COMPARATIVE BREEDING ECOLOGY OF THE LITTLE EGRET (*EGRETTA G. GARZETTA*) IN THE AXIOS DELTA (GREECE) AND THE CAMARGUE (FRANCE)

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INTRODUCTION

In the Mediterranean region the Little Egret (*Egretta garzetta*) has a patchy breeding distribution (Cramp & Simmons, 1984 ; Hafner *et al.,* 1987). Since the seventies the species has generated considerable interest for the study of the breeding and feeding ecology, in the Camargue in southern France (e.g. Voisin, 1978, 1979 ; Hafner, 1977, 1978 ; Hafner & Britton, 1983 ; Hafner *et al.,* 1982, 1986, 1993, 1994 ; Kersten *et al.,* 1992), in Italy (e.g. Fasola, 1986 ; Fasola & Ghidini, 1983 ; Fasola & Barbieri, 1978 ; Fasola & Alieri, 1992), in Spain (Fernandez-Cruz, 1995 ; Fernandez-Cruz *et al.,* 1992), in Greece (Tsachilidis, 1990 ; Kazantzidis & Goutner, 1996) and in Croatia (Mikuska, 1992). Egrets carrying wing marks and originating from the Camargue are frequently observed in Spain but there is also evidence of dispersal in an easterly direction (Pineau, 1992), and some of these birds have been observed in Greece (Hafner, unpubl. data). According to migration movements analysed by Voisin (1985, 1991) Little Egrets from the different breeding areas in southern Europe are most likely to mix during migration and wintering and are part of a metapopulation system.

We compare data on the breeding biology of Little Egrets in two Mediterranean wetlands of international importance. The physical and biotic characteristics of foraging habitat differ considerably between the two wetlands and we investigate whether the breeding performance and chick condition reflect this inter-regional variation. The results may contribute towards the conservation of these birds as part of wetland management and conservation programmes.

STUDY AREAS

The study areas which are separated by approximately 1 500 km show considerable differences in their habitat structure and management.

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The Camargue (43° 30' N, 4° 30' E), is a Ramsar site of international importance, especially as waterfowl habitat (Jones, 1993). The whole wetland complex comprises over some 1 500 km^2 formed by the mouth of the river Rhône. Each year 1 000 (1985) to 3 000 (1994) pairs of Little Egrets nest in small copses, together with Cattle Egrets (*Bubulcus ibis*), Night Herons (*Nycticorax nycticorax*) and Squacco Herons (*Ardeola ralloides*). The major feeding area considered in this study lies between the two arms of the river and around the large central lagoon « Vaccarès ». This part of the Camargue consists of a mosaic of diverse and shallow water habitats, particularly freshwater marshes (about 75 km^2), ricefields (70 km^2) and, to the south of Vaccarès, brackish and saltwater habitat dominated by *Salicornia* flats (90 km^2) (Table I). Three or four Little Egret colonies used this extensive feeding area each year. Most of the freshwater marshes are managed for hunting purposes and water levels are closely controlled. Many are grazed by cattle and horses and some reed cutting occurs. About 40 per cent of the surface of these marshes are permanent with a dominant vegetation of reed *Phragmites australis*. The other 60 per cent are temporary and dominated by *Scirpus maritimus*. Some of them constitute important feeding sites at the time of their summer drying out, as prey concentrated in pools become easily accessible. Water levels in most of these marshes are maintained through pumping, until the breeding season is well advanced and the chicks are near fledging. Ricefields are exploited during a shorter period, mainly from the end of May to the end of June. In the southern part of the delta, the brackish and saltwater feeding area, water levels are largely dependent upon rainfall and there is considerable variation between years in the extent of exploitable feeding habitat (Hafner *et al.*, 1994).

TABLE I

Extent of foraging habitats of Little Egrets in the two areas studied.

	Extent (km^2) and (%)	
	Axios	Camargue
Brackish and Salwater	16 (45)	90 (38)
Freshwater habitat	2 (6)	75 (32)
Ricefields	17 (49)	70 (30)
Total	35	235

The Axios Delta (40° 30' N, 22° 53' E) extends over 68.7 km^2 (Athanasiou, 1990) and is part of a large wetland complex situated at the west coast of Thermaikos Gulf, including the estuarine and deltaic areas of the rivers Axios, Aliakmon, Loudias and Gallikos. This wetland complex is of international importance for waterbirds and protected under the Ramsar Convention. The Axios Delta comprises a variety of habitats such as salt- and freshwater marshes, ricefields, lagoons, open sea, vegetated coastal islets, sandy shores, riparian forest and tamarisk scrub. The study area was about 53 km^2 of which 35 km^2 constitued

foraging habitats of the Little Egret (Table I). Of these, *Salicornia* dominated habitats are mainly made up by tidal and non-tidal saltmarshes, mudflats and shallow sea shore. Freshwater habitat includes river edges, artificial canals and a few natural marshes. Water levels of this habitat are dependent on rainfall and management through pumping from the river for agriculture. Reed *Phragmites australis* and *Typha* spp. form the dominant vegetation. Ricefields are an important habitat becoming available to the egrets in late April. The Little Egrets (270-700 pairs) breed in the riverine forest of Alder (*Alnus glutinosa*), Willow (*Salix* sp.) and Tamarisks (*Tamarix* spp.), together with Night Herons, Squacco Herons, Spoonbills (*Platalea leucorodia*), Glossy Ibises (*Plegadis falcinellus*), Cormorants (*Phalacrocorax carbo*) and Pygmy Cormorants (*Phalacrocorax pygmeus*). Human activities in the study area are intense and include agriculture, cattle grazing, fishing, aquaculture, hunting (in winter), sand extraction, building, garbage and sewage damping. The effluents from the city of Thessaloniki and the neighbouring industrial area, result in coastal pollution.

METHODS

Foraging distribution

The comparison of the foraging distribution between the two wetlands is based on counts of Little Egrets during three breeding seasons in both the Camargue and the Axios.

Because the feeding areas are extensive and often inaccessible in the Camargue, aerial surveys were carried out in order to assess the distribution of foraging Little Egrets. The method aims at measuring the true density and distribution of Little Egrets within 10 km of each study colony. Three well trained observers are needed to carry out these surveys and it is important that they be familiar with the area surrounding the colonies. One of them guides the pilot whilst the other two count and map the birds around the colonies. During each flight, all potential feeding sites were inspected from variable altitudes and as often as necessary in order to obtain a complete count. Name of sites, numbers of Little Egrets and foraging habitat type used were recorded on tape and later transcribed. All surveys took place at about the same time, in mid-morning. A total of six flights (1991-1993) were analysed, three during the incubation period and three during the chick raising period. The results are consistent with the patterns described earlier from ground counts in the area (Hafner, 1977 ; Hafner *et al.,* 1987 ; Hafner & Fasola, 1992).

In the Axios, the study area was surveyed within the same morning hours once every ten days from 1st April to 30 June (1988, 1989, 1990) from raised dykes and the numbers of Little Egrets foraging were recorded in each habitat type (as defined in Table I). Because numbers of birds per ten-day periods did not differ significantly in each habitat between years, numbers were averaged for further comparisons.

Breeding parameters

Data inside the colonies were collected in both areas from 1988 to 1990. Nests were individually marked and their content was checked at least once a

week. Numbers of eggs laid and hatched were recorded at each nest (clutch size given is the number of eggs present in a nest before hatching).

Data on brood size shortly before fledging were collected from the ground, using binoculars, when the chicks were about 20-25 days of age. At about 30 days a Little Egret is able to fly (Hafner *et al.,* 1994) and a whole brood is not necessarily being fed on the same tree. The number of chicks begging for food were counted when a parent attended the nest to feed the brood. Chicks were marked individually and their tarsus length (except for 1988 in the Axios) and weight recorded. In order to avoid variation in chick weights due to food provisioning, chicks were marked and measured during the early morning hours. Their body condition was evaluated using the method developed by Hafner *et al.* (1994) which is to : (1) calculate the regression of body weight on tarsus length, an independent measure of size for all the chicks measured ; (2) calculate an index of chick condition as the ratio of the actual body weight to the predicted body weight for a chick of a given tarsus length, using the regression.

Chick diet

Chick regurgitations were collected throughout the nestling period. Samples of food items found in the regurgitations were collected from the feeding grounds by standard techniques (Kushlan, 1974 ; Kjelson *et al.,* 1975 ; Fasola, 1994). Food items from such samples were used to estimate the dry mass of each prey type. Dry mass was measured by weighing food items dried in an automatic electric oven at 70 °C until steady mass (about 48 hours).

Statistical analysis

Data on clutch and brood sizes were normally distributed and were not transformed for the analysis. Comparison between the two study areas was made using the non-parametric Jonckheere-Terpstra test. The body condition index was calculated from log-transformed data and mean values were compared using appropriate t-tests. Comparisons of the regressions of chick weight against tarsus length were made using the analysis of covariance (ANCOVA). Data on feeding destribution were submitted to χ^2-tests for intra- and inter-study areas comparisons. Data on numbers of items in each prey category determined in the chick regurgitations and the relative abundance of different prey categories expressed as biomass (dry weight), were compared using the non parametric Kappa statistic K (Siegel & Castellan, 1988).

RESULTS

Use of foraging habitats

In the Camargue the available foraging habitat was almost seven times greater than in the Axios Delta (Table I). In the Axios the distribution of foraging Little Egrets between the different types of foraging habitat was similar between the

incubation and chick periods (χ^2_2 = 10.17, P = 0.06) but differed significantly in the Camargue (χ^2_2 = 48.98, P < 0.001, Table II). Highly significant differences were also found between the Axios Delta and the Camargue in the use of foraging habitats both during incubation (χ^2_2 = 280.15, P < 0.001) and the chick period (χ^2_2 = 80.67, P < 0.001). During incubation, there was higher use of freshwater marshes in the Camargue and of ricefields in the Axios whereas the use of brackish and saltwater, *Salicornia* dominated habitats was similar in both areas. During the chick period, the use of the latter habitat and of ricefields was higher in the Axios and the use of freshwater habitat was again higher in the Camargue (Table II).

TABLE II

Habitat use of Little Egrets in the two study areas.
Figures are percentages of average number of birds per habitat.

	Axios	Camargue
Incubation period		
Brackish and saltwater habitats	31.9	32.8
Fresh water habitats	7.2	61.5***
Ricefields	60.9***	5.7
Average total number of birds	138	612
Nestling period		
Brackish and saltwater habitats	44.8***	27.8
Fresh water habitats	13.6	57.0***
Ricefields	41.6***	18.2
Average total number of birds	125	658

*** : P < 0.001, χ^2 tests (on numbers of birds).

BREEDING PARAMETERS

Clutch size

Clutches were significantly greater in the Axios Delta than in the Camargue. The difference was due to higher numbers of large clutches in the Axios Delta (Table III).

Hatching success

The distribution of the number of eggs hatched per nest was similar in the two study areas (χ^2 tests) (Table IV). Three and four eggs per clutch were most commonly hatched.

Brood size

Broods of three chicks were most frequent in the Axios Delta whereas broods of three and four chicks were most commonly observed in the Camargue. As a

TABLE III

Size distribution of clutches in the two study areas.

Clutch Size	Axios	Camargue
2	2	9
3	36	47
4	107	144
5	98	74
6	13	11
Total number of nests	256	285

Jonkheere-Terpstra test standardized JT = – 3.114, $P < 0.01$.

TABLE IV

Percentage distribution of the number of eggs hatched per nest in the two study areas.

Number of eggs hatched per nest	% Number of clutches	
	Axios	Camargue
0	7.8	6.7
1	1.9	2.1
2	8.6	8.5
3	26.6	28.9
4	41.8	44.4
5	12.9	9.2
6	0.4	0.4
Total number of nests	256	284

TABLE V

Distribution of brood sizes at chick age 25 days in the two study areas.

Brood Size	Axios	Camargue
1	10	4
2	46	38
3	89	92
4	63	91
5	6	8
Total number of nests	214	233

Joonkheere-Terpstra test standardized JT = 2.6, $P < 0.01$.

result the brood sizes were significantly greater in the Camargue than in the Axios. The difference is due to a greater number of four-chick broods in the Camargue (Table V).

CHICK DIET

The percentage (in numbers) of the main prey categories differed significantly between the study areas. This difference was due to greater proportions of invertebrates, amphibians and salt and brackish water fish taken by the egrets in the Axios and also to greater proportions of freshwater fish taken in the Camargue (Table VI).

TABLE VI

Main prey categories of Little Egrets in the study areas.

Prey	Axios	Camargue
Percentages (in numbers)		
Difference between Greece and France : Kappa statistic, K = 0.122, P < 0.001.		
Invertebrates	42.6	31.2
Amphibians	19.2	6.3
Freshwater fish	6.2	57.9
Brackish & Salt Water fish	32.0	4.6
Total number of items	2 595	18 707
Biomass (% dry weight) :		
Difference between Greece and France : Kappa statistic, K = 0.0034, P = 0.002.		
Invertebrates	17.9	43.1
Amphibians	28.3	32.9
Freshwater fish	19.8	14.8
Brackish & Salt Water fish	34.0	9.2
Total weight (g)	505.7	2 702.6

Dry mass of prey categories (all the data combined) was also significantly different between the areas. This difference was mainly due to higher proportions of invertebrates and to lesser extent of amphibian prey-mass in the Camargue and higher proportions of salt and brackish water fish prey-mass in the Axios Delta (Table VI). Although invertebrates were less represented by numbers in the Camargue than in the Axios, they contributed more to the mass taken in the former than in the latter. Despite the fact that the diet of Egrets in the Camargue was dominated by freshwater fish, the dry mass corresponding to this category was similar in both areas suggesting that in the Axios Delta freshwater fish preyed upon had a greater size on average. Proportions of salt and brackish water fish were significantly higher in the Axios Delta both numerically and by mass.

BODY CONDITION OF CHICKS

The relationship between tarsus and weight for all the chicks measured is given by the regressions :

Camargue : Weight = 7.164 (tarsus)-102.043 (R^2 = 0.875, N = 1 199).
Axios : Weight = 6.071 (tarsus)-80.324 (R^2 = 0.956, N = 600).

Comparison of these regressions revealed a significantly higher slope in the Camargue (F = 10.812, P = 0.001) (Fig. 1). The relationship between tarsus (for tarsus > 50 mm, representing large chicks during their main growth period) and weight is given by the regressions :

Camargue : Weight = 6.335 (tarsus)-47.676 (R^2 = 0.666, N = 460).
Axios : Weight = 5.634 (tarsus)-53.943 (R^2 = 0.749, N = 187).

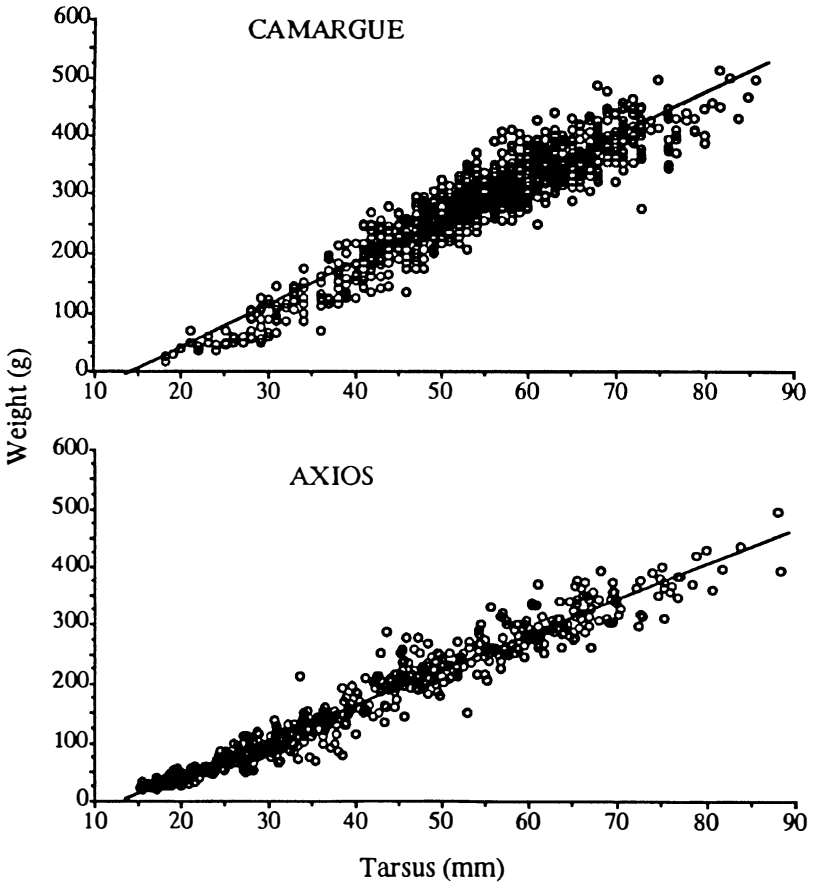

Figure 1. — Relationship between tarsus length and weight of Little Egret chicks in the two study areas.

The slopes of these regressions are similar ($F = 0.321$, NS) but the analysis of covariance revealed a significantly higher intercept in the Camargue (ANCOVA, $F = 381.369$, $P < 0.001$, Fig. 2).

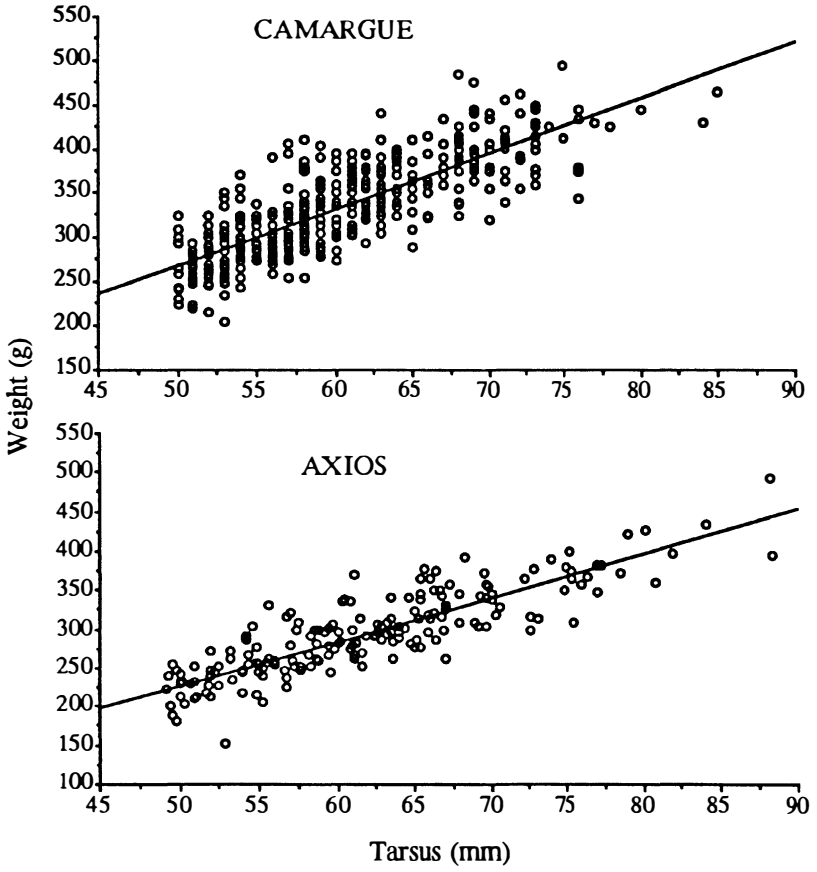

Figure 2. — Relationship between tarsus length and weight during the main growth period of Little Egret chicks in the two study areas.

The mean body condition index was higher in the Camargue (1.038 ± 0.096 (SD), $N = 460$) than that in the Axios (0.999 ± 0.096, $N = 187$) ($t = 4.61_{645}$, $P < 0.001$). This difference concerns only a relatively short period during the peak development of chicks (at age 14 days) (Fig. 3).

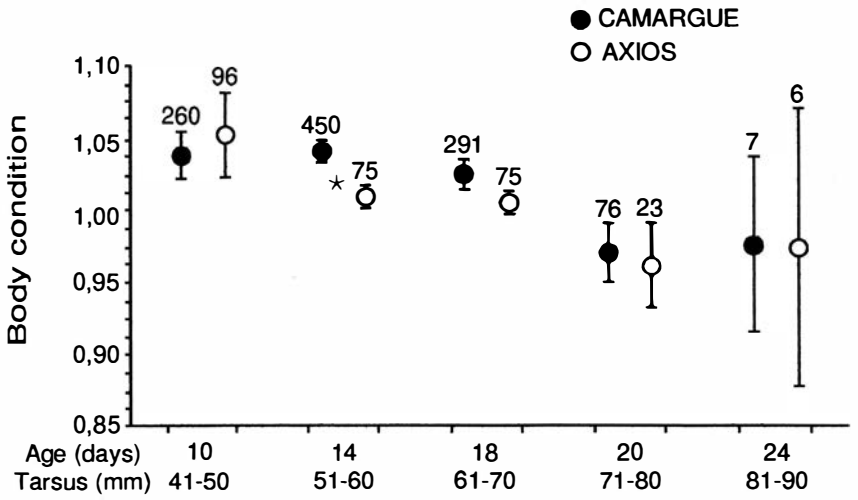

Figure 3. — Comparison of the mean body condition of Little Egret chicks in the two study areas. Vertical lines indicate 95 % confidence intervals and numbers above the means are samples sizes. An asterisk indicates a significant difference between adjacent dots.

DISCUSSION

Although the extent of each type of foraging habitat in the Camargue is similar, by far the highest proportion of Little Egrets was observed in the freshwater habitats both during incubation and chick raising. This preference for freshwater habitat in the Camargue, particularly marshes, has been emphasized in former studies (Hafner, 1977 ; Hafner *et al.,* 1986 ; Kersten *et al.,* 1992 ; Hafner *et al.,* 1993 ; Hafner & Fasola, 1992). In contrast, in the Axios Delta, the use of natural freshwater habitat was limited but ricefields and brackish and saltwater lagoons were heavily exploited both during incubation and chick raising. This difference in habitat use is reflected by the chick diet : freshwater fish (by number), predominated largely in the diet of the egrets in the Camargue chicks. In the Axios, invertebrates and amphibians were primarily taken in the ricefields where fish were never found (Kazantzidis, unpubl.). Proportionately more invertebrates and amphibians were present in the chick diet of egrets in the Axios but their mass was inferior to that in the Camargue. These differences are attribuable to the size and type of prey taken in each area : in the Camargue, adult frogs rather than tadpoles were taken (Hafner, unpubl. data) whereas the inverse took place in the Axios where the chicks received mainly tadpoles (96.3 per cent out of 840 amphibians collected in the regurgitates). The considerable quantities of brackish and saltwater fish in the Axios regurgitates reflects the importance of the *Salicornia* dominated, coastal feeding areas during the chick raising period in Greece.

The difference in clutch size between the study areas was mainly due to a greater proportion of large clutches in the Axios Delta. In the Camargue, the amount of rainfall during January-February preceding the breeding season was found to be positively correlated to the mean clutch size of Little Egrets,

suggesting that rainfall early in the season improves feeding condition (Hafner *et al.,* 1994). In the Axios Delta Little Egrets feed mainly during the pre-breeding season in the brackish and saltwater coastal areas, with water levels being less dependent on rainfall (Kazantsidis & Goutner, 1996). There, the accumulation of energetic reserves for egg production may therefore depend less on rainfall than in the Camargue. Production of larger clutches in birds is related to adequate feeding conditions at the onset of breeding which improve the condition of the females (Drent & Daan, 1980 ; Martin, 1987 ; Bolton, 1990). In the Camargue a considerable proportion of the birds present in summer overwinters on or near the area (Pineau, 1992 ; Hafner *et al.,* 1994) avoiding the stress of migration. Thus, it is possible that after a mild and wet winter (case of the study years) these adults are able to build up a good body condition for breeding. In contrast winter conditions are generally harsh in the Axios and the birds breeding there are migrants which arrive mainly at the end of March (Kazantzidis & Goutner, 1996). As there is evidence that herons reduce clutch size when food is scarce (Lack, 1947 ; Powell, 1983 ; Powell & Powell, 1986), a considerably higher proportion of five-egg clutches in the Axios suggests that food is not a limiting factor there at the onset of breeding. On the other hand, variation in clutch size in the Camargue in certain years (1982-1989, Hafner, unpubl. data) suggests variation in feeding conditions during the pre-nesting season. During the study years analysed here, Camargue Little Egrets, in spite of lower clutches than in the Axios, were able to « catch up » and produce larger broods with chicks of better body condition than the Axios birds. Camargue birds perhaps lay clutches of fewer eggs but of higher quality (Martin, 1987) but another more likely mechanism is that with rising temperatures in May and June numbers of prey such as coleoptera larvae and fish develop fast in the numerous freshwater marshes. This is certainly true for the Mosquitofish from the second half of June onwards (Reeders, 1983 ; Crivelli, unpubl. data), when normally the demand for food by the broods is highest. This is also the period when Camargue chicks were found to be fatter than in the Axios where freshwater marshes are rare and the overall feeding area more uniform than the complex mosaic of habitats available in the Camargue. The differences revealed by this study in clutch size, brood size and chick condition between the two wetlands are presumably related to local ecological conditions, in particular the trophic situation. Nevertheless, although significant, the difference in mean brood size was only slight and the overall chick production in the Axios for a given colony size is similar to chick production elsewhere in the Mediterranean (see data in Prosper & Hafner, 1996). Little Egrets are typically opportunistic foragers, responding flexibly to changes in food resources in time and space (Hafner & Britton, 1983 ; Dugan *et al.,* 1986 ; Kersten *et al.,* 1992 ; Hafner *et al.,* 1993). They adapt well to different habitat types.

In future the carrying capacity of the Axios Delta will depend largely on the management of the ricefields and on the conservation of the coastal, brackish and saltwater area. Further encroachment on the latter habitat by human pressure, in form of reclamation and increasing pollution, could seriously affect the local breeding population. Regarding the ricefields, the present situation provides clear evidence of their importance as a wetland habitat for the Little Egrets. However, any reduction in the surface area of these fields, or modification in their management could have detrimental effects on the nesting Little Egrets. The importance of ricefields to nesting Little Egrets in the Axios is such that they should be considered an important wetland habitat and consequently deserve

environmentally sensitive management. Thus in the Axios Delta, the future of the Little Egret population depends on the conservation of the last remaining natural parts of this wetland on the one hand, and on future agricultural policy on the other hand.

The Camargue still offers extensive areas of natural and semi-natural foraging habitats which are heavily used by the Little Egrets. In contrast, a considerable decline in the use of ricefields has taken place since the mid-eighties. The reason for this development is not clear. At least during the mid-eighties it might have been due to increased use of pesticides (Hafner *et al.,* 1986). However, irrigation practices in the Rhône delta have changed in recent years in order to reduce the cost of irrigation. As a result, with less inflow and outflow of water, oxygenation of the fields is reduced and this no doubt affects prey populations as well (Crivelli, pers. comm.). The monitoring programme on Camargue Little Egrets which is carried out annually since 1967 will be continued. It provides invaluable information on ecosystem conditions and changes and their influence on this bird population.

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SUMMARY

Data on the breeding biology of Little Egrets (*Egretta garzetta*) are compared between two internationally important Mediterranean wetlands for waterbirds : the Camargue in southern France and the Axios Delta, Macedonia, Greece. During the incubation and chick-rearing periods, Camargue Little Egrets fed mainly in freswhater marshes and secondarily in brackish and saltwater lagoons. In the Axios Delta, ricefields were particularly important, followed by brackish and saltwater habitat. These differences in feeding habitat use are reflected in chicks diet. Freshwater fish predominated (by number) in the Camargue while Axios chicks regurgitated mostly invertebrates and tadpoles from ricefields and saltwater fish. Clutches in the Axios were significantly greater than in the Camargue. This may be attributable to favourable feeding conditions offered by the coastal saltmarshes. These are heavily exploited during the pre-breeding season, before the ricefields become available. Brood sizes were significantly greater in the Camargue than in the Axios due to a greater proportion of four-chick broods. Furthermore, Camargue chicks at age 14 days, when the demand of food is highest, were fatter than the Axios chicks of the same age. Thus, after having laid fewer eggs than the egrets in the Axios, the Camargue birds were finally able to produce more young

and in better condition during a crucial moment of the breeding season. These differences in breeding success are related to conditions for feeding which, during the chick period, are very favourable in the Camargue. In the Axios it is essential that ricefields be part of future wetland conservation programmes.

RÉSUMÉ

Des données sur la biologie de reproduction de l'Aigrette garzette (*Egretta garzetta*) sont comparées entre deux zones humides méditerranéennes d'importance internationale pour les oiseaux d'eau : la Camargue en France et le delta de l'Axios en Grèce. Pendant l'incubation et l'élevage des poussins, les aigrettes de Camargue s'alimentent principalement dans les marais d'eau douce et, dans une moindre mesure, dans les lagunes d'eau saumâtre et salée. Dans l'Axios, les rizières constituent des lieux d'alimentation particulièrement importants, les milieux d'eau saumâtre et salée se plaçant en deuxième position. Les différences dans l'exploitation des divers types de milieux d'alimentation apparaissent dans le régime des poussins. En Camargue, les poissons d'eau douce constituent l'essentiel (en nombre) de leur alimentation alors qu'en Grèce, le régime est surtout composé d'invertébrés et de tétards provenant des rizières ainsi que de poissons d'eau salée. La taille des pontes est significativement plus élevée dans l'Axios qu'en Camargue. Ce résultat pourrait refléter une situation trophique favorable offerte par les marais salants côtiers de l'Axios, principaux milieux exploités par les aigrettes pendant la saison pré-nuptiale, avant la mise en eau des rizières. En Camargue, les nichées sont significativement plus élevées que dans l'Axios, une proportion plus élevée de nichées de quatre poussins ayant été enregistrée en France. De plus, à l'époque où les poussins ont besoin d'un maximum de nourriture pour survivre, vers deux semaines, ceux de Camargue sont en meilleure condition que ceux de Grèce. Par conséquent, à partir d'une ponte moins élevée que celle enregistrée dans l'Axios, les aigrettes de Camargue élèvent plus de jeunes qui sont en meilleure condition à l'époque cruciale de l'élevage. Ces différences dans le succès de la reproduction sont liées à une situation trophique très favorable en Camargue en période d'élevage. Dans l'Axios, il est essentiel que les rizières soient intégrées dans les programmes futurs de conservation de cette importante zone humide.

REFERENCES

ATHANASIOU, H. (1990). — *Wetland habitat loss in Thessaloniki plain, Greece.* MSc Dissertation, University College London, London, 90 pp.

BOLTON, M. (1990). — Experimental evidence for food limits on egg production in Lesser Black-backed Gulls *Larus fuscus. Acta XX Congressus Internationalis Ornithologici* (Supplement) : 349.

CRAMP, S. & SIMMONS, K.E.L. (1984). — *Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic.* Vol. I. Oxford University Press, Oxford.

DRENT, R.H. & DAAN, S. (1980). — The prudent parent : energetic adjustments in avian breeding. *Ardea,* 68 : 225-252.

DUGAN, P., HAFNER, H., BOY, V. (1986). — Habitat switches and foraging success in the Little Egret (*Egretta garzetta*). *In* Ouellet, H. (ed.). *Proceedings 19th International Ornithological Congress,* 2 : 1869-1877.

FASOLA, M. (1986). — Resource use in agricultural and non-agricultural habitats in Italy. *Colonial Waterbirds,* 9 : 139-148.
FASOLA, M. (1994). — Opportunistic use of foraging resources by heron communities in southern Europe. *Ecography,* 17 : 113-123.
FASOLA, M. & BARBIERI, F. (1978). — Factors affecting the distribution of heronries in Northern Italy. *Ibis,* 120 : 337-340.
FASOLA, M. & ALIERI, R. (1992). — Conservation of heronry sites in North Italian agricultural landscapes. *Biol. Conserv.,* 62 : 219-228.
FERNANDEZ-CRUZ, M. (1975). — Revisión de las actuales colonias de Ardeidas de España. *Ardeola,* 21 : 65-126.
FERNANDEZ-CRUZ, M., FERNANDEZ-ALCAZAR, G., CAMPOS, F. & DIAS, P.-C. (1992). — Colonies of Ardeids in Spain and Portugal, p. 76-78. *In* Finlayson, C.M., Hollis, G.E. & Davis, T.J. (eds.). *Managing Mediterranean Wetlands and their birds.* IWRB Special Publication No 20.
HAFNER, H. (1977). — *Contribution à l'étude écologique de quatre espèces de hérons* (Egretta g. garzetta *L.,* Ardeola r. ralloides *Scop.,* Ardeola i. ibis *L.,* Nycticorax n. nycticorax *L.*). Unpublished Thesis. Toulouse, France : University of Toulouse, 183 pp.
HAFNER, H. (1978). — Le succès de reproduction de quatre espèces d'Ardeidés *Egretta g. garzetta* L., *Ardeola r. ralloides* Scop., *Ardeola i. ibis* L., *Nycticorax n. nycticorax* L., en Camargue. *Rev. Ecol. (Terre Vie),* 32 : 279-289.
HAFNER, H., BOY, V. & GORY, G. (1982). — Feeding methods, flock size and feeding success in the Little Egret *Egretta garzetta* and the Squacco Heron *Ardeola ralloides* in Camargue, Southern France. *Ardea,* 70 : 45-54.
HAFNER, H. & BRITTON, R.H. (1983). — Changes of foraging sites by nesting Little Egrets (*Egretta garzetta* L.) in relation to food supply. *Colonial Waterbirds,* 6 : 24-30.
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 : 126-127.
HAFNER, H., DUGAN, P.J. & BOY, V. (1987). — *Herons and wetlands in the Mediterranean : Development of indices for quality assessment and management of Meditterranean wetland ecosystems.* Final report to the IIIrd Environment Research Programme of the Commission of the European communities, 46 pp.
HAFNER, H. & FASOLA, M. (1992). — The relationship between feeding habitat and colonially nesting Ardeidae, p. 194-201. *In* Finlayson, C.M., Hollis, G.E. and Davis, T.J. (eds). *Managing Mediterranean Wetlands and their birds.* IWRB Special Publication No 20.
HAFNER, H., DUGAN, P.J., KERSTEN, M., PINEAU, O. & WALLACE, J.P. (1993). — Flock feeding and food intake in Little Egrets *Egretta garzetta* and their effects on food provisioning and reproductive success. *Ibis,* 135 : 25-32.
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. *Rev. Ecol. (Terre Vie),* 49 : 53-62.
KAZANTZIDIS, S. & GOUTNER, V. (1996). — Feeding ecology and conservation of feeding habitats of Little Egrets (*Egretta garzetta*) in the Axios Delta, Macedonia, Greece. *Colonial Waterbirds* 19 (special publication 1) : 115-121.
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. *J. Anim. Ecol.,* 60 : 241-252.
KJELSON, A.M., TURNER, R.W. & JOHNSON, N.G. (1975). — Description of a stationary drop net for estimating nekton abundance in shallow waters. *Trans. Amer. Fish. Soc.,* 104 : 46-49.
KUSHLAN, A.J. (1974). — Quantitative sampling of fish populations in shallow, fresh water environments. *Trans. Amer. Fish. Soc.,* 348-352.
LACK, D. (1947). — The significance of clutch size. *Ibis,* 89 : 302-352.
MARTIN, T.E. (1987). — Food as a limit on breeding birds : a life history perspective. *Ann. Rev. Ecol. Syst.,* 18 : 453-487.
MIKUSCA, T. (1992). — The population of nesting herons in Croatia, p. 68-69. *In* Finlayson, C.M., Hollis, G.E. and Davis, T.J. (eds). *Managing Mediterranean Wetlands and their birds.* IWRB Special Publication No 20.
PINEAU, O. (1992). — Key wetlands for the conservation of Little Egrets breeding in the Camargue, p. 210-214. *In* Finlayson, C.M., Hollis, G.E. and Davis, T.J. (eds). *Managing Mediterranean Wetlands and their birds.* IWRB Special Publication No 20.
POWELL, G.V.N. (1983). — Food availability and reproduction by Great White Blue Herons, *Ardea herodias :* a food addition study. *Colonial Waterbirds,* 6 : 139-147.
POWELL, G.V.N. & POWELL, A.H. (1986). — Reproduction by Great White Herons (*Ardea herodias*) in Florida Bay as an indicator of habitat quality. *Biological Conservation,* 36 : 101-113.

PROSPER, J. & Hafner, H. (1996). — Breeding aspects of the colonial Ardeidae in the Albufera de Valencia : Population changes, phenology and reproductive success of the three most abundant species. *Colonial Waterbirds* 19 (special publication 1) : 98-107.

REEDERS, H.H. (1983). — *Spatial and temporal distribution of prey species of the Little Egret* (Egretta garzetta) *in a French Mediterranean wetland.* Nature Conservation Department report number 710, Agricultural University Wageningen, The Netherlands. 64 pp.

SIEGEL, S. & CASTELLAN, N.J. (1988). — *Nonparametric statistics for the behavioral sciences.* McGraw-Hill Book Company, New York.

TSACHALIDIS, P. (1990). — *Biology and behavioral ecology of the Little Egret.* Unpublished thesis, University of Thessaloniki, Greece.

VOISIN, C. (1978). — Utilisation des zones humides du delta rhôdanien par les Ardéidés. *L'Oiseau et R.F.O.,* 48 : 217-261, 239-380.

VOISIN, C. (1979). — Les populations d'Ardéidés arboricoles dans le delta du Rhône de 1968 à 1977 : Evolution des effectifs et période de reproduction. *Alauda,* 47 : 151-156.

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. & A.D. Poyser Ltd., London.