

DO BREEDING SITE CHARACTERISTICS INFLUENCE BREEDING PERFORMANCE OF THE PURPLE HERON *ARDEA PURPUREA* IN THE CAMARGUE?

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RÉSUMÉ

La biologie de la reproduction du Héron pourpré, *Ardea purpurea*, a été étudiée en Camargue durant les années 1997-1998. La date de ponte a été significativement différente entre les colonies pour une des deux années alors que la taille de ponte, constamment faible (2.9-3.4), n'a présenté aucune différence ni entre les colonies, ni entre les années. La mortalité des poussins a été similaire entre les colonies sur une même année mais significativement plus élevée en 1997. La taille des nichées, le rang de naissance et la date de ponte ont un effet significatif sur la croissance des poussins. Les analyses de nourriture régurgitée ont révélé une grande variété de proies et de façon surprenante peu de poissons. Les données de baguage ont aussi montré que les jeunes hérons peuvent parfois coloniser des nids voisins pour améliorer leurs conditions. Des études postérieures doivent permettre de préciser les connaissances relatives à l'écologie alimentaire, et de mieux connaître les facteurs qui affectent la disponibilité des sites potentiels de nidification.

SUMMARY

The breeding biology of the Purple Heron, *Ardea purpurea*, was studied in 1997-1998 in the Camargue delta complex in southern France. The mean laying date differed significantly between colonies in only one of the two years while clutch size remained constantly low (2.9-3.4) and showed no significant inter-colony or inter-annual differences. Chick mortality was similar among colonies the same year but was significantly higher in 1997 than in 1998. Brood size, hatching rank order and laying date had a significant effect on chick growth. Analyses of food regurgitated by chicks revealed a large variety of prey categories and surprisingly few fish. Ringing data provided evidence on several occasions that young herons can colonize foreign nests to improve their conditions. Future studies should focus on the feeding ecology and on factors affecting the availability of suitable nest sites.

INTRODUCTION

Between 1970 and 1990 most European breeding colonies of the Purple Heron (*Ardea purpurea*) declined (Mestre & Ferrer, 1974; Kayser *et al.*, 1994; Tucker & Heath, 1994; Hagemeyer & Blair, 1997; Fasola *et al.*, in press). Drought

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in the wintering areas of West Africa has frequently been considered responsible of the population fluctuations of this long-distant migrant (Den Held, 1981; Cavé, 1983). However, it has also been suggested that local breeding conditions in Europe could play a role in the population dynamics of this colonial breeding bird (Kayser *et al.*, 1994; Prosper & Hafner, 1996; Hafner & Fasola, 1997; Deerenberg & Hafner, in press; Fasola *et al.*, in press). For instance, several breeding populations in Europe were stable during the mid-1980s whereas the breeding population of Mediterranean France showed a further decline in the early 1990s (Hafner & Fasola, 1997). Although studies are few, information on clutch size across Europe (Manuel, 1957; Williams, 1959; Ferry & Blondel, 1960; Haverschmidt, 1961; Kral & Figala, 1966; Moser, 1986; Gonzalez-Martin *et al.*, 1992) provides evidence that productivity differs significantly between breeding areas. According to Moser (1986) the Camargue population in the early 1980s had the smallest clutch-size in Europe by almost one egg. Despite high numbers of Purple Herons breeding in the Camargue at that time (i.e. up to 60 % of the total breeding population in France, Hafner *et al.*, 1985), this wetland area produced disproportionately fewer young to the potential breeding population than other areas (Moser, 1986). Assessing the importance of the ecological conditions for the reproduction of the Purple Heron remains difficult mainly because the breeding ecology of this vulnerable species is poorly documented in most areas (Kral & Figala, 1966; Tomlinson, 1975; Moser, 1986; Gonzalez-Martin *et al.*, 1992; Gonzalez-Martin, 1994).

The objective of this study was to assess several aspects of the breeding biology of Purple Herons nesting in a variety of reedbeds of the Camargue. 15 years ago (Moser, 1983, 1984) reedbed characteristics (surface, vegetation structure, water levels and regime) were suggested to be key determinants of colony establishment, size and persistence, but the question of whether or not ecological differences between breeding sites result in a differential breeding success has not been determined. Therefore we attempted to analyse breeding parameters of the Purple Heron in relation to habitat characteristics likely to influence breeding performance.

METHODS

DATA COLLECTION

In order to obtain information on possible variation in breeding success between different parts of the Camargue delta complex (1 600 km²), we studied one colony in the Plan du Bourg to the East of the Rhône, three colonies in the Ile de Camargue, and one colony in the Petite Camargue West of the delta (Fig. 1). In order to locate the colonies over such an extensive area we used a single-engine airplane carrying two observers plus the pilot. Aerial counting techniques were developed in 1979 and used to survey all suitable reedbeds and assess the number of nests along the Mediterranean coast of France. Counting techniques are detailed in Moser (1984), Kayser *et al.* (1994) and Deerenberg & Hafner (in press.). In brief, three or four flights each lasting three to four hours are made each breeding season on dates which coincide with the periods of optimal visibility of Grey and Purple Heron nests respectively. Reedbeds are surveyed from 100-300 meters. On

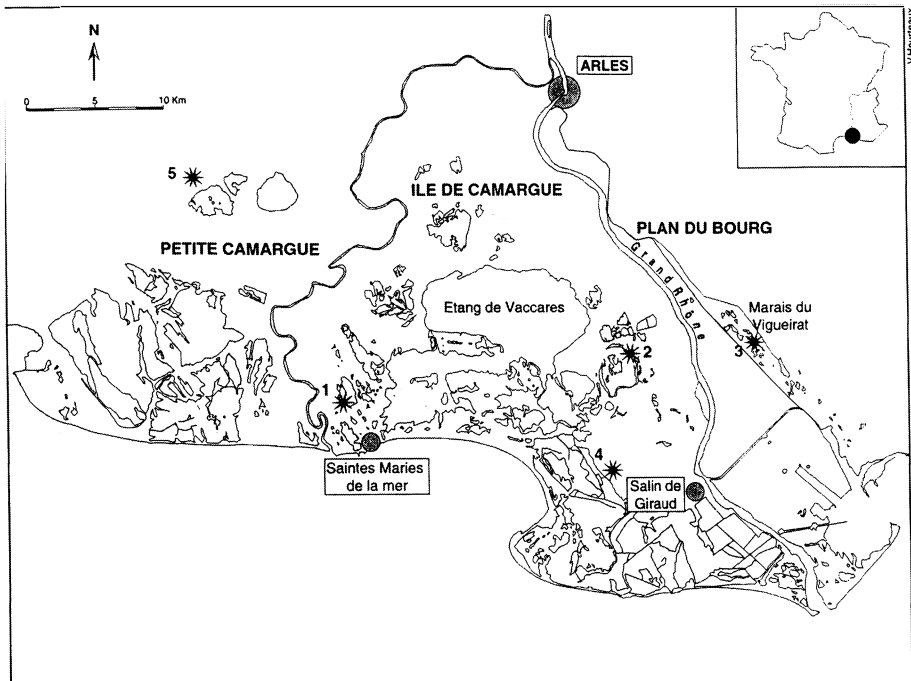


Figure 1. — The study area of the Camargue showing the location within France (inset). Asterisks and numbers mark the location of colonies studied.

locating of a colony, altitude is increased slightly before the aircraft is banked steeply to allow vertical photographs of the nests to be taken. At the end of the season the photos are projected on paper in order to mark and to count each individual nest.

The colonies were visited on the ground and nests were located by walking transects determined from the aerial photographs. The nests were marked with numbered tags (tied to the reed below the nest). In order to avoid excessive disturbance (1) colonies were not visited prior to incubation, (2) colony visits were limited to one hour between 06-09.00^{hrs}. The best method consists of one small group of three to four persons moving slowly and quietly from one nest to another. In such a way, adults attended their nests undisturbed at only few meters distance. Our presence went unnoticed also because of the density of the reeds. Another advantage of this method is that the chicks remain quiet in their nest until their capture. When measuring chicks, noise and rapid movements must be avoided. An experienced team can place the chicks back into the nest and leave with the whole brood remaining in the nest. In very small colonies (< 10 nests) laying may be almost simultaneous by the different pairs while in the larger colonies laying is spread over several weeks. Visiting a colony at the very start of incubation should be avoided since it will almost certainly cause desertion of the site. Our first visits to the individual colonies were made about two weeks after the start of incubation. Due to asynchrony in laying dates, the number of visits per individual nests varied

from three to six. At each visit, nest contents were recorded, the eggs weighed and numbered with a non-toxic marker pen. Whenever possible we noted which chick came from which egg. The entire broods were ringed for individual recognition. At each visit, nestlings were weighed and measured (length of culmen, ala and tarso-metatarsus). Because it was not always possible to relocate a marked nest in the dense reed structure, some nest histories are fragmentary. To obtain information on chick diet we collected the food items regurgitated by chicks in 1998. The prey samples were sorted in 95 % alcohol for examination in the laboratory where the prey were identified and their length measured to the nearest mm. Sizes of fish were measured from the tip of the snout to the fork of the tail. Samples of food items found in the regurgitations were collected from the feeding grounds and the items 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). For large prey such as snakes and fish, dry weights were read from length/dry weight calibrations calculated from samples of prey captured in the field (Moser, 1984).

Water levels in the reedbeds occupied by the nesting herons were measured on a weekly basis. Other physical characteristics (i.e. surface area of reed, distance to surrounding land from which terrestrial predators can penetrate the marsh, and management such as reed cutting) were determined from aerial photographs and from a Landsat-5 TM satellite image taken in July 1995.

DATA ANALYSIS

Given that nests were not visited daily, we could not determine the laying dates exactly. However, this information could be estimated from the age of the oldest chick in the brood based on tarsus length (see Moser, 1984) and knowing that the incubation period lasts about 26 days. For each colony the data were pooled for all the chicks since we were unable to determine their sex. In addition, there was no evidence of bimodality in our measurements.

Given the semi-altricial character of the Purple Heron (i.e. nestlings leave the nests well before fledging to hide from predators), we measured survival only until chicks were 16 days old, the earliest age at which they are able to leave the nest. Estimates of chick survival are therefore minima.

The contribution of different variables to the growth of chicks (bill, wing and weight) was derived by backward and stepwise multiple regression procedure (Draper & Smith, 1981). We studied the following independent variables: age (estimated from tarsus length), laying date, brood size, hatching rank order, colony site and year. At each iteration, the variable showing the lowest partial correlation with the dependent variable was removed from the model if the correlation was not significant. When no variable could be removed from the model, the procedure came to an end. Statistical analyses were performed using Systat 5 version 5.2.1 for the Macintosh (Wilkinson, 1990). Other statistical tests were performed following Sokal & Rohlf (1995) and Siegel & Castellan (1988). All tests were two-tailed. Results were considered significant at the 5 % level.

RESULTS

The results are based on records from 62 nests in three colonies in 1997 and 101 nests in four colonies in 1998. Reedbeds occupied by Purple Herons differ considerably in structure (Table I).

TABLE I

Colony characteristics and breeding parameters of the Purple Heron in 1997 and 1998.

Year	1997			1998			
	1	2	3	2	3	4	5
N° colony							
Surface area of reed (ha)	6	1.5	30	1.5	30	13	70
Water depth (cm)	40	65	55	80	60	10	5
Distance to terrestrial habitat (m)	30	15	220	15	220	25	700
Colony size (pairs)	23	29	45	6	50	20	263
Laying date	129.2 ± 8.1	121.1 ± 6.5	123.5 ± 9.6	123.2 ± 4.5	123.3 ± 10.3	114.7 ± 7.8	121.2 ± 8.7
(n)	20	14	24	6	23	3	45
Clutch size	3.2 ± 0.4	3 ± 0	2.9 ± 1.1	3.2 ± 0.4	3.0 ± 0.8	3.4 ± 0.9	3.2 ± 0.6
(n)	5	1	7	6	26	14	44
Hatching success	100 %	no	91 %	90.5 %	83 %	45.5 %	92.6 %
(n)	16	data	22	21	47	33	135
Brood size	2.7 ± 0.8	2.4 ± 0.5	3.0 ± 0.9	2.8 ± 0.7	2.8 ± 1.2	0.5 ± 1.1	2.9 ± 0.8
(n)	16	13	24	6	26	14	44
Nestling mortality	26.5 %	25 %	25.6 %	6 %	11.6 %	100 %	10.6 %
(n)	49	32	74	17	69	7	141

THE NEST

Data on nest structure could be collected in the two largest colonies studied in 1998. The mean diameter of nests did not differ between these two colonies (mean \pm s.d., S1: 50.1 ± 6.4 , $N = 15$, S2: 50.6 ± 6.4 , $N = 40$, ANOVA, $F_{1,53} = 0.06$, $P > 0.05$). However, there was a significant difference in the mean height of nests between the two colonies (mean \pm s.d., S1: 85.5 ± 13.9 , $N = 15$, S2: 72.3 ± 11.5 , ANOVA, $F_{1,53} = 12.9$, $P < 0.001$). There was no significant relationship between the diameter and the height of nests (Spearman rank order correlation, S1: $r_s = -0.20$, $P = 0.23$; S2: $r_s = -0.03$, $P = 0.41$). In both S1 and S2, there was however a negative and significant relationship between the diameter of the nest and the laying date (Spearman rank order correlation, S1, $r_s = -0.47$, $P = 0.03$, S2, $r_s = -0.37$, $P = 0.01$) indicating that early initiation results in larger nests than late initiation. Although significant only in S2, there was furthermore a positive relationship between laying date and height of the nest in the reed (Spearman rank order correlation, S1, $r_s = 0.32$, $P = 0.12$, S2, $r_s = 0.34$, $P = 0.01$). For both S1 and S2, there was no significant relationship between the clutch or brood size and the diameter of the nest or its height in the reed (Spearman rank order correlation, $P > 0.05$ in all cases).

LAYING DATES

In 1997, the mean laying date differed between colonies (Table I, ANOVA, $F_{2,55} = 4.33$, $P = 0.014$), due to a late start in the smallest colony. There was no significant difference in 1998 (Table I, ANOVA, $F_{3,73} = 0.98$, $P > 0.05$).

CLUTCH SIZE AND EGG WEIGHT

Clutch size varied from two to five eggs in 1997 and from two to eight eggs in 1998, with clutches of three and four eggs accounting for more than 75 % in each of the two years. In 1998, two exceptionally large clutches, of seven and eight eggs in colonies 3 and 5 respectively, were probably due to two females laying in the same nest. There was no significant difference in the mean clutch size between colonies in 1997 (Table I, ANOVA, $F_{2,10} = 0.22$, $P > 0.05$) nor in 1998 (Table I, ANOVA, $F_{3,68} = 0.76$, $P > 0.05$), nor between the two years (mean \pm s.d. 1997: 3.0 ± 0.82 , 1998: 3.2 ± 0.68 , ANOVA, $F_{1,72} = 0.84$, $P > 0.05$). No significant relationship could be detected between clutch size and laying date: 1997 (Spearman rank order correlation, $r_s = -0.14$, $N = 11$, $P > 0.05$), and in 1998 (Spearman rank order correlation, $r_s = -0.04$, $N = 57$, $P > 0.05$).

In clutches for which both egg-weight and order of hatching were known, the lightest egg was not systematically the last to hatch in the brood (Wilcoxon signed rank test, $Z = 0.04$, $P = 0.97$). The mean egg weight among clutches of two eggs (42.7 ± 4.1 , $N = 8$), three eggs (40.5 ± 5.9 , $N = 13$) and four or more eggs (43 ± 5.4 , $N = 5$) was not significantly different (ANOVA, $F_{2,23} = 0.65$, $P > 0.05$).

HATCHING SUCCESS

Hatching success in 1997 could be computed for the colonies 1 and 3 and was not significantly different (Table I, Fisher's exact test $P = 0.50$). Hatching success

in 1998 differed significantly between the four colonies (Table I, Fisher's exact test $P < 0.0001$). However, for the colony 4, we observed predation of all marked nests by Polecats (*Putorius putorius*). When colony 4 was excluded from the comparison, the difference of hatching success between the three other colonies was not significantly different (Fisher's exact test $P = 0.15$). Between the two years, there was no significant difference of hatching success (Fisher's exact test $P = 0.27$).

BROOD SIZE

Mean brood sizes (Table I) between colonies (1997: ANOVA $F_{2,50} = 2.96$, $P > 0.05$; 1998 with colony 4 excluded: ANOVA $F_{2,15} = 0.10$, $P > 0.05$) and between years (colony 4 in 1998 excluded, ANOVA $F_{1,141} = 2.01$, $P > 0.05$) were not significantly different. However, the nestling mortality was significantly higher in 1997 than in 1998 (Table I, colony 1 in 1998 excluded, Fisher's exact test $P < 0.001$). The poor condition of chicks which died in 1997 strongly suggests that food shortage was the cause of their death.

GROWTH RATE

As expected, the age of chicks was the main predictor of the body weight, the bill- and wing-length (Table II). However, growth differed according to the hatching rank order of chicks (Table II). Within a same nest, early hatched chicks had a higher growth than late-hatched chicks (Fig. 2). Among the other explicative variables, a positive effect of brood size and laying date on growth was observed while colony site and year had no significant influence.

NESTLING DIET

In Table III we have grouped the regurgitates collected by Moser (1984) and during the present study to give a broad picture of chick diet. The percentage

TABLE II

Summary statistics of multiple regression analysis (Stepwise procedure, weight, bill and wing as dependent variable successively). Forward and backward multiple regressions yielded similar results. Interactions terms were not significant.

	Weight			Bill			Wing		
	SC	F	P	SC	F	P	SC	F	P
Year	0.036	3.731	0.054	0.009	0.406	0.524	0.013	1.404	0.236
Locality	—	2.435	0.046	—	1.025	0.393	—	2.077	0.082
Brood	0.086	34	< 0.0001	0.066	32	< 0.0001	0.008	0.940	0.333
Rank	—	25	< 0.0001	—	11	< 0.0001	—	8.967	< 0.0001
Laying date	0.035	5.207	0.023	0.035	8.646	0.0034	0.037	17	< 0.0001
Age	0.925	3 900	< 0.0001	0.985	7 000	< 0.0001	0.999	13 000	< 0.0001

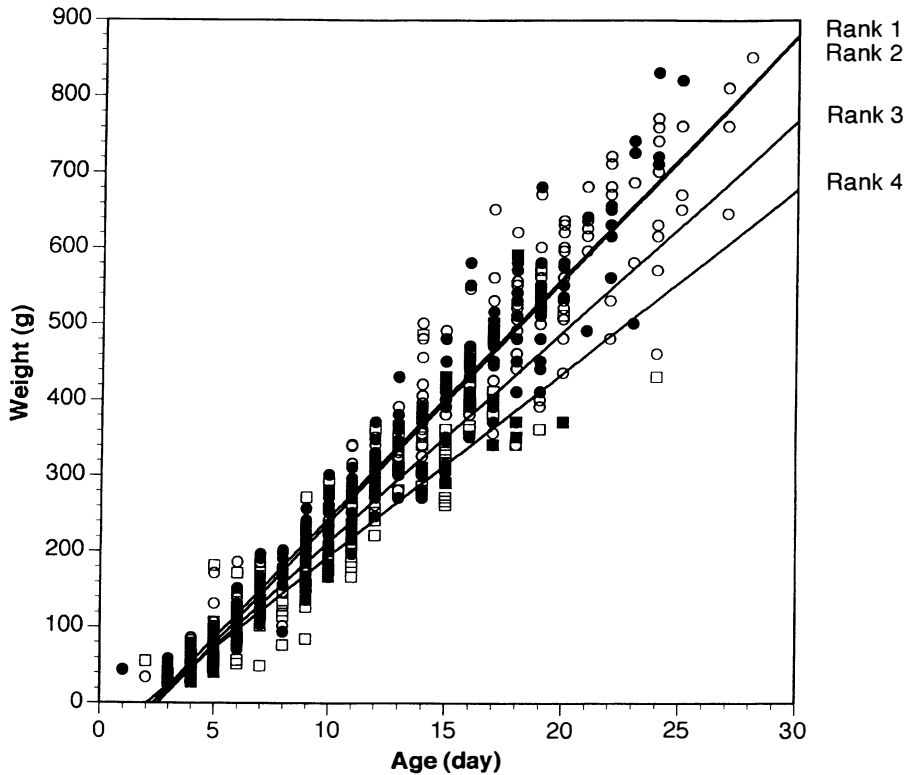


Figure 2. — Growth rate evolution of Purple Heron chicks (weight) through time according to their hatching rank order.

(Kolmogorov-Smirnov two-sample test, $D = 0.4$, $P < 0.01$) and dry mass (Kolmogorov-Smirnov two-sample test, $D = 0.3$, $P < 0.01$) of prey categories differed significantly between the two periods. This difference was due to higher proportions of invertebrates, particularly coleoptera larvae, in 1998 and higher proportions of fish in 1979-1980.

BROOD PARASITISM

On three occasions, metal and colour ringed chicks aged about 20 days were found in nests belonging to neighbours of their true parents. A rank 3 chick in the brood hierarchy in its nest of birth (according to its tarsus length) was upgraded to rank 2 in the foreign nest. The two other birds had rank 1 in their own nest and conserved this position in the foreign nest where, however, they enjoyed a greater size advantage.

DISCUSSION

Relationships between breeding parameters and the distribution pattern of Purple Heron colonies of the Camargue have not previously been investigated.

TABLE III

Main prey categories of Purple Herons in 1980-1982 (N = 1 720 preys, Moser, 1984) and at present (N = 145 preys).

Prey	% items		% by dry weight	
	Moser, 1984	Present	Moser, 1984	Present
Freshwater fish	61.7 %	26.9 %	85.4 %	61.3 %
Reptiles and amphibians	11.0 %	9.7 %	11.1 %	6.7 %
Birds and mammals	1.0 %	—	0.4 %	—
Crustacea	4.3 %	1.4 %	0.1 %	0.4 %
Orthoptera	2.6 %	8.3 %	0.9 %	8.0 %
Coleoptera larvae	12.8 %	46.9 %	1.9 %	21.7 %
Other invertebrates	6.6 %	6.8 %	0.2 %	1.9 %

LAYING DATES

In 1997 we found a significant difference in the mean laying date between the three colonies studied. This phenomenon could indicate that habitats are heterogeneous in quality and that better sites tend to be occupied before sites of low quality. We cannot exclude this hypothesis since the latest laying dates occurred in the smallest colony.

NEST LOCATION AND PREDATION

We found a negative and significant relationship between the diameter of the nest and the laying date. This could be expected since adults supply nesting material throughout the incubation and chick raising period (Hafner, unpubl. data). In the colony with the lowest water level, there was also a significant tendency with time to build the nests higher and higher in the reed. With decreasing water levels the risk of predation by mammals increases and Purple Herons may well adjust the height of their nest to the threat of predation during laying and incubation. By constructing their nests at a certain height, however, they are probably more exposed to avian predation. Alternatively, the tendency observed could also result from a compromise for late breeders between limiting the risk of predation by avian predators and limiting the risk of being predated by terrestrial predators.

For only one colony in 1998, we observed a major nest predation by Polecats on eggs and chicks in all the marked nests. The low water level in this colony and its proximity to terrestrial habitat probably favoured the access to the nests by this predator (Table I, Colony 4). Other colonies with low water levels were far from land and therefore much better protected against predators such as Polecat, Fox (*Vulpes vulpes*) and Boar (*Sus scrofa*). Colony 5 is a good example (Table I). Losses of eggs and nestlings in the Camargue colonies due to predation seem to be negligible providing that the nest site is well flooded or, in absence of high

water level, far from terrestrial habitat. If these ecological requirements are not met, a colony may be totally destroyed as was the case with colony 4 and as previously seconded by Hafner (1970).

CLUTCH SIZE

In agreements with Moser's observations (1986), we found that low productivity in the Camargue colonies resulted from a reduced clutch size rather than high chick mortality. Thus, 15 years after his study, mean clutch size of the Purple Heron in the Camargue has remained unchanged. Energetic constraints on egg production could explain this phenomenon (i.e. Martin, 1987; Monaghan & Nager, 1997). However, no information is available on female conditions nor on the trophic potential of the Camargue on arrival of the herons in spring. In general, the reproductive rate of birds is broadly determined by the productivity of the ecosystem in which they live (Ricklefs, 1980). Therefore, the reduced clutch size could illustrate an adaptive adjustment to the local conditions of the Camargue. Purple Herons could for instance predict from conditions at the time of arrival on the breeding grounds the conditions which are likely to occur during the nestling phase and then lay the appropriate number of eggs.

GROWTH RATE

The similarity in chick growth patterns between colonies suggests that conditions on a colony scale are of minor importance. The positive effect of brood size on chick growth is a priori a surprising result since we would expect chicks to experience a more severe food shortage in large broods rather than small ones. However, a positive correlation may exist between clutch size (and subsequent brood size) and parental quality. If this is true, brood size and growth of chicks may well be positively correlated. Information on adult conditions and/or age would be important to address this point. We also found a strong effect of the hatching rank order on chick growth. Because of the staggered age of the chicks (and consequently their size) due to asynchronous hatching, competitive asymmetries exist among siblings of Purple Herons. As in most altricial and semi-altricial bird species, the smallest chicks are often reported to suffer from food shortage (e.g. Inoue, 1985; Mock & Parker, 1986; Stenning, 1996). This phenomenon appears likely to explain growth difference between chicks according to their rank (e.g. Fujioka, 1984; Mock, 1985).

BROOD PARASITISM

On three occasions, the marking scheme provided evidence that young Purple Herons can leave their nest and occupy, at least temporally, neighbouring nests. This phenomenon may simply result from young herons committing mistakes when attempting to return to their own nests. Alternatively, we would a priori expect natural selection to favour individual chicks which are disadvantaged in their nest to move to a neighbouring brood in order to improve their chances of growth and survival (e.g. Morris *et al.*, 1991; Avital *et al.*, 1998; Saino *et al.*, 1994). Late-hatched and therefore small individuals usually obtain less food than

their siblings. By moving to other nests as soon as possible, late-hatched chicks could improve their rank position in the brood hierarchy and would then obtain more food.

Knowing that food shortage was an important cause of mortality among rank 3 and 4 chicks (especially in 1997), we cannot reject this hypothesis.

This aspect deserves further study. It requires a different approach (i.e. a behavioural study during the nestling period).

NESTLING DIET

The diet of Purple Heron chicks is usually characterized by a high proportion of fish (Moser, 1984, Rodriguez & Canavate, 1985, Gonzalez-Martin *et al.*, 1992, Gonzalez-Martin, 1994, Fasola *et al.*, 1993, Campos & Lekuona, 1997). The small amount of fish and the large quantities of invertebrates regurgitated by Camargue chicks in 1998 may indicate scarcity of fish (possibly resulting into poor feeding conditions). This aspect merits further investigation. We are presently planning to complete future studies of chick diet and condition by experimental work involving supplementary food provisioning to sample broods.

CONCLUSION

These results first confirm the work by Moser 15 years earlier that the clutch size of the Purple Heron in the Camargue remains the smallest in Europe. The higher mortality observed for rank 3 and rank 4 chicks suggests that the Camargue offers relatively poor conditions for rearing nestlings. Knowing that the colony location has a negligible influence on these processes (this study), factors regulating the reproductive success of Purple Herons in the Camargue are probably of general nature affecting the whole Camargue.

Future studies will focus on the feeding ecology of this species in the Camargue and on factors affecting the availability of suitable breeding sites.

In the Camargue, Purple Herons nest only in mature Phragmites stands that must be inundated throughout the breeding season. Management of these marshes which represent some 40 potential breeding sites is totally unpredictable. Most of them are on private properties and used for hunting of waterfowl. Therefore, in addition to the study of food and feeding habitat, the physical characteristics of the nest sites and surrounding feeding areas will be investigated from March to July.

This implies measures of water levels, extent of flooded areas and reed structure (effects of reed-cutting, grazing, and management practices). Long-term data collected for all the 40 potential breeding sites in the area will further our understanding on local factors affecting the distribution of nesting Purple Herons.

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