Does foraging habitat quality affect reproductive performance in the Little Egret, *Egretta garzetta*?

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Abstract
Does foraging habitat quality affect reproductive performance in the Little Egret, Egretta garzetta*?*— In order to understand the role of foraging habitat quality on fecundity parameters we measured habitat use, breeding parameters, and body condition of chicks in six colonies of Little Egrets in southern France. The foraging habitat available differed between colonies; it was mainly natural marshes around the Carrelet colony, agricultural lands (rice fields and dry crops) around the Agon colony, a mix of agricultural and natural lands around the Redon and Fiélouse colonies, a mix of natural and urbanised/industrial lands around the Palissade colony, and mainly cultivated and urbanised lands around the Chaumont colony. The habitat attractiveness to adult Little Egret breeding was higher for natural marshes than for other habitat types. Agricultural marshes (rice fields) came next. Other human–made habitats came last. Clutch size and body condition index of chicks did not differ between colonies. Brood size was influenced by both the association of the proportion of natural marshes in the foraging area and clutch size, and the association of clutch size and the total number of heron pairs in the colony. The effect of the proportion of natural marshes could not be distinguished from the effects of the colony size. The potential influence of other parameters not taken into account in this study is discussed.

Key words: *Egretta garzeta*, Foraging habitat, Reproductive parameters, Body condition, Natural marshes.

Resumen
¿Afecta la calidad del hábitat alimentario a la capacidad reproductiva de la garceta común, Egretta garzetta*?*— Con la finalidad de conocer el papel que ejerce la calidad del hábitat alimentario sobre los parámetros de fecundidad, se evaluaron el uso del hábitat, los parámetros reproductivos y las condiciones físicas de los polluelos de seis colonias de garceta común en el sur de Francia. El hábitat alimentario disponible variaba de unas colonias a otras, siendo principalmente marismas naturales en el entorno de la colonia de Carrelet, terrenos agrícolas (campos de arroz y cultivos de secano) alrededor de la colonia de Agon, una combinación de terrenos agrícolas y naturales alrededor de las colonias de Redon y Fiélouse, una combinación de terrenos naturales y urbanizados/industriales alrededor de la colonia de Palissade, y principalmente terrenos cultivados y urbanizados alrededor de la colonia de Chaumont. En la época de reproducción, los adultos de garceta común se sienten atraídos principalmente por las marismas naturales, en detrimento de otros tipos de hábitat. Las tierras agrícolas anegadas (campos de arroz) siguen en orden de preferencia, mientras los hábitats construidos por el hombre ocupan el último lugar. El tamaño de la puesta y el índice de estado físico de los polluelos no mostraron diferencias entre las colonias. El tamaño de la nidada estuvo influenciado tanto por la asociación de la proporción de marismas naturales en el hábitat alimentario y el tamaño de la puesta, como por la asociación del tamaño de la puesta y el número total de parejas de garzas de la colonia. El efecto de la proporción de marismas naturales no se puede diferenciar del ejercido por el tamaño de la colonia. Se discute también la influencia potencial de otros parámetros que no se han tenido en cuenta en este estudio.

Palabras clave: *Egretta garzeta,* Hábitat alimentario, Parámetros reproductores, Condiciones físicas, Marismas naturales.

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Introduction

The distribution of food and the ability of individuals to exploit it have major implications on animal population dynamics (STEPHEN & KREBS, 1986). The exploitation of favourable patches with good foraging efficiency is linked to the structure of the habitat (CARTER & ABRAHAMS, 1997) and, on a broader scale, to the landscape (DOOLEY & BOWERS, 1998). Human activities, such as agricultural practices (soil management or pesticides and fertiliser use), affect the abundance, quality and availability of food resources for birds (e.g. AEBISCHER, 1990; TUCKER, 1992; WILSON et al., 1996; PETERSEN, 1998; CHAMBERLAIN et al., 1999). Although farmland has often been viewed in a rather dichotomic way as the juxtaposition of more or less isolated patches of suitable (non cultivated) areas within a matrix of non–suitable (cultivated) habitats (FARINA, 1997; PETERSEN, 1998), farmland can be considered, from an animal species'perspective, as a whole made up of a mosaic of habitat patches providing resources of varying abundance and quality. This raises the question of the function and value of the farmed component of the landscape in the functioning of these animal populations.

In birds, some fitness components related to reproductive parameters (e.g. clutch size, brood size, breeding success) or chicks'condition and growth, may be directly connected to the availability and quality of foraging habitats in the vicinity of nesting sites (e.g. CLAMENS & ISENMANN, 1989; TIAINEN et al., 1989; BURGER & GOCHFELD, 1991; HAFNER et al., 1993) and can, therefore be used as estimators of habitat quality.

One of the main crops on a global scale is rice (*Oryza* spp.), which covers over 11% of the farmed lands (FASOLA & RUIZ, 1997). Rice fields often replaced natural wetlands and numerous wetland bird species use the agricultural wetlands provided by rice cultivation (FASOLA & RUIZ, 1997). In some regions (e.g. the Ebro Delta in Spain or the Po Valley in Italy), rice fields have actually become the only significant wetland available for waterbirds (FASOLA & RUIZ, 1997). This prompted several studies to understand the consequences of rice field use on the ecology and population dynamics of such species (see FASOLA & RUIZ, 1997; TOURENQ et al., 2001).

As one of the main wetland complexes of the Western Palearctic, the Camargue, southern France, is a major area of rice production in Europe (FASOLA & RUIZ, 1997). It also contains one of the largest industrial salt pans in the Mediterranean and is bordered by a large industrial complex (BATTY et al., 1996; BERNY et al., in press). This mosaic consists of natural, agricultural and industrial wetlands and offers a rather unique opportunity to study the respective value of man–made and more natural wetlands on the health of water bird populations.

Among the species which extensively use rice fields, the Little Egret (*Egretta garzetta*), a common heron in the Camargue, provides a good study model. The Little Egret is a colonial species that uses a wide range of habitats for foraging, including all types of wetlands (TOURENQ et al., 2000). In this context, artificial wetlands such as rice fields may consequently provide food resources, especially during the breeding period in the Camargue (HAFNER et al., 1986; HAFNER & FASOLA, 1992). TOURENQ et al. (2000) have shown that egret numbers have increased over the past decades together with an increase in the area cultivated in rice. At first glance, rice cultivation seems therefore to have been beneficial to egrets. However, BENNETTS et al. (2000) and LOMBARDINI et al. (2001) showed that this correlation may be misleading. Respectively, these authors found that reproductive parameters have decreased during the past decades and that this species preferentially used natural marshes rather than anthropized habitats for foraging. To investigate this point further: 1. The foraging habitat use of adult Little Egrets around breeding colonies was investigated in order to identify the habitat selected in relation to its availability; and 2. Clutch size, brood size and the condition of Little Egret chicks were hypothesized that were influenced by the proportion of this habitat.

Material and methods

Study area

The Camargue deltaic complex, southern France (43°40'–43°30' N, 4°10'–4°30' E; ca. 1,450 km²), is renowned as one of the most important wintering and breeding grounds in Europe for water birds (HEATH & EVANS 2000). Natural habitats cover some 60,000 ha (±41% of total surface) and salt pans some 21,000 ha (±15% of total surface) in the southern region. Some 24,000 ha (±16% of total surface) are devoted to rice farming, whereas dry crops cover 26,000 ha (±18% of total surface). Located in the south–eastern area, the industrial complex of Fos–sur–Mer (metal transformation and refineries) covers about 9% of the total surface of the delta (CHAUVELON, 1996).

This study was carried out in 1998 and 1999 in six colonies of tree–nesting herons located within, or adjacent to, the Camargue: Agon, Fiélouse and Chaumont in 1998, and Carrelet, Redon, Palissade in 1999 (fig. 1). Palissade is situated in the south–eastern part of the delta, between the industrial complex of Fos–sur–Mer and the industrial salt pans of Salin de Giraud. Colonies of Agon, Fiélouse, Redon and Carrelet are located in the semi–natural central area of the delta. The Chaumont colony is situated outside the delta within a vineyard cultivation area near a coastal tourist resort.

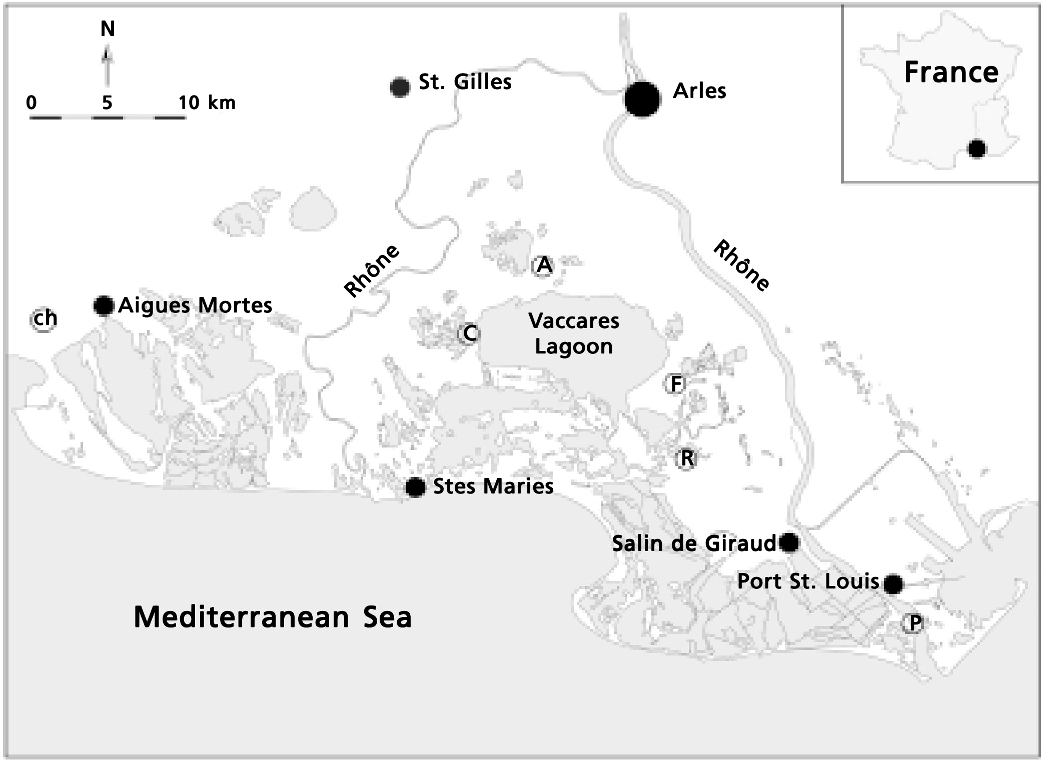

Fig. 1. Study area with the location of Little Egret colonies sampled in 1998 and 1999: C. Carrelet, A. Agon; F. Fiélouse; R. Redon; P. Palissade; ch. Chaumont. (Inset shows the location of the study area in France.)

Fig. 1. Área de estudio con la localización de las colonias de garceta común muestreadas en 1998 y 1999: C. Carrelet; A. Agon; F. Fiélouse; R. Redon; P. Palissade; ch. Chaumont. (El mapa del recuadro muestra la localización del área de estudio en Francia.)

Foraging habitat composition and habitat use by egrets

Digitised aerial photographs of the study area (scale 1:20,000) were ortho–rectified, geo-referenced and gathered (software Geoimage, on a UNIX workstation; SANDOZ & CHAUVELON, 1998). A total of 18,500 agricultural plots and natural areas and marshes were digitised with GIS MapInfo. Land–use was updated each year during the study through integration of classified satellite images. MapInfo was used to calculate the area of habitats available within the foraging range of colonies (radius = 10 km; HAFNER & FASOLA, 1992). For each colony, the proportions of each habitat type were estimated: rice fields (RICE), dry cultivation lands such as vineyards, corn, pastures,... (DRY), urbanised and industrial areas (URB), flooded surfaces of natural marshes (NM) and other natural lands such as salt flats called "sansouïre" (SAN). The proportion of woodlands, sea, as well as central parts of lagoons and Rhône river arms were not included in the analysis, as they are not used by Little Egrets when foraging. The one meter shore zone of lagoons and river arms which is used by foraging Little Egrets were only considered (C. Toureng, pers. obs.).

For the five colonies within the delta (Agon, Carrelet, Fiélouse, Redon, Palissade), foraging individuals were counted by aerial surveys (at 400 ft above ground) of the foraging range of each colony in the morning. Each flock or individual counted on one of the habitat types was recorded and plotted on a map. In order to take into account the variation in foraging habitat use that may occur during the reproductive season (LOMBARDINI et al., 2001), aerial surveys were conduced at the egg–laying stage, the brooding stage and at the fledging stage. In 1998, nine aerial surveys (three per reproductive stage) were made for Agon and Fiélouse but in 1999, due to meteorological and technical hazards and airforce exercises over the study area, were only able to perform eight surveys for Redon, Carrelet and Palissade colonies. Due to flight authorizations (proximity of the Montpellier international civil and Nîmes military airports), we could not carry out aerial survey over the Chaumont colony foraging range.

Breeding parameters and chicks measurements

For the six colonies, we measured clutch size, brood size and nest success. Little Egrets nests were individually tagged at the beginning of the season (early May) and monitored weekly. The clutch size was defined as the number of eggs per nest after laying was completed. The brood size was defined as the number of chicks remaining alive at 20–25 days of age for successful nests. After 20–25 days, chicks are capable of escaping by walking and may not be present in the nest (BENNETTS et al., 2000). Nest success was estimated as the proportion of active nests (i.e. nests with at least one chick) that were successful (i.e. nests that fledged at least one chick).

Measurements included tarsus length (mm), taken from the middle of the mid–tarsal joint to the distal end of the tarso–metatarsus, and body mass (g). Chicks were aged according to tarsus length (THOMAS et al., 1999). All birds were released unharmed at the site of capture.

Statistical analysis

Habitat selection by Little Egrets was determined using a chi–square goodness–of–fit test to compare the observed distribution of foraging adults with that expected, relative to the proportion of each suitable habitat available within the foraging range of colonies.

The body condition index (BCI) was calculated as the residuals from the model II (reduced major axis) regression of body mass (W) on the tarsus length (T) (GREEN, 2000). The use of model II regressions is likely more appropriate to study body condition since the use of residuals from ordinary least square linear regression of body mass against a linear measure of size is subject to errors due to measurements and violation of assumptions (SOKAL & ROHLF, 1997; GREEN, 2000).

Clutch size and brood size were compared between colonies using one–way analyses of variance (ANOVA) and Tukey–Kramer (HSD) post-hoc tests (SOKAL & ROHLF, 1997). The effects of habitat types selected by foraging adult Little Egrets and their interactions on the clutch size and brood size of egrets for each colony were assessed using a generalised linear model (GLM) approach. Because the brood size is at least partially limited by clutch size (HAFNER et al., 2001), the clutch size (CS) was considered as an explanatory variable of brood size. Little Egrets nest in mixed colonies with Cattle Egret (*Bubulcus ibis*), Squacco Heron (*Ardeola ralloides*), Black–crowned Night Heron (*Nycticorax nycticorax*) and Grey heron (*Ardea cinerea*) in the Camargue (TOURENQ et al., 2000). Because of possible density–dependent effects on brood size (BENNETTS et al., 2000; HAFNER et al., 2001), the total number of breeding pairs of herons (PAIR) was also considered as an explanatory variable of brood size. Since 1967, all heron colonies have been censused each year in the Camargue. The census is based on direct nest counts and counting error increases with colony size, with up to 10% under–estimation of larger colonies, while over–estimation is unlikely (TOURENQ et al., 2000). Using a generalized linear model procedure with a identity link function, we explored the effects of clutch size, total number of breeding pairs and habitat types selected by foraging breeding adults on the breeding parameters. Models with non–identifiable or non–estimable effects were ignored. Model selection was based on Akaike's Information Criteria (AIC AKAIKE, 1973; SHIBATA, 1989) and multi–model inference (MMI; ANDERSON et al., 2000). AIC is defined as:

$$-2\ln(L) + 2np$$

where $-2\ln(L)$ represents the deviance and np is the number of parameters estimated in the model. Models with AIC scores differing by < 2 were not considered statistically different (SAKAMOTO et al., 1986).

Multi–model inference is based on the entire set of models, using AIC differences ($\cong_i$) between the best model, i.e. with the minimum AIC, and each model and using Akaike weights (Δ_i; ANDERSON et al., 2000). Akaike weights are calculated as:

$$\Delta_i = \exp(-0.5\cong_i) \ / \ \Sigma^R_{r=1} \exp(-0.5\cong_i)$$

where $\exp(-0.5\cong_i)$ is the likelihood of a model i given the data for i = 1, 2,... R models.

Results

Foraging habitat and habitat use

The foraging habitat composition differed significantly among the five colonies aerial-surveyed (table 1). The foraging range of the Agon colony mainly consisted of pastures, dry cultivation lands (sunflowers) and rice fields. The Fiélouse colony was mainly surrounded by salt flats ("sansouïres") and pastures. The Palissade colony was located between the industrial salt pans of Salin de Giraud and the industrial zone of Fos–sur–Mer, but near the large natural marshes of they de Roustan and Palissade. The foraging range of the Redon colony mainly consisted of "sansouïres" from the Vaccarès lagoon system, rice fields, salt pans and some natural marshes. More than 50% of the Carrelet foraging habitats were natural marshes, the rest being pastures, rice fields and "sansouïres"(table 1).

Table 1. Composition of the foraging habitat and selection of habitats within the foraging range by Little Egrets during the reproductive seasons 1998 and 1999. Number of individuals observed (N) and number of individuals expected relative to the proportion of habitat available (Exp) are given. * Indicate the highest selected habitats in a greater proportion than their availability for a given colony. Indices indicate the preference rank of habitats by increasing order: RICE. Rice fields; DRY. Dry cultivated lands; URB. Urbanised lands; NM. Natural marshes; SAN. "Sansouïres"; § To avoid problems due to empty cells and oversmoothing the data, the constant 10^{-8} was added to all the cells for χ^2 computations (AGRESTI, 1990).

*Table 1. Composición del hábitat alimentario y selección de hábitats dentro de la gama alimentaria de la garceta común durante las estaciones reproductoras de 1998 y 1999. Se presentan el número de individuos observados (N) y el número de individuos esperados (Exp) según la proporción de hábitat disponible. * Indican los hábitats seleccionados en mayor proporción que su disponibilidad para una colonia indicada. Los índices indican en rango de preferencia de hábitats y en orden creciente: RICE. Campos de arroz; DRY. Tierras cultivadas de secano; URB. Tierras urbanizadas; NM. Marismas; SAN. "Sansouïres"; § A fin de evitar problemas debidos a celdas vacías y uniformizar los datos, se añadió la constante 10^{-8} a todas las celdas para los cálculos de las χ^2 (AGRESTI, 1990).*

		Habitat				
Colony		RICE	DRY	URB	NM	SAN
Agon	ha (%)	5,177 (21.49)	10,169 (42.22)	16 (0.07)	3,958 (16.43)	4,765 (19.78)
	N (Exp)	177 (38.03)$_2$	1 (0.44)$_3$	0 (0)$_4^{\S}$	1396 (229.36)$_1^*$	0 (0)$_5^{\S}$
Palissade	ha (%)	345 (2.13)	1,113 (6.87)	7,403 (45.72)	2,209 (13.64)	5,122 (31.63)
	N (Exp)	20 (0.42)$_2$	16 (1.10)$_3$	24 (10.97)$_4$	635 (86.61)$_1^*$	9 (2.84)$_5$
Fiélouse	ha (%)	3,209 (13.04)	6,739 (27.37)	16 (0.07)	2,090 (8.49)	12,564 (51.04)
	N (Exp)	140 (18.25)$_2$	124 (33.93)$_3$	0 (0)$_5^{\S}$	1467 (124.54)$_1^*$	181 (92,.38)$_4$
Carrelet	ha (%)	3,489 (14.88)	4,159 (17.74)	16 (0.07)	13,446 (57.34)	2,339 (9.97)
	N (Exp)	47 (7)$_3$	37 (6.56)$_4$	0 (0)$_5^{\S}$	2619 (1501.73)$_1^*$	38 (3.78)$_2$
Redon	ha (%)	3,877 (14.37)	3,617 (13.41)	3,256 (12.07)	10,121 (37.50)	9,378 (37.74)
	N (Exp)	49 (7.03.)$_2$	18 (2.41)$_3$	0 (0)$_5^{\S}$	1293 (484.87)$_1^*$	61 (21.97)$_4$

The foraging habitat surrounding the Chaumont colony consisted of a few natural marshes (2,060 ha; 7.03%) dispersed in an intensive dry cultivation area (vineyards, asparagus; 12,000 ha; 41%), near the industrial salt pans of Aigues–Mortes and a highly developed tourist coastal zone (6,357 ha; 21.7%). The rest of the habitat consisted of salt flats and pine woods (8,755 ha; 29.87%).

Overall, adult Egrets from aerial–surveyed colonies selected natural marshes first and agricultural marshes (rice fields) second. Foraging adult egrets were found in higher numbers than expected in natural marshes in all the colonies considered (table 1). Rice fields were used more often in relation to "sansouïres" and dry cultivated lands (mostly pastures) in the Agon, Carrelet and Palissade colonies whereas "sansouïres" were used more often than rice fields and dry cultivated lands by egrets in the Redon and Fiélouse colonies.

Breeding parameters

Clutch size, brood size and nest success were checked for 123 nests in the five colonies within the Rhône delta and the Chaumont colony. The mean clutch size per colony ranged from 3.74 to 4.22 eggs per nest (Agon and Redon colonies, respectively). There was no significant difference of mean clutch size between colonies (ANOVA, $F_{[5,122]} = 1.45$, $P = 0.21$; table 2).

The mean brood size ranged from 1.12 to 2.63 chicks per nest (Carrelet and Agon colonies, respectively). A significant difference of brood size was observed between colonies (ANOVA, $F_{[5,122]} = 4.20$, $P = 0.001$; table 2). Post–hoc tests (Tukey–Kramer HSD) indicated that Carrelet nests had a lower brood size than Agon, Redon and Fiélouse nests, but this was not significantly different from Palissade and Chaumont (table 2).

Table 2. Number of nests sampled in the studied colonies and corresponding estimates of total number of pairs (Np), mean clutch size (CS ± SE), mean brood size (BS ± SE) and proportion of nests successful (NS). Same letters indicates that brood size values are not different (Tukey–Kramer HSD test, P<0.05).

Tabla 2. Número de nidos muestreados en las colonias estudiadas y correspondientes estimaciones del número total de parejas (Np), tamaño medio de la nidada (CS ± desviación estándar), tamaño de las crías (BS ± desviación estándar) y porporción de nidos llenos (NS). Las mismas letras indican que los valores del tamaño de las crías no son diferentes (test de Tukey–Kramer HSD, P < 0,05).

Colony	N	Np	CS	BS	NS
Agon	27	1,237	3.74 (±0.13)	2.63 (±0.21)[a,]	0.92
Redon	18	1,108	4.22 (±0.16)	2.55 (±0.26)[a]	0.88
Fiélouse	17	1,452	3.76 (±0.16)	2.41 (±0.27)[a]	0.88
Palissade	20	118	4.15 (±0.15)	1.60 (±0.26)[a,b]	0.65
Chaumont	31	548	3.93 (±0.12)	2.10 (±0.30)[a,b]	0.90
Carrelet	16	470	3.87 (±0.17)	1.12 (±0.28)[b]	0.63

The highest value of nest success was obtained for the Agon colony (0.92) and the lowest for the Carrelet colony (0.63; table 2). The total number of pairs of herons also varied between colonies (table 2). The Fiélouse colony (1,452 pairs) was the largest while the smallest was the Palissade colony (118 pairs).

Chick body condition

For both years (1998 and 1999), a total of 172 chicks aged between 6 and 21 days (mean = 12.97±0.24 SE) were measured in the five colonies within the Rhône delta (Agon, Carrelet, Fiélouse, Redon, Palissade) and the Chaumont colony.

Body mass (W) was significantly correlated with tarsus length ($r^2 = 0.89$, $N = 167$, $P < 0.001$). The body condition index (BCI) was obtained from the residuals of the model II regression:

$$W = 7.49T - 153.26$$

The corrected body condition index was not significantly different between colonies (ANOVA, $F_{[5,161]} = 1.25$, P = 0.28).

Subsequently, preliminary univariate tests showed that the mean age of chicks varied between colonies (ANOVA, $F_{[5,166]} = 8.61$, $P < 0.001$). Post–hoc test (Tukey–Kramer HSD) indicated that Palissade chicks were older than chicks from other colonies (table 3).

Relation between environmental and colonial parameters

As the body condition and the clutch size (CS) were not significantly different between colonies, we concentrated our analysis on the brood size (BS) as the variable to investigate. The habitat selected by adult breeding Little Egrets being natural marshes (NM), we considered the effect of this habitat on the brood size. Using a generalised linear model procedure, we obtained the best (i.e. lowest) scores of AIC for the model PAIR+CS+NM (AIC = 366.62; table 4). Second and third models PAIR+CS and NM+CS showed identical AIC (376.62). The examination of Akaike weights suggests that the model PAIR+CS+NM is the best. However Δ_i was increased by 10 units by the subtraction of one effect (PAIR or NM). Finally, the model PAIR+CS+NM was rejected on the basis of the large number of parameters not estimated. The fact that the model PAIR+NM had a higher AIC score (382.26) and that PAIR+CS and NM+CS models had identical scores suggests that the proportion of natural mashes (NM) was not estimable in presence of the size of colony (PAIR). This is linked with the fact that these effects are confounded; i.e. each level of NM is included exclusively in a level of PAIR.

Discussion

In regions where natural marshes are scarce, the proportion of rice fields available in the foraging range affects the distribution and size of colonies. In this context, rice fields provide suitable foraging habitats for tree–nesting herons (Hafner & Fasola, 1992; Fasola & Ruiz, 1997). Hafner et al. (1986) showed that in the Camargue region, rice fields were intensively used by the Little Egret during the reproductive season, especially when adults were feeding chicks. However, natural habitats (i.e. marshes) in this area still cover a great proportion of the landscape mosaic.

Table 3. Number of individuals (N), mean age ± SE of Little Egret chicks from the colonies studied in 1998–1999 in the Camargue, France. Same letters indicates that ages are not different (Tukey–Kramer HSD test, $P < 0.05$).

Tabla 3. Número de individuos (N), edad media ± desviación estándar de los pollos de las colonias de garceta común estudiadas en 1998–1999 en la Camarga francesa. Las mismas letras indican que las edades no son diferentes (test de Tukey–Kramer HSD, P < 0,05).

Colony	N	Age (days)
Palissade	21	16.33 (0.66)^a
Chaumont	30	13.10 (0.52)^b
Fiélouse	12	13.08 (0.53)^b
Redon	28	11.21 (0.61)^b
Carrelet	49	12.43 (0.44)^b
Agon	27	12.48 (0.44)^b

More recent studies revealed that cultivated habitats such as rice fields were avoided (in relative terms) throughout the year, whereas natural marshes were the habitat preferred by foraging Litte Egrets (LOMBARDINI et al., 2001). It was thus suggested that rice fields might be of lower value than natural marshes.

In this study, aerial surveys revealed that for all monitored colonies, natural marshes were the habitat preferred (selected more than expected regard to its proportion in the landscape) by adult Little Egrets during the breeding season, even in an agricultural or industrial environment. Most natural marshes (about 40% of the Camargue surface area) are presently situated in protected areas but also in private properties devoted to waterfowl hunting (TOURENQ et al., 2000). Thus, valuable foraging habitats for the Little Egret depend on the maintenance of these natural marshes and wildfowling in the Camargue. Nevertheless, rice fields were the anthropised habitats most preferred by egrets. The importance of ricefields for waterbirds may be most pronounced during extremely dry years when natural marshes are dry. Our study included a relatively dry year (1998, with a total annual rainfall = 471.10 mm) and a relatively wet year (1999, with a total

Table 4. Modelling the influence of total number of pair of herons (PAIR), clutch size (CS), natural marshes (NM) on the brood size of Little Egrets in the Camargue: Dev. Deviance of the model; Np. Number of parameters; AIC. Akaike Information Criteria; $\cong_i$ AIC – minAIC; Δ_i Akaike weight; * The model had higher number of estimates non–estimated; [1] Model including two–way interactions; [2] Model including three–way interactions.

*Tabla 4. Modelos de influecia del número total de parejas de garzas (PAIR), tamaño de la nidada (CS), marismas (NM) en el tamaño de las crías de garceta común en la Camarga: Dev. Desviación del modelo; Np. Número de parámetros; AIC. Criterio de información de Akaike; $\cong_i$ AIC – minAIC; Δ_i Peso de Akaike; * Modelo con gran número de valores no estimados; [1] Modelo con dos tipos de interacciones; [2] Modelo con tres tipos de interacciones.*

Model	Dev	Np	AIC	$\cong_i$	Δ_i
PAIR+CS+MN*	358,62	4	366,62	0	0.98
CS+MN	358,62	9	376,62	10	0.006
PAIR+CS	358,62	9	376,62	10	0.006
MN	370,26	6	382,26	15,64	0.0001
PAIR	370,26	6	382,26	15,64	0.0001
PAIR+MN	370,26	6	382,26	15,64	0.0001
CS	382,52	4	390,52	23,9	< 0.0001
PAIR/CS/MNΔ2*[1]	352,96	20	392,96	26,34	< 0.0001
PAIR/CS/MNΔ3*[2]	352,96	20	392,96	26,34	< 0.0001

annual rainfall = 719.10 mm) compared to the mean annual rainfall of 625.40 mm for the 1963–99 period (Chauvelon, unpub. data). However, colonies surveyed in 1998 (Agon, Fiélouse and Chaumont) presented among the highest reproductive performances (see table 2). Moreover, extremely dry years have been recorded in the Camargue (e.g., 252.00 mm and 325.60 mm for 1989 and 1992, respectively; Chauvelon unpub. data). Our results are therefore applicable to a relatively dry year, but do not allow us to extend reliable inference to extreme conditions which may periodically occur.

TIAINEN et al. (1989) suggested that the intensification of farming induced a decrease in the Finish Starling (*Sturnus vulgaris*) population as the result of a reduction in nestling fitness (i.e. growth and survival). In Little Egrets, chick body condition and reproductive success are said to be a function of food quality and abundance in the foraging range and of food quantity collected by adults (HAFNER et al., 1993). Despite the conversion of many natural marshes into rice fields and other artificial habitats in the past 30 years, a general increase in population numbers of Little Egrets has been observed in the Camargue (TOURENQ et al., 2000). The analysis of a series of reproductive parameters in this species revealed no clear stresses in habitats of little appeal to egrets. The mean clutch size and chick body condition did not differ between colonies. In birds, the number of eggs laid by the female is partly related to the body condition of the female before ovulation (e.g. DRENT & DAAN, 1980; MONAGHAN et al., 1989; CHASTEL et al., 1995). However, Little Egrets may be "income breeders" (sensu MEIJER & DRENT, 1999) like purple herons, (*Ardea purpurea ;* MOSER, 1986): eggs are relatively small in relation to female body weight (5%, Hafner et al., unpubl. data), thus requiring small reserves before their production (MOSER, 1986), and both sexes participate in incubation during laying (HAFNER et al., 1993). Moreover, the Little Egret is a partial migrant (TOURENQ et al., 2000). Thus, females may feed on breeding areas just before and/or during egg production. Further studies are needed to confirm this hypothesis.

Brood size among birds is supposed to reflect local conditions (DRENT & DAAN, 1980) and our results suggest that brood size may vary with the proportion of natural marshes around colonies. However, we could not separate the effect of the proportion of natural marshes from the effect of the colony size. Whereas the Carrelet colony was surrounded mainly by natural marshes, it was also the colony with one of the lowest number of breeding pairs, the lowest mean brood size and the lowest nest success. The brood size of Carrelet was similar to the mean brood size of colonies with a significant amount of anthropised habitat in their foraging range (Chaumont, Palissade).

One possible stressor not taken into account in this study could be the ingestion of pesticides through the consumption of food collected in rice fields. Little Egrets are mainly insectivorous–piscivorous (TOURENQ et al., 2000) and non–negligible concentrations of organochlorine pesticides typically used in rice farming were detected in tissues of fish from the Camargue (ROCHE et al., 2000). Organochlorines were also found in the eggs of Little Egrets in colonies with a «rice environment» (BERNY et al., in press). Through the quality of the food ingested (GRASMAN et al., 1998), contaminants are known to influence reproductive parameters (NEWTON, 1986; BURGER & GOCHFELD, 1991; BERNY et al., 2001). This might also be the case for the Carrelet colony where brood size and nest success were low. The presence of industrial areas set upstream and near the mouth of the Rhône river (Fos sur Mer complex), generates exposure to heavy metal or polychlorinated byphenyls (PCBs) and may account for the presence of contaminants found in eggs (BATTY et al., 1996; BERNY et al., in press.). This is especially valid for the Palissade colony where brood size and nest success were low. Studies are in progress to confirm the impact of contaminants on egrets reproduction in the Camargue.

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