Espanjassa

Kirjoittajat tutkivat silkkihaikaran pesintää kolmessa espanjalaisessa Extremaduran alueen haikarakoloniassa, joissa pesi myös muita haikaralajeja. Silkkihaikaroiden pesimämenestykseen vaikuttavia tekijöitä ei ole juuri tutkittu aikaisemmin yksityiskohtaisesti, vaikka lajin suojelun kannalta pesimämenestykseen vaikuttavien tekijöiden tunteminen on oleellista. Badajozin koloniassa pesi 60 (vuonna 1996) ja 95 (vuonna 1997) silkkihaikaraparia. Kahdessa muussa koloniassa pesi molempina tutkimusvuosina 30 (Montijon kolonia) tai 20 (Moranten kolonia) silkkihaikaraparia. Keskimääräisessä pesyekoossa, pesäpoikasten lukumäärässä 20–25 vuorokauden iässä ja poikaskuolleisuudessa ei havaittu eroja eri kolonioiden välillä. Silkkihaikaroiden pesimämenestyksessä ei havaittu eroja myöskään tutkimusvuosien välillä, vaikka muninnan aloituspäivän mediaaneissa oli eroja tutkimusvuosien välillä. Euroopan muihin silkkihaikarakolonioiden verrattuna Extremaduran haikaroiden pesimämenestys on alhaisin, vaikka pesinnän aloitusajankohta on aikaisin Palearktisella alueella. Pesän sijaintikorkeudessa ei ollut eroja vuosien välillä, mutta pesän sijaintikorkeudessa havaittiin eroja eri kolonioiden välillä. Pesän sijaintikorkeus ei kuitenkaan poikennut missään koloniassa tarjolla olevien pesäpaikkojen korkeudesta. Pesän sijaintikorkeus tai pesien tiheys eivät vaikuttaneet silkkihaikaroiden pesimämenestykseen Extremadurassa.

References

Baxter, G. S. 1994: The influence of synchronous breed-

- ing, natal tree position and rainfall on egret nesting success. — *Colonial Waterbirds* 17: 120–129.
- Burger, J. 1982: On the nesting location of Cattle Egret *Bubulcus ibis* in South African heronries. — *Ibis* 124: 523–529.
- Butler, R. W. 1994: Population regulation of wading Ciconiiform Birds. — *Colonial Waterbirds* 17: 189–199.
- Cézilly, F., Boy, V. & Hafner, H. 1990: Group foraging in Little Egrets (*Egretta garzetta*): from field evidence to experimental investigation. — *Behav. Proc.* 21: 69–80.
- Cramp, S. & Simmons, K. 1977: The birds of the western Palearctic. Volume I: Ostrich to Ducks. — Oxford University Press, Oxford.
- Fasola, M. & Alieri, R. 1992: Nest site characteristics in relation to body size in herons in Italy. — *Colonial Waterbirds* 15: 185–192.
- Fasola, M. & Barbieri, F. 1975: Aspetti della biologia riproduttiva degli Ardeidi gregari. *Ricerche di Biologia della Selvaggina* 62. — Laboratorio di Zoologia Applicata alla Caccia, Bologna.
- Fasola, M. & Pettiti, L. 1993: Optimal clutch size in *Nycticorax nycticorax* and *Egretta garzetta*. — *Bollettino di Zoologia* 60: 385–388.
- Fernández-Cruz, M. 1975: Revisión de las actuales colonias de Ardeidas de España. — *Ardeola* 21: 65–126.
- Hafner, H. 1980: Etude écologique des colonies de hérons arboricoles (*Egretta g. garzetta* L., *Ardeola r. ralloides* Scop., *Ardeola i. ibis* L., *Nycticorax n. nycticorax* L.) en Camargue. — *Bonner Zoologische Beiträge* 31: 249–287.
- Hafner, H., Dugan, P. J. & Boy, V. 1986: Use of artificial and natural wetlands as feeding sites by Little Egrets (*Egretta garzetta*, L.) in the Camargue southern France. — *Colonial Waterbirds* 9: 149–154.
- Hafner, H., Dugan, P. J. & Boy, V. 1987: Herons and wetlands in the Mediterranean: Development of indices for quality assesment and management of Mediterranean wetland ecosystem. Final report to the IIIrd Environment Research Programme of the Commission of the European communities, 46 pp.
- Hafner, H., Dugan, P. J., Kersten, M. & Wallace, J. P. 1993: Flock feeding and food intake in Little Egrets (*Egretta garzetta* L.): the effects of food provisioning and reproductive success. — *Ibis* 135: 25–32.
- Hafner, H., Kayser, Y., Boy, V., Fasola, M., Julliard, A.-C., Pradel, R. & Cézilly, F. 1998: Local survival, natal dispersal, and recruitment in Little Egrets *Egretta garzetta*. — *Journal of Avian Biology* 29: 216–227.
- Hafner, H., Kayser, Y. & Pineau, O. 1994: Ecological

- determinants of annual fluctuations in numbers of breeding Little Egrets *Egretta garzetta* in the Camargue, S. France. — *Revue d'Ecologie (Terre Vie)* 49: 53–62.
- Järvinen, A. 1989: Clutch-size variation in the Pied Flycatcher *Ficedula hypoleuca*. — *Ibis* 131: 572–577.
- Jehl, J. R., Jr. 1994: Absence of nest density effects in a growing colony of California Gulls. — *Journal of Avian Biology* 25: 224–230.
- Kersten, M., Britton, R. H., Dugan, P. J. & Hafner, H. 1991: Flock feeding and food intake in Little Egrets: the effects of prey distribution and behaviour. — *Journal of Animal Ecology* 60: 241–252.
- Kazantzidis, S., Goutner, V., Pyrovetsi, M. & Sinis, A. 1997: Comparative nest site selection and breeding success in two sympatric ardeids, Black-Crowned Night-Heron (*Nycticorax nycticorax*) and Little Egret (*Egretta garzetta*) in the Axios Delta, Macedonia, Greece. — *Colonial Waterbirds* 20: 505–517.
- Kazantzidis, S., Hafner, H. & Goutner, V. 1996: Comparative breeding ecology of the Little Egret (*Egretta g. garzetta*) in the Axios Delta (Greece) and the Camargue (France). — *Revue d'Ecologie (Terre Vie)* 51: 313–327.
- Maddock, M. & Baxter, G. S. 1991: Breeding success of egrets related to rainfall: a six-year Australian study. — *Colonial Waterbirds* 14: 133–139.
- Parejo, D., Costillo, E., Fuentes, C. 1997: Evolución de los ardeidos coloniales en la cuenca extremeña del Guadiana (suroeste de España). — *Butlletí del Grup Català D'Anellament* 14: 31–35.
- Parejo, D. & Sánchez, J. M. 1999: Effects of agricultural development on colonial Ardeidae populations in Southwestern Spain. — *Waterbirds* 22: 302–306.
- Parejo, D., Sánchez, J. M. & Avilés, J. M. 1999: Factors affecting the nest height of three heron species in heronries in the south west of Spain. — *Ardeola* 46: 227–230.
- Perennou, C., Sadoul, N., Pineau, O., Johnson, A. Hafner, H. 1996: Management of nest sites for colonial waterbirds. Conservation of Mediterranean wetlands. No. 4. — *Tour du Valat, Arles (France)*.
- Prósper, J. & Hafner, H. 1996: Breeding aspects of the Colonial Ardeidae in the Albufera de Valencia, Spain: Population changes, phenology, and reproductive success of the three most abundant species. — *Colonial Waterbirds* 19: 98–107.
- Rice, W. R. 1989: Analyzing tables of statistical tests. — *Evolution* 43: 223–225.
- Rivas-Martínez, S. 1987: Memoria y mapa de las series de vegetación de España 1:400.000. — ICONA, Madrid.
- Schönwetter, M. 1967: *Handbuch der Oologie*, vol. I. — Akademie Verlag, Berlin.
- Tucker, G. M. & Heath, H. F. 1994: *Birds in Europe: their conservation status*. — Birdlife International, Cambridge.
- Voisin, C. 1976: Etude de Comportement de l'Aigrette garzette (*Egretta garzetta*) en période de reproduction. — *L'Oiseau et R. F. O.* 46: 387–425.
- Voisin, C. 1985: Migration et stabilité des populations chez l'Aigrette garzette (*Egretta garzetta*). — *L'Oiseau et R. F. O.* 55: 291–311.
- Voisin, C. 1991: *The herons of Europe*. — T & AD POYSER, London.
- Zar, J. H. 1996: *Biostatistical analysis*. Third edition. — Prentice Hall, New Jersey.