# BREEDING PARAMETERS, FEEDING HABITS AND NESTLING GROWTH IN A RECOVERING POPULATION OF PURPLE HERONS FROM THE EBRO DELTA, SPAIN

## M. GONZÁLEZ-MARTÍN, X. RUIZ & G. A. LLORENTE

González-Martín, M., Ruiz, X. & Llorente, G. A., 1992. Breeding parameters, feeding habits and nestling growth in a recovering population of Purple Herons from the Ebro Delta, Spain. *Misc. Zool.*, 16: 147-160.

Breeding parameters, feeding habits and nestling growth in a recovering population of Purple Herons from the Ebro Delta, Spain.— In this paper the first data on breeding biology and ecology for Purple Herons nesting in the Iberian peninsula are presented. Such data are used to test the prevailing ecological conditions in the Ebro Delta for the recovery of a population of Ardea purpurea which has suffered dramatic changes in size, falling from more than 1000 pairs in the 1960's to 60 pairs at the beginning of 1970's. In the Ebro Delta Purple Herons feed mainly on cyprinid fish. The existence of a latitudinal cline in mean clutch size variation is confirmed and used to test whether Camargue breeders are less productive than expected. The mortality rates (during the incubation and nestling periods, for nests, eggs and chicks) are similar to, or significantly lower, than those obtained for the Camargue in all cases. The overall growth rate of body mass is the same for the Ebro Delta nestlings and for nestlings reared in captivity in "ad libitum" food conditions, indicating that the ecological conditions were good in 1983 for the recovery of the species.

Key words: Breeding, Food, Growth, Conservation, Ardea purpurea, Ebro Delta.

(Rebut 20 II 92; Acceptació condicional: 22 IX 92; Acc. definitiva: 27 X 92)

M. González-Martín, X. Ruiz & G. A. Llorente, Dept. de Biologia Animal (Vertebrats), Fac. de Biologia, Univ. de Barcelona, Avgda. Diagonal 645, 08028 Barcelona, Espanya (Spain).

The final development of this paper was funded by a DGICYT research grant (PB86-0171) from the Spanish Government.

## INTRODUCTION

Although Purple Herons are among the most conspicuous species breeding in the Western Palearctic and in spite of the existence of a number of papers dealing with clutch size or other punctual data, their breeding biology and ecology as a global trait remained relatively unknown until the studies of KRAL & FIGALA (1966) in Hungary and MOSER (1986) in the Camargue. An analysis of breeding parameters, feeding habits and growth of nestlings is presented for a population of nesting Purple Herons Ardea purpurea in the Ebro Delta (Northeast Spain). Thus, giving the first data concerning several aspects of the breeding biology of this species in the Iberian peninsula. Also, the growth curves of other structures than body mass are first time described for this species.

The studied population size has experienced dramatic changes: during the 1960s more than 1000 pairs nested in the Ebro Delta (MALUQUER, 1971), by the early 1970s the

population fell to only 60 + pairs (MESTRE & FERRER, 1974), though from the late 1970s to the present (1991) it has gradually recovered to reach ca. 400 pairs (MARTÍNEZ-VILALTA, 1990). Our analysis aim to assess the suitability of the ecosystem for the recovery of this species and so could be of great interest for conservation policies.

The existence of a latitudinal cline in mean clutch-size values for this species is examined and, as suggested by MOSER (1986), the question of whether Camargue breeders are less productive than expected is investigated using regression analysis. Finally, this study provides data on Purple Herons' reproductive fitness, the need for which has also been stressed by MOSER (1986).

## STUDY AREA AND METHODS

Data were recorded on two heronries in the Ebro Delta during the breeding season of 1983. Colony 1 was located at the Encanyissada Lagoon and Colony 2 in Buda Island (fig. 1). Both colonies were in reedbeds Phragmites australis. The Ebro Delta is an alluvial plain of 250 km<sup>2</sup>, situated in the south of the Tarragona province (Spain) between 40° 37'- 40° 48'N and 0° 21'- 0° 60'E. Approximately 75% of the Delta surface area is covered by farmland, and in the remaining 25% there are littoral lagoons surrounded by reed beds (10%), sandy ground (9%) and salt marshes (6%). The main crop of the Delta (nearly 40% of the total surface area) is rice, and its farming cycle marks the production rhythm of the ecosystem (Ruiz, 1985; FERRER & MARTÍNEZ-VILALTA, 1986).

Colony 1 held 23 pairs of Purple Heron and two pairs of Black-Crowned Night Heron *Nycticorax nycticorax* in 1983. All nest platforms were constructed with reed where the vegetation was taller. Colony 2 comprised four species of Ardeidae: Purple Heron (at least 50 pairs), Cattle Egret *Bubulcus ibis*, Squacco Heron *Ardeola ralloides* and Little Egret *Egretta garzetta*. Purple Heron nests were longer and in taller vegetation than those of the other species.

During the study the Purple Heron population of the Ebro Delta was just initiating a weak recovery (150 pairs in 1983). So, we were cautious not to create detrimental disturbance, therefore we selected a small independent colony and avoided regular visits until the presence of the first hatchlings, which can be heard from the distance. In such a way the heronry was externally monitored during April and May. This is the reason why phenology data were estimated by backcalculation using literature and our own data (i.e. laying date of an egg is estimated assuming that the incubation period is about 26 days on average (CRAMP & SIMMONS, 1977) and the laying period assuming that laying interval is similar to the hatching interval). Data corresponding to egg-size, clutch-size, brood-size, growth and survival rates at different stages were recorded during the months of June and July 1983, visiting the Encanyissada colony every five days (seven visits). Unless otherwise specified we worked with all the Purple Heron nests of the colony (n=23). Each visit was made between 17h and 19h to homogeneize data recording and minimize the effects of our disturbance to broods and breeding pairs (e.g. avoiding overheating of nestlings). The Illa de Buda colony was visited only twice, in order to obtain food boluses regurgitated by nestlings. For the breeding parameters study, some unpublished data referring to a heronry studied by Ruiz, Montori and Jover in 1978 were added. This heronry was located in the Alfacada lagoon (fig. 1).

To assess diet 28 regurgitations were collected. In order to avoid biasses such as

prey-size variation with nestling size (RODRÍGUEZ DE LOS SANTOS & CAÑAVATE, 1985), sampling was designed to comprise boluses coming from nestlings of different ages up to 30 days. These samples were preserved individually in 70% alcohol. Prey items were identified to taxonomic order and quantified following the methods of RUIZ (1985). Numerical values were transformed into biomass values through average conversion factors obtained from sets of prey items collected in the field, following the procedures of RUIZ (1985). Mathematical methods of analysis are those described by RUIZ & JOVER (1981, 1983) and RUIZ (1985).

Eggs were measured with a Vernier calliper to the nearest 0.1mm, and volume estimated by Hoyt's formula (HoyT, 1979). Once hatched, chicks were marked (first with ink and from the second week of life with PVC rings) to permit individual recognition. Data on body mass, and lengths of culmen, tarsus, third toe without claw, and wing (from the carpal joint to the longest primary feather) were recorded from each individual every five days for growth studies. Masses were obtained with a Pesola spring balance to the nearest 1g when less than 100g and to the nearest 5g when heavier. Culmen, tarsus and toe lengths were also recorded with a Vernier calliper to the nearest mm. Wing length was measured with a stop-ruler to the nearest mm. These interval data were employed to obtain mixed-longitudinal data sets following the procedures of RICKLEFS & WHITE (1975). To do so, we used the average weights and measures of recent hatched (wet) nestlings found during our visits as values for the age 0. In this way we can fit growth functions to a real age scale (RICKLEFS, 1983). These methods were specially designed to obtain average growth curves with few visits to colonies. As it has been pointed out (RICKLEFS, 1983) these type of data do not permit inferential

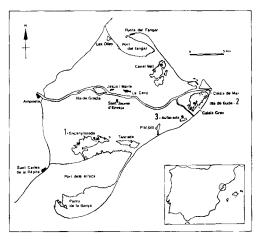


Fig. 1. Map of the Ebro Delta, showing the location of the three colonies studied: 1. The Encanyissada Lagoon; 2. The Illa de Buda Lagoon; 3. The Alfacada Lagoon.

Mapa del delta del Ebro en el que se muestra la localización de las tres colonias estudiadas: 1. Laguna de l'Encanyissada; 2. Isla de Buda; 3. Laguna de l'Alfacada.

statistical analyses but are useful in comparing populations, as well as in fitting curve functions to time course of growth. This method is of special interest when visits to colonies are difficult (remote sea-bird colonies), or as in our case, when frequency of visits can affect the breeding success in an endangered species. Data were analyzed using the graphic method of RICKLEFS (1967) to establish the best fitting model (logistic, Gompertz or Von Bertalanffy) and calculate the corresponding growth parameters.

Breeding success was estimated using Mayfield's method (MAYFIELD, 1961, 1975) improved by MILLER & JOHNSON (1978) and JOHNSON (1979), taking the nest as the unit and, also, for eggs and chicks individually to the age of 16 days. This limit on the age for mortality analysis is due to the semialtricial character of the species. From this age until independence, nestlings leave the nest when disturbed, and move to hide sometimes at considerable distances. So, when a chick of this age or older is not found its fate cannot be ascertained, unless its corpse is found. To compare survival probabilities we used the t statistic as proposed by JOHNSON (1979). The associated degrees of freedom of this statistic are equal to exposure days minus two and, since the degrees of freedom are greater than 120 in all cases, the z-statistic distribution was used (SOKAL & ROHLF, 1981).

In his paper MOSER (1986) suggested that, in the Camargue, Purple Herons are less productive than in other parts of Europe. But, how do we ascertain whether mean clutchsize values in a particular case are within the expected variation range, or significantly different? To answer this question we used regression analysis with latitude as a metric variable to predict mean clutch-size. Although it is only a quantitatively restricted approximation, this will allow us to identify any point which differs significantly from the line defining the general trend in latitudinal mean clutch size variation (outside its 95%) confidence intervals). Because regression analysis of mean clutch-size with latitude is predictive rather than functional, it was performed using the least squares method (Model 1) (RICKER, 1973; SOKAL & ROHLF, 1981).

The rationale behind this analysis is supplied by Ashmole's hypothesis concerning the relationship between clutch-size and relative productivity of the environment (ASHMOLE, 1963; RICKLEFS, 1980) together with the consideration that latitude could be taken as a way to represent the tendency of ecosystems to show higher Production/ Biomass quotients the further they are from the equator (MARGALEF, 1974). That is, the existence of greater differences in resource availability between the non-breeding season (which regulates the numbers of adult population) and the breeding season, resulting in an increase of resources available for reproduction as latitude increases.

## RESULTS

In the Ebro Delta, Purple Herons feed mainly on cyprinid fish. The other prey taken are complementary, the most notable being Coleoptera (mainly big larvae and adults of *Hydrous piceus*) and Rodentia (table 1). There is a homogeneous pattern of resource consumption both at population and individual levels, as indicated by the upper profile

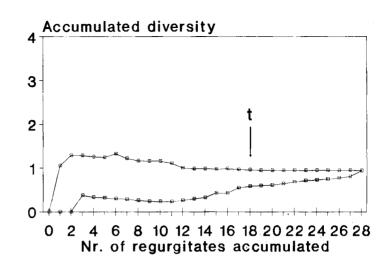
Table 1. Importance of the different prey items in the diet of Purple Heron nestlings in the Ebro Delta: %P. Frequence of occurrence; %N. Numeric abundance; %B. Biomass abundance;  $\lambda$  "N. Values of probabilistic index ( $\lambda$ ) developed by RUIZ & JOVER (1981, 1983) to measure prey importance in the diet composition of a predator population.

Importancia de las diferentes presas en la dieta de los pollos de garza imperial en el delta del Ebro: %P. Frecuencia de presencia; %N. Abundancia numerica; %B. Abundancia en biomasa;  $\lambda$ "N. Valor del índice probabilístico ( $\lambda$ ) desarrollado por RUIZ & JOVER (1981, 1983) para medir la importacia de las presas en la composición de la dieta de una población depredadora.

Prey type	%P	%N	%B	λ"Ν
Cypriniformes	<b>96.</b> 43	75.71	80.07	87.00
Coleoptera	64.29	21.76	15.95	10.74
Orthoptera	35.71	1.58	0.80	0.07
Odonata	10.71	0.32	0.03	0.17
Rodentia	17.86	0.63	3.14	2.01

Fig. 2. Accumulated trophic diversity functions. The upper line corresponds to maximum to minimum individual diversity ordering and the lower to the converse. t. Point from which it has been calculated the Hp average value (RUIZ, 1985).

Funciones de diversidad trófica acumulada. La curva superior corresponde a las diversidades tróficas individuales ordenadas de mayor a menor y la curva inferior a las ordenaciones de menor a mayor. t. Punto a partir del cual se ha calculado el valor Hp promedio (RU17, 1985).



of cumulative diversity function obtained (fig. 2), which reaches stability from 12 accumulated samples onwards. Note that such stability indicates that information added from this point is redundant (RUIZ, 1985) and therefore, that our sample size was large enough to describe the diversity in food of Purple Heron nestlings in the Ebro Delta in 1983. Furthermore, the average value of estimated population trophic diversity is much lower than accumulated diversity value (Hp=0.59 < Hz=0.95) a result typical for homogeneity and dominance in diet composition (RUIZ & JOVER 1983; RUIZ, 1985).

Phenology data are summarized in fig. 3. The reproductive period begins and ends nearly a month earlier in the Ebro Delta than in Central Europe (data in CRAMP & SIMMONS (1977). A similar early phenology has been reported for the Camargue population (MOSER, 1986), but the overall reproductive period is slightly longer (by a month) there than in the Ebro Delta.

Egg measures of 47 eggs from the Encanyissada heronry are combined with those from the Alfacada colony (n=98) to

obtain the sample of 145 eggs used to describe Purple Heron egg size and its variability in the Ebro Delta (table 2).

Clutch size ranged from four to six eggs in our study. Mean clutch size was 5.06 (sd=0.77; n=15) in the Encanyissada lagoon. In the Alfacada lagoon (data from 1978) mean clutch size was 4.77 (sd=0.70; n=13). Other data available for the Ebro Delta correspond to a colony in the Illa dc Buda (Haller in BAUER & GLUTZ, 1966) where mean clutch size was 4.2 (sd=0.77; n=300) and to those recorded by MUNTANER et al. (1984) from all over the Ebro Delta, for which mean clutch size was 4.3 (sd=1.08, n=102).

Mean clutch sizes of Camargue (3.48; sd=0.66; n=242) (MOSER, 1986) and Ebro Delta in 1983 (see above) differ significantly: Mann-Whitney U-test, two tailed, U=293, p<0.001.

A regression analysis of latitude (degrees away from the equator) vs. mean clutch size was performed (data shown in table 3). In order to obtain comparable data series we calculated average values for those areas in which we have more than one sample. The correlation is significant (r=0.78; n=13; p<0.002) and fits the equation: Mean clutch-size=0.054\*Latitude+1.909; r<sup>2</sup>=0.608. Finally, assuming that these relationship is linear, Transvaal, the southwest Cape and the Camargue differ clearly from the general tendency indicated by the regression line, i.e. are out of its 95% confidence limits (fig. 4).

The average growth functions for structures analyzed in this study are given in fig. 5, comparisons are given in table 4. The third toe was the structure, among those monitored, with the highest growth rate, followed in order by tarsus-metatarsus, body mass, wing and culmen. So, this last structure would be the best indicator of age from hatching until fledging.

Table 2. Descriptive statistics of 145 eggs of Purple Heron from the Ebro Delta. Volume has been estimated by Hoyt's formula: vol= $0.51 L*B^2$ .

Estadística descriptiva de 145 huevos de garza imperial del delta del Ebro. El volumen ha sido estimado a partir de la fórmula de Hoyt: vol= $0.51 L^*B^2$ .

	Length	Breadth	Volume
Max.	64.40	43.00	58.01
Min.	50.30	37.00	35.87
Range	14.10	6.00	22.14
Mean	55.23	40.36	45.94
S.D.	2.49	1.30	3.82
Var. Coeff.	4.51	3.23	8.31

Table 3. Latitude and mean clutch size values for Purple Heron in different localities of the World. Where there are different records, average values are given: (\*) Haller in BAUER & GLUTZ (1966), present study (1983), MUNTANER et al. (1984), LLIMONA & MARTÍNEZ-VILALTA (1987), unpublished data of 1988 and 1989; (\*\*) Makatsch (1950) in CRAMP & SIMMONS (1977); (\*\*\*) Williams in MOSER (1986).

Latitud y valores del tamaño medio de la puesta de la garza imperial en diferentes localidades del mundo. Si hay diferentes registros de una misma localidad se da el valor promedio: (\*) Haller in BAUER & GLUTZ (1966), este estudio (1983), MUNTANER et al. (1984); LLIMONA & MARTÍNEZ-VILALTA (1987), datos no publicados de 1988 y 1989; (\*\*) Makatsch (1950) in CRAMP & SIMMONS (1977); (\*\*\*) Williams in MOSER (1986).

Localities	Nests	Latitude	Mean C-S.	Reference	
Eastern Africa	22	1° <b>S</b>	2.6	<b>B</b> ROWN et al. (1982)	
Zimbawe	113	17° S	3.2	TOMLINSON (1975)	
Bostwana	15	20° S	2.9	BROWN et al (1982)	
Transvaal	40	23° S	2.1	BROWN et al (1982)	
Southwest Cape	24	33° S	2.5	BROWN et al (1982)	
Ebro Delta	543	40° N	4.4	(*)	
Macedonia	30	41° N	4.8	(**)	
Camargue	269	44° N	3.5	(***)	
Western France	92	45° N	4.4	Ferry & Blondel (1960)	
Switzerland	305	45° N	4.2	MANUEL (1957)	
Central France	96	46° N	5.1	Ferry & Blondel (1960)	
Hungary	76	49° N	5.3	Kral & Figala (1966)	
Netherlands	27	52° N	4.5	HAVERSCHMIDT (1961)	

From the comparison of overall growth rates (indicated by body mass growth function) between our study and that of TOMLINSON

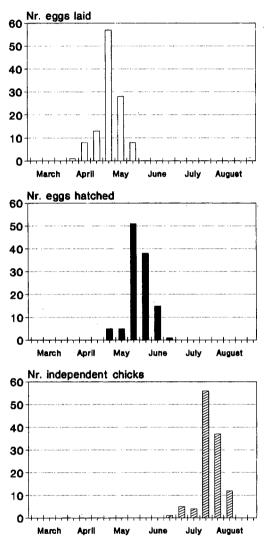


Fig. 3. Seasonal distribution of: A. Clutch initiation dates; B. Hatching initiation dates; C. Independence of nestlings initiation dates for two colonies (the Encanyissada and the Illa de Buda) of Purple Heron in the Ebro Delta, in 1983.

Distribución estacional de: A. Fechas de inicio de puesta; B. Fechas de inicio de eclosión; C. Fechas de inicio de la independencia de los pollos en dos colonias (l'Encayissada y l'Illa de Buda) del Delta del Ebro, en 1983. (1975) with animals reared in captivity (table 4), it is clear that there were only small differences in the form of growth equation and in the instantaneous growth rate constant.

In tables 5 and 6 the results of comparative mortality analysis between the Camargue data (MOSER, 1986) and our own study in the Encanyissada lagoon, are given. When we take the nest as study unit, mortality is very low, being slightly greater for eggs than for nestlings. This difference is significant (t=6.0, p<0.05) in the case of the Camargue, but not for the Ebro Delta, nor between localities. Taking the individual as the study unit (egg or nestling according to the period considered) the mortality rates are also very low, but in this case the probability of survival is significantly greater (t=7, p<0.05) for nestlings of the Ebro Delta than for those of the Camargue. The daily survival probability is significantly greater (t=4.9, p<0.05) during the egg stage than during the nestling stage in the Camargue, but not in the Ebro Delta.

### DISCUSSION

The feeding habits of Purple Herons in the Ebro Delta indicate the existence of high prey availability, as they have the narrowest trophic niche recorded for the species in the Western Palearctic (table 7), and there was no food segregation among individuals (PIANKA, 1986). These results are consistent with the observations reported by FASOLA (1987) who made direct measurements of prey availabilities in the Ebro Delta rice-fields during the spring, and compared the feeding ecology of four species of herons (Little Egrets, Cattle Egrets, Squacco Herons and Purple Herons). From such comparisons he concluded that

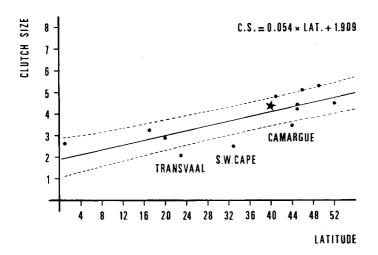


Fig. 4. Regression line of mean clutch size on latitude. (95% confidence intervals). Each point represents the average value when there are several records for the same place (see table 3). ★ Ebro Delta.

Recta de regresión del tamaño medio de la puesta en relación a la latitud. (intervalos de confianza al 95%). Cada punto representa el valor promedio cuando hay varios registros para un mismo lugar (ver tabla 3). ★ Delta del Ebro.

Purple Herons feed on large fish without overlap. Thus in 1983, food supply was probably not a constraint for Purple Herons in the Ebro Delta.

MOSER (1986) showed a significant seasonal decrease in average clutch-size for the Camargue colonies, so it could be argued that our data on mean clutch size in the Encanyissada present a bias, because we lack information from the earlier nests in the colony. This bias, however, was probably small because seasonality effects are only significant when comparing the extremes of the reproductive period and our data correspond to the central period of reproduction. In any case that bias would be irrelevant to our conclusions, because unbiased mean clutch size should reach higher values, reinforcing the differences detected.

As shown by the coefficient of determination ( $r^2=0.608$ ), latitude explains 60% of the mean clutch size variation in Purple Herons, and the relationship between both variables could no longer be considered weak, in spite

Table 4. Growth model and parameters fitted to different structures analyzed for Purple Heron nestlings in the Ebro Delta. Body mass is compared for Ebro Delta (this study) and captivity data (TOMLINSON, 1975).

Modelo y parámetros de crecimiento correspondientes a las diferentes estructuras analizadas en pollos de garza imperial del Delta del Ebro. Se compara el crecimiento en peso de los pollos en el Delta del Ebro (este estudio) con datos en cautividad (TOMLINSON, 1975).

	Ebro Delta					Captive	
	Body mass	Wing	Culmen	Tarsus	Digit III	Body Mass	
Asymptote	1000 g	306 mm	120 mm	120 mm	111mm	1000 g	
Model	Gompertz	V.Bertal.	V. Bertal.	Logistic	Logistic	Gompertz	
Slope	0.030	0.024	0.021	0.032	0.054	0.029	
Origin	-0.433	-0.328	-0.166	-0.378	-0.467	-0.432	
Rate (K)	0.081	0.054	0.047	0.128	0.215	0.081	
t <sub>10-90</sub> (days)	37.320	<b>5</b> 1.650	56. <b>9</b> 60	34.310	20.410	39.270	

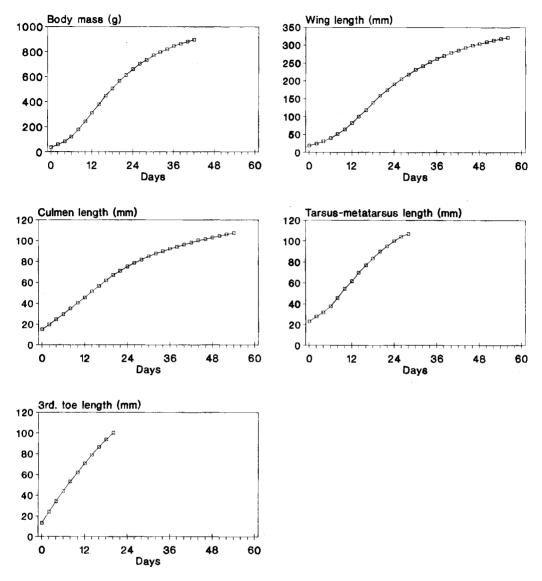


Fig. 5. Average growth curves (until 90% growth) for Purple Heron nestlings in the Encanyissada Heronry in 1983. Measures are defined in the text (methods).

Curvas de crecimiento en promedio poblacional (hasta el 90% de la asíntota) para los pollos de garza imperial en la colonia de l'Encanyissada en 1983. Los parámetros están definidos en el texto (métodos).

of the arguments given by MOSER (1986). Latitude is not a proper biological parameter, but has a direct effect on daylength, climate, seasonality, etc. and can be used as a rough estimator of the ecosystem productivity (MARGALEF, 1974), which in turn broadly determines mean clutch size in birds (RICKLEFS, 1980). Furthermore, note that the estimate of interception at latitude 0 is very near to two eggs, the most usual clutch size for terrestrial birds in equatorial ecosystems (CODY, 1966).

The regression analysis shows that productivity of Purple Herons in the Camargue is lower than the estimated values comprised in the 95% confidence band for mean prediction, as well as in the case of Transvaal and the Southwest Cape. In these two latter cases, however, there are two uncontrolled sources of error which can explain, at least in part, their position in the graphic. First, latitude values are not given where values of mean clutch size are reported, so in both cases, we have estimated an approximate latitude  $(\pm 1^\circ)$ .

Table 5. Estimates of survival probabilities for Purple Heron nests during the incubation and nestling periods (16 days). Values indicated by (\*) differ significantly between them at 0.05 level.

Estimaciones de la probabilidad de supervivencia en nidos de garza imperial durante el periodo de incubación y el periodo de crianza de los pollos hasta 16 días de edad. Los valores señalados con (\*) se diferencian significativamente al nivel del 0,05%.

Locality	Nest-day	Losses	Survival probability by nest-day (%)	Survival probability during this period (%) with 95% confidence limits
Incubation period				
Encanyissada	121	1	99.2	80.6 (100-52.6)
Camargue	4874	44	99.1 (*)	19.0 (84.4-73.6)
Nestling period				
Encanyissada	216	0	100	100
Camargue	3654	2	99.9(*)	99.1 (100-97.9)

Table 6. Estimates of survival probabilities for eggs and nestlings of Purple Herons during the incubation and nestling periods. Values indicated by (\*) or (#) differ significantly between them at 0.05 level.

Estimaciones de la probabilidad de supervivencia para huevos y pollos de garza imperial durante los periodos de incubación y crianza de pollos. Los valores señalados por (\*) o (#) se diferencian significativamente al nivel del 0,05%.

Locality	Egg-day	Losses	Survival probability by egg-day (%)	Survival probability during incubation period (%) with 95% confidence limits
Incubation period				
Encanyissada	694	4	99.4	86.0 (99.5-73.4)
Camargue	16027	60	99.6 (*)	90.7 (93-88.5)
Nestling period				
Encanyissada	1171	1	(#) 99.9	98.6 (100-95.9)
Camargue	11143	96	(#) 99.1(*)	87.1 (89.6-84.6)

Second, values of mean clutch size for these places are, as far as we know, punctual estimates and could represent extreme values (BROWN et al., 1982). Clearly, more information is needed to elucidate these points. But this is not the case for the Camargue, because the latitude value estimated is free of error at the degree level used in our analysis, and values of mean clutch size have not changed significantly for Purple Herons in the Camargue during the last 25 years (MOSER, 1986). Further studies are needed to assess why this difference for Camargue breeders exists.

The Ebro Delta values of productivity are comprised between the 95% confidence intervals of those predicted by the latitudinal trend in that species (fig 4). This clutch size combined with a high nestling survival rate (see table 6) indicate that productivity and survival conditions does not seem to be a constraint to recover past population numbers.

When taking into account the degree of relative development of controlled structures at hatching, we found that legs (tarsus, third toe) and bill (culmen) are the most developed among them. This pattern of development can be interpreted as adaptive for the early locomotion of nestlings due to their semialtricial condition (WERSCHKUL, 1979). Also, it is worth noting that the third toe is nearly equal in length to the tarsus-metatarsus, thus facilitating movement over soft surfaces, such as

Table 7. Diet composition in percentages by numbers and trophic diversity values for Purple Herons in: 1. AMAT & Herrera, 1978; 2. Rodríguez de los Santos & Cañavate, 1985; 3. This study; 4. Owen & Phillips, 1956; 5. Moser, 1984, 1986.

Composición de la dieta pollos de garza imperial según los porcentajes numéricos de las presas que la forman y los valores de diversidad trófica en: 1. AMAT & HERRERA, 1978; 2. RODRÍGUEZ DE LOS SANTOS & CAÑAVATE, 1985; 3. This study; 4. OWEN & PHILLIPS, 1956; 5. MOSER, 1984, 1986.

	Localities				
Prey type	1 Doñana-1	2 Doñana-2	3 Ebro Delta	4 Netherlands	5 Camargue
Mammals	_	1.00	0.63	26.16	0.10
Birds	4.54	-	-	0.42	0.10
Reptiles	0.58	11.00	_	_	3.40
Amphibians	0.49	-	-	4.22	7.60
Fish	56.40	78.00	75.71 .	57.80	<b>6</b> 1.60
Arachnida	_		_	-	0.50
Crustacea	0.74	4.00	-	-	1.90
Odonata	6.27	-	0.32	-	8.20
Orthoptera	0.74	6.00	1.58	-	2.60
Coleoptera	30.22		21.76	11.39	12.90
Hemiptera	_	-	-	-	0.30
Diptera	-	_	-	-	0.30
Lepidoptera	-	_	_	_	0.10
Total prey items	1211	100	1264	237	1720
Number of regurgitates	?	?	28	73	302
Trophic diversity	1.63	1.12	0.95	1.55	1.92

Table 8. Cumulative survival probabilities across the early life stages (egg and nestling) for Purple Heron in the Camargue and the Ebro Delta. (\*) 0.05.

Probabilidad de supervivencia acumulada a lo largo de los primeros estadios de vida (huevos y pollos) de la garza imperial en La Camarga y en el Delta del Ebro. (\*) 0,05%

Locality	Probability that a nest yields a 16 days old nestling	Probability that a laid egg reaches hatching	Hatching pro- bability of a non lost egg	Probability that a nestling can survive to the age of 16 days	Probability of a laid egg to become a 16 days old nestling
Encanyissada	80.6 (n=121)	69.3 (n=121)	95.9 (n=49)	(*) 98.7 (n=75)	68.4 (n=49)
Camargue	78.3 (n=3654)	71.6 (n=4874)	94.3 (n=829)	(*) 87.7 (n=782)	59.0 (n=782)

reed-beds, in which the Purple Herons feed and breed. This situation is well apparent in the adult, where the third toe length is greater than tarsus length. An opposite trait is found in Grey Herons *Ardea cinerea*, which indicates that such species are different ecological morphotypes: Purple Herons are more adapted to soft surfaces and Grey Herons to deeper waters (BOEV, 1988).

The fact that average growth rates in the Ebro Delta are the same as those found by TOMLINSON (1975) for animals reared in captivity with "ad-libitum" food conditions, clearly indicates that conditions for chick rearing in the Ebro Delta were excellent in 1983.

Furthermore, when making a comparative analysis of cumulative survival probabilities between the Ebro Delta and the Camargue a significant difference (t=5.023, p<0.05) is found in the probability of a nestling reaching 16 days, which is greater in the Ebro Delta (table 8). So, it can be concluded that the Purple Herons nesting in the Ebro Delta are significantly more productive than those breeding in the Camargue, not only due to a greater mean clutch size, but also to the fact that these differences are maintained because the probabilities of egg/nestling survival are equal or significantly greater for the Ebro Delta than for the Camargue.

The same could be said when comparing the Ebro Delta in 1983 (mean clutch size=5.06, egg stage mortality=14%) with Zimbabwe (TOMLINSON, 1975) (mean clutch size=3.32, egg stage mortality=49.56%) even though in that case data cannot be tested for statistical inferences. It would be more interesting to compare the Camargue with Zimbabwe, because mean clutch size is, in that case, very similar (Camargue=3.4; Zimbabwe=3.3), but there is a great difference (40%) in mortality percentages during the egg stage (Camargue=9.4%, Zimbabwe= 49.56%). Thus the number of hatchlings per nest is much higher for Camargue pairs (3.1) than for those of Zimbabwe (1.6).

All the parameters monitored: feeding habits, clutch size, growth rates and mortality rates, are consistent, indicating the absence of constraints or favourable outcomes when compared with other studies. So we may conclude that ecological conditions in the Ebro Delta ecosystem for the recovery of the Purple Heron population were excellent in 1983. If maintained, the recovery of Purple Heron population may thus depend more on availability of adequate areas to breed and on the existence of good conditions in their wintering areas (DEN HELD, 1981).

#### ACKNOWLEDGMENTS

We thank H. Hafner, M. Moser, Ll. Jover and seven anonymous reviewers for their critical reading and comments on earlier drafts of this paper. The field work was done with the cooperation of Encanyissada Lagoon wardens. We are especially grateful to Mr. José Martí for his helpful assistance inside the Encanyissada heronry and to Mrs. Nuria Borés for permission to work at the Buda Island heronry. The English text was improved by Robin Rycroft (S.A.L. of the University of Barcelona). A summary of this paper was presented at the IWRB Symposium held in Grado (1991) thanks to an invitation of Tour du Valat Foundation.

### RESUMEN

Parámetros de reproducción, alimentación y crecimiento de los pollos de una población de garza imperial en proceso de recuperación en el delta del Ebro, España.

En este trabajo se aportan los primeros datos sobre algunos aspectos de la biología reproductiva y la ecología de la garza imperial (Ardea purpurea) en la península ibérica. Mediante dichos datos se analizan las condiciones ecológicas en el delta del Ebro para la recuperación de una población de garza imperial que ha sufrido drásticos descensos en su tamaño. Se examinan, también, algunas hipótesis propuestas por MOSER (1986). En el delta del Ebro, la garza imperial se alimenta principalmente de ciprínidos. La amplitud de su nicho trófico (diversidad trófica) es la menor de las registradas en el Paleártico occidental. Se ha confirmado la existencia de una tendencia latitudinal en la variación del tamaño medio de la puesta, definida por la ecuación: tamaño medio de puesta=0,054\*Lat.+1,909, r<sup>2</sup>=0,608, y se ha identificado a la Camarga como un lugar en el que la producción de huevos es mucho menor a la esperada, mientras que las tasas de productividad en el delta del Ebro se situan dentro de la banda del 95% de valores predichos por la ecuación. Las tasas de mortalidad obtenidas en este estudio son similares o significativamente más bajas que las obtenidas en la Camarga. Las funciones de crecimiento muestran un modelo de desarrollo postnatal adaptado a las necesidades locomotoras correspondientes a la condición semialtricial de la garza imperial. Finalmente, la tasa de crecimiento global (incremento de la masa corporal) es la misma para el delta del Ebro que para pollos en cautividad, con unas condiciones alimenticias "ad-libitum".

Se concluye que las condiciones ecológicas en el delta del Ebro en 1983 fueron muy buenas para la recuperación de la especie.

#### REFERENCES

- AMAT, J. A. & HERRERA, C. M., 1978. Alimentación de la Garza imperial (*Ardea purpurea*) en las marismas del Guadalquivir durante el periodo de nidificación. *Ardeola*, 24: 95-104.
- ASHMOLE, N. P., 1963. The regulation of numbers of tropical oceanic birds. *Ibis*, 103(b): 458-473.
- BAUER, K. M. & GLUTZ, U. N., 1966. Handbuch der Vögel Mitteleuropas. Vol. 1. Akademische Verlagsgesellschaft, Wiesbaden.
- BOEV, Z. N., 1988. Morphological characteristics of the adaptation of herons (Aves, Ardeidae) in relation to their movement along the substrate. Acta Zoológica Bulgarica, 36: 63-71.
- BROWN, L. H., URBAN, E. K. & NEWMAN, K. (Eds), 1982. The birds of Africa. Vol. 1. Academic Press, London.
- CODY, M. L., 1966. A general theory of clutch size. Evolution, 20: 174-184.
- CRAMP, S. & SIMMONS, K. E. L. (Eds.), 1977. The birds of the Western Palearctic. Vol. 1. Oxford University Press, Oxford.
- FASOLA, M., 1987. Preliminary report on the feeding ecology of Herons in the Ebro Delta. *Butlletí Parc Natural Delta de l'Ebre*, 2(1): 30-31.
- FERRER, X. & MARTÍNEZ-VILALTA, A., 1986. Le Delta de l'Ebre: Un milieu aquatique règlé par la culture du riz. L'oiseau et R.F.O., 57(1): 13-22.
- FERRY, C. & BLONDEL, J., 1960. Sur le nombre d'oeufs du héron pourpré. Alauda, 28: 62-64.
- HAVERSCHMIDT, F., 1961. Sur le nombre d'oeufs du héron pourpré. Ardea purpurea. Alauda, 29: 68.
- HELD, J. J. DEN, 1981. Population changes in the Purple Heron in relation to drought in the wintering area. Ardea, 69: 185-191.
- HOYT, D. F., 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk, 96: 73-77.
- JOHNSON, D. H., 1979. Estimating nesting success: the Mayfield's method and an alternative. Auk, 96: 651-661.
- KRAL, B. & FIGALA, J., 1966. Breeding biology of the Purple Heron, Ardea purpurea, in the Velky and Maly Tisy Reserve. Zoologické Listy, 15(1): 33-46.
- LLIMONA, F. & MARTÍNEZ-VILALTA, A., 1987. Cens d'ardeids nidificants al Delta de l'Ebre 1986. Butlletí Parc Natural Delta de l'Ebre, 2(1): 7-12.

- MALUQUER, S. M., 1971. La avifauna en el Delta del Ebro en primavera-verano. Ardeola, vol. esp.: 191-319.
- MANUEL, F., 1957. Nouvelle vue d'ensemble sur l'héron pourpré. Nos oiseaux, 24:35-39.
- MARGALEF, R., 1974. *Ecología*. Editorial Omega, Barcelona.
- MARTÍNEZ-VILALTA, A., 1990. Cens d'ardeids nidificants al delta de l'Ebre 1990. Butlletí Parc Natural Delta de l'Ebre, 5: 22-23.
- MAYFIELD, H. F., 1961. Nesting success calculated from exposure. Wilson Bulletin, 73: 255-261.
- 1975. Suggestions for calculating nesting success. Wilson Bulletin, 87: 456-466.
- MESTRE, P. & FERRER, X., 1974. Censo de algunas aves coloniales del delta del Ebro en 1972-1973. *Misc. Zool.*, 3: 143-149.
- MILLER, H. W. & JOHNSON, D. H., 1978. Interpreting the results of nesting studies. *Journal Wildlife Management*, 42: 471-476.
- MOSER, M. E., 1984. Resource partitioning in colonial herons with particular reference to the Grey Heron *Ardea cinerea* L. and the Purple Heron *Ardea purpurea* L., in the Camargue, S. France. Ph.D. Thesis, University of Durham.
- 1986. Breeding strategies of Purple Herons in the Camargue, France. *Ardea*, 74: 91-100.
- MUNTANER J., FERRER, X. & MARTÍNEZ, A., 1984. Atles dels ocells nidificants de Catalunya i Andorra. Ketres Editora, Barcelona.
- OWEN, D. F. & PHILLIPS, G. C., 1956. The food of nesting Purple Heron in Holland. *British Birds*, 49: 494-499.
- PIANKA, E. R., 1986. Ecology and natural history of desert lizards. Princeton University Press, New Jersey.
- RICKER, W. E., 1973. Linear regressions in fishery research. J. Fish. Res. Board Can., 30: 409-434.

- RICKLEFS, R. E., 1967. A graphical method of fitting equations to growth curves. *Ecology*, 48: 978-983.
- 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk, 97: 38-49.
- 1983. Avian postnatal development. In: Avian Biology, 7: 1-83 (D.S. Farner, J.R. King & K.C. Parkes, Eds.). Academic Press, New York.
- RICKLEFS, R. E. & WHITE, S. C., 1975. A method for constructing nestling growth curves from brief visits to seabird colonies. *Bird-Banding*, 46(2): 135-140.
- RODRÍGUEZ DE LOS SANTOS, M. & CAÑAVATE, J. P., 1985. Sélection des proies par le Héron pourpré Ardea purpurea pendant la période de reproduction dans les marais du Guadalquivir (Espagne). L'oiseau et R.F.O., 55(3): 195-203.
- RUIZ, X., 1985. An analysis of the diet of Cattle Egrets in the Ebro Delta, Spain. Ardea, 73: 49-60.
- RUIZ, X. & JOVER, LL., 1981. Sobre la alimentacion otoñal de la garcilla bueyera, Bubulcus ibis (L., 1978), en el delta del Ebro, Tarragona (España). Publicaciones del Departamento de Zoología de la Universidad de Barcelona, 6: 65-72.
- 1983. Tipificación trófica de las poblaciones mediante estimas de la dominancia y de la diversidad. Actas XV Congreso Internacional de Fauna Cinegética y Silvestre: 695-707. Trujillo (Cáceres) 1981.
- SOKAL, R. R. & ROHLF, F. J., 1981. *Biometry*. 2nd. edition. W.H. Freeman & Co, New York.
- TOMLINSON, D. N. S., 1975. Studies of the Purple Herons. Part 3: Egg and chick development. *Ostrich*, 46(2): 157-167.
- WERSCHKUL, D., 1979. Nestling mortality and the adaptative significance of early locomotion in the Little Blue Heron. *Auk*, 96: 116-130.