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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.

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being a thesis presented in candidature for the degree of Doctor
of Philosophy in the University of Durham,

October, 1984.



-1. MAY 1985

To my parents and

Jo, my wife.

ABSTRACT.

Resource Partitioning in Colonial Herons, with particular reference to the Grey Heron Ardea cinerea and the Purple Heron Ardea purpurea in the Camargue, S. France.

Author: Michael E. Moser.

There have been major changes in the relative abundance of the six species of colonial Ardeidae (herons and egrets) which breed in the Camargue, since 1968. Two species, the Grey Heron and the Cattle Egret, started nesting in the delta in the mid-sixties and have increased dramatically in numbers, whilst there has been a simultaneous decline in the breeding population of Purple Herons.

Examination of counts and of the patterns of resource use by these species show that although Grey and Purple Herons overlap extensively in morphology, breeding sites (reedbeds), feeding sites and diet, competition during the breeding season cannot have been responsible for the observed changes, since numbers of Purples have remained stable in those areas where the greatest increases of Greys have occurred, whilst they have completely disappeared in some areas where there were no Greys. Instead, breeding sites have been destroyed to such an extent within the delta that they now limit the number of Purple Herons below the level set by winter mortality, which has been shown to limit breeding populations in other areas.

For Purple Herons, the relationship between colony size and food resources was examined at a breeding-site where colony size was not limited by the availability of adequate breeding habitat. Adults exploited feeding areas near (<2km) to the colony in

preference to those further away (max. 15km); near areas were the first to be filled and remained filled throughout the breeding season. Early breeders held feeding territories in areas adjacent to the colony, to the exclusion of later breeders. Breeding partners did not share the same feeding territories, nor associate in any way on the feeding areas. It is suggested that the increasing costs of flight-time and flight-energy incurred by adults foraging further from the colony may set an upper limit to colony size.

Aspects of the breeding biology of the Purple Heron are described. The average clutch-size in the Camargue is the lowest reported for Europe, and declined significantly through the summer. Siblings differed considerably in size as a result of the asynchronous hatching of the clutch, and not of egg-size differences. The first two chicks in broods of three, and the first three chicks in broods of four, grew fastest and a high proportion of the youngest chicks in a brood died of starvation. It is argued that the number of young fledged is limited by the ability of the adults to deliver food to the nest. Changes in clutch-size are used to adjust brood-size to predictable changes in food availability, while brood reduction through sibling hierarchies provides a fine tuning at the time of peak nestling demand.

The diet of Grey and Purple Herons was examined from nestling regurgitations; both species are highly piscivorous. The Grey Heron specialises on large Eels, Carp and Mullet whilst the Purple Heron takes Eels and a wide variety of other fish, plus some invertebrates. Mechanisms of prey selection were examined

for the Grey Heron. Large Carp and similar fish are the most profitable prey for adults whilst small fish and species which possess protective spines, such as Catfish, are of low profitability. Young chicks cannot consume prey as large as can the adults, although this ability develops by the time they are ca 30 days old. Evidence is presented that adults select prey in relation to the age of their chicks.

The results of this study are discussed in relation to the conservation of breeding heron populations in Europe. Recommendations for the management of breeding areas are proposed.

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ACKNOWLEDGEMENTS

Throughout this study, I was financed by the B.O.U. David Lack studentship. I am very grateful to all those who have contributed to this fund, for giving me the opportunity to carry out my work in the Camargue. I would like to thank Peter Wilkinson (BOU Treasurer) for his part in ensuring the smooth administration of this grant. I am also extremely grateful for funds made available through the Biological Station of Tour du Valat. These covered the costs of transport, and at times my accommodation while on fieldwork in the Camargue. I would particularly like to thank Dr Luc Hoffmann for his help in these matters, and for allowing me use of the facilities at the Biological Station. A small grant was also awarded for field-expenses by Sigma Xi, to whom I am very grateful.

During fieldwork, I was assisted by many people. In particular, I must thank Nick Whitehouse, Andy Webb and Jonathan Wallace. I was also assisted in many ways by John Walmsley, Pat Dugan, Heinz Hafner, Denis Bredin, Vincent Boy and the technical and secretarial staff at Tour du Valat. I thank them all for making my time in the Camargue so stimulating, enjoyable and memorable. The CRBPO greatly assisted this project with their administration of the french bird-ringing scheme. I am particularly grateful to M Francis Roux, for his help in obtaining licences.

I am indebted to the owners and employees of the estates in the Camargue where I did my fieldwork. Without their cooperation this study could not have been done. In particular, I would like to

thank M Courlas (La Société de la Chasse de Stes. Maries), M Grand(Les Bruns), M Blohorn (Carrelet), and M Coulet (Réserve Nationale de la Camargue). For his considerable help, hospitality and friendship, I offer my sincerest thanks to M Baldo, the guard at the Etg. de Landre, where I carried out a large part of this study. René Lameroux helped in many ways, particularly by allowing me to observe captive herons at his ornithological park.

I am very grateful to Professor D. Barker for the facilities provided by the Department of Zoology, University of Durham. I would also like to thank the technical staff at the University for their help, in particular Chris Moore(Dept. of Physics) for constructing radio transmitters. I am grateful to the British Museum (Bird Section), at Tring, for allowing me to measure herons. Dr R.J. O'Connor advised me on my analysis of nest success.

My father and my wife, Jo, helped to type the text of this thesis. To both I am very grateful - to the latter in particular, for bearing with my antisocial habits during the latter stages of writing-up. Dr P.J. Dugan helped in innumerable ways through discussions and help with fieldwork; I am particularly grateful for his assistance and friendship. I thank also Dr. A. Crivelli for his advice concerning fish populations in Camargue.

Finally, I owe my deepest gratitude to my two supervisors, Dr P.R. Evans and Dr H. Hafner, for their encouragement, stimulation and advice. Dr H. Hafner divulged to me much of his knowledge and

enthusiasm of herons, during many hours spent together in the field. He also gave a great deal of his time in helping to obtain permits to work on various estates in the Camargue. Dr P.R. Evans encouraged me to work in the Camargue in the first place, followed and supervised the project with much enthusiasm and interest, and gave invaluable support and advice during the writing-up stages.

INTRODUCTION

The Camargue, S. France, is an area of outstanding conservation importance for populations of wetland birds. The habitats and associated avifauna have been described by Hoffmann (1958, 1970) and more recently by Blondel and Isenmann (1981). Of particular significance are the wintering populations of ducks (Anatidae), the wintering and breeding populations of flamingos (Phoenicopteridae), and the breeding populations of herons and egrets (Ardeidae). The latter form the subject of this thesis, which was stimulated by recent, apparently large changes in the relative abundance of the different Ardeid species which breed in the Camargue. One group of these, the tree-nesting species, have already been studied in considerable detail (Hafner 1975, 1977, Hafner et al. 1982, Bredin 1983), while the ecology of the species which nest in reedbeds remains poorly known. A baseline study of this second group was desirable for conservation purposes, to identify any factors limiting the size of the breeding populations in the Camargue. In addition, the characteristics of these species provide opportunities for the examination of theoretical questions regarding resource use by colonial species during the breeding season.

The aims of my study were fourfold: first, to examine population changes and the patterns of resource overlap between the six species of colonial Ardeidae which breed in the Camargue, to identify whether interspecific competition during the breeding season has been an important factor in guiding changes in the



relative abundance of the individual species; second, to examine the factors which limit the number of reed-nesting herons at individual breeding sites, and in the Camargue as a whole; third, to examine the patterns of resource use and reproductive biology of the reed-nesting herons to identify at which phase of the breeding cycle reproductive output is limited, and by what resources; finally, to formulate, from these studies, management/protection recommendations for the conservation of reed-nesting herons on their breeding areas in the Camargue and elsewhere.

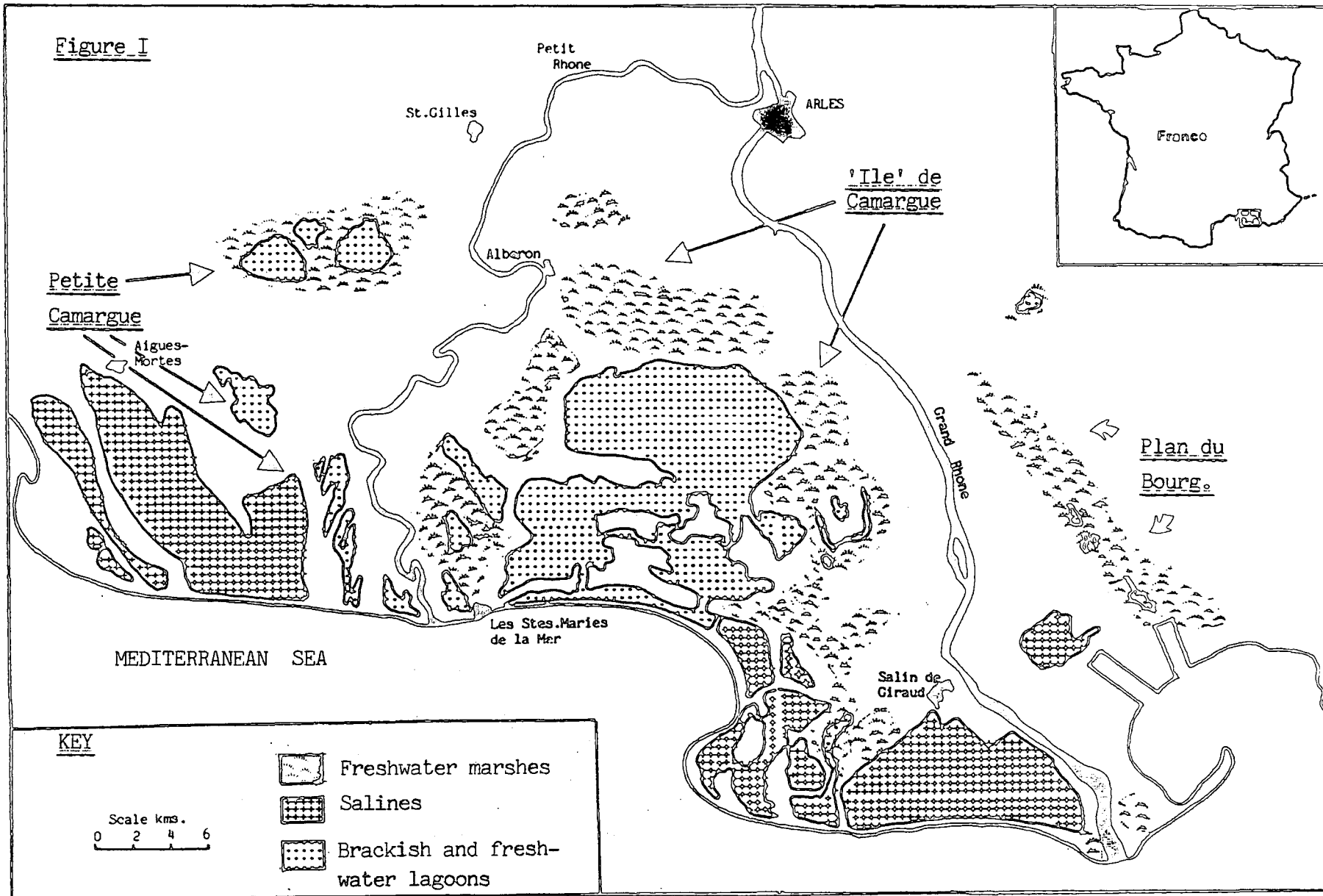
My thesis takes the form of an introductory chapter describing recent population changes and broad patterns of overlap in resource use for all six species of colonial herons in the Camargue; the following four chapters focus on the ecology of the two species of reed-nesting herons; and the final chapter discusses the relevance of my findings to the conservation of reed-nesting heron populations in the Camargue and western Europe.

The Study Area. (Figure I).

The Camargue ($43^{\circ} 30' N$ $4^{\circ} 30' E$) is the delta of the river Rhone, lying on the Mediterranean seaboard of France, approximately midway between the Spanish and Italian borders. The delta, or 'Ile de Camargue', is triangular in shape, and defined by the two remaining arms of the river Rhone, the Grand Rhone and the Petit Rhone. The distance from the head of the delta to the sea is about 35km, while at its base the delta is some 40km across. The

Figure I. The study area of the Camargue, showing the location within France (inset), and the distribution of the main wetland habitat types.

Figure I






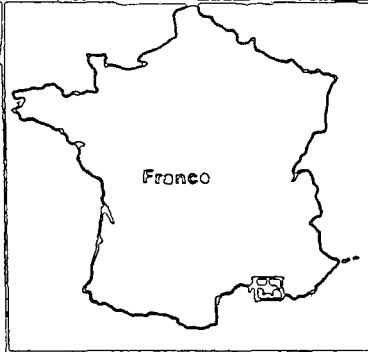
Petite
Camargue

MEDITERRANEAN SEA

KEY

Scale kms.
0 2 4 6

-  Freshwater marshes
-  Salines
-  Brackish and fresh-water lagoons



Plan du
Bourg.

total area enclosed by the river Rhone is about 780km². Immediately outside the delta are two areas generally taken to be included in 'The Camargue'. These are, to the east, the Plan du Bourg (240 km²), and to the west the Petite Camargue (380km²). Throughout this study, I include these two areas in 'The Camargue', and specifically use the term 'delta' when concerned solely with the 'Ile' de Camargue.

The Camargue delta is a low plain of both fluvial and marine origin, which is now protected from incursions of the sea and the Rhone by numerous banks and ditches. It is extremely flat, and about one-third is covered by ^{natural} wetland habitats, which have been described in detail by Britton and Podlejski (1981). The entire area is greatly influenced by mans activities, and some of the salient influences have been described by Aguesse and Marazanoff (1965). The climate is typical of Mediterranean areas, with a low and unpredictable rainfall which occurs mainly in the autumn, winter and spring, and hot, dry summers. It is an extremely windy area, and in summer evaporation rates are high. Details of the climatic conditions are given by Heurteaux (1976), while a useful summary is given by Blondel and Isenmann (1981).

Approximately one half of the Camargue is covered by wetland habitats (including the man-made saline lagoons and ricefields). Much of the dry land area is cultivated (cereals, vines, etc..) particularly in the north of the delta, whilst further south, high soil-salinity levels have resulted in extensive plains supporting a thin halophile vegetation (particularly Arthrocnemum

spp.). Four principal wetland habitat types can be recognized:

1. Saline lagoons. These form a complex of shallow artificial lagoons, covering 120km² within the delta, created for the industrial exploitation of salt by evaporation. They are flooded early each spring with sea-water, which then evaporates throughout the summer months until salt crystals form and can be harvested in the Autumn. Fish occur in the lowest salinity lagoons only, although invertebrates are very numerous in all but the most saline.

2. Brackish marshes and lagoons. These cover the large area which is not used for salt-extraction immediately inland from the sea, and include the vast Etang de Vaccares. They are generally very shallow (<1m deep), with little emergent vegetation. In summer many dry out causing rapid changes in water depth, salinity, and density of fish and invertebrates.

3. Freshwater habitats. These occur in three main areas: in a broad band surrounding the Etang de Vaccares; to the north of the Petit Camargue; and on the Plan du Bourg. They comprise a mosaic of permanent lagoons, temporary marshes, ditches and canals. In hot, dry, windy summers, a high proportion of these marshes will dry out, causing short-term concentrations of invertebrates and fish, while in cooler, wetter years most will remain inundated. The timing and extent of changes in water levels and densities of fish and invertebrates are thus highly unpredictable both within and between years. The ditches, canals and deeper lakes usually remain full of water, and provide a 'prey reservoir' to allow

repopulation of the marshes once these become flooded again. The dominant vegetation of the marshes is usually either Scirpus maritimus, Phragmites australis or Typha sp. but varies with their hydrology and particularly the grazing regime. Most freshwater habitats in the Camargue are intensively managed for wildfowl hunting purposes and/or reed exploitation. Detailed studies of the fish communities have been carried out by Crivelli (1981, 1981a)

4. Ricefields. These artificial 'wetland' habitats cover some 8000 ha. within the delta. They are flooded in April and for a short period provide shallow, open water conditions, before rapid growth of the riceplants produces a dense sward. The crop is harvested in August, and the fields remain dry for the rest of the year. Many irrigation ditches supply these and other cultivated habitats with water.

CHAPTER ONE.Ecological relationships between the six species of colonial Ardeidae which breed in the Camargue.INTRODUCTION.

Eleven species of Ardeidae have been recorded in the Camargue, of which six are relatively numerous during the breeding season. These are Grey Heron Ardea cinerea, Purple Heron Ardea purpurea, Night Heron Nycticorax nycticorax, Little Egret Egretta garzetta, Cattle Egret Ardeola ibis, and Squacco Heron Ardeola ralloides. All are colonial nesters. The Bittern Botaurus stellaris and Little Bittern Ixobrychus minutus also breed. Both are territorial breeders whose ecology and status remain poorly known. The latter is certainly rare, and probably fewer than ten pairs breed each year (see Blondel and Isenmann 1981). Bitterns were censused in 1979 (Hafner and Moser unpublished) and in 1983 (Hafner et al. 1984), when totals of 29 and 24 booming males were located within the delta, respectively. Both species are therefore of low numerical status, very widely dispersed, and are thus unlikely to affect the distributions or abundance of the other species, although the converse may not be true. In addition to the breeding species, the Great White Heron Egretta alba occurs each year as a non-breeding visitor (Blondel and Isenmann 1981), whereas the other two species recorded (Reef Heron Egretta gularis and Black-headed Heron Ardea melanocephala) are accidental.

Dramatic changes have occurred recently in the relative abundance

of the six colonial species in the Camargue. An important question, both for their conservation and from an academic viewpoint is to determine to what extent these changes can be accounted for by competition. I define competition in terms of its effects on population dynamics (sensu Williamson 1972). Hence, 'two species compete if they overlap in their use of the same limited resource, such that the population dynamics of one species is adversely affected by the presence of the other'. Such competition can occur either directly, through interference between individuals, or indirectly, because a resource which has been exploited by one individual is no longer available to another.

Krebs(1978) showed that mixed-species coloniality occurs frequently amongst Ardeidae. Burger(1981) discussed the evolution of this habit, and suggests that the benefits fall into two categories: those relating to a reduction in the probability of nest predation, and those related to an enhancement of resource utilisation efficiency, particularly in food gathering. There may also be considerable costs associated with mixed-species coloniality, as by definition individuals will be clumped in relation to space and other resources. Thus, the probability of competition between individuals for those resources, both by interference and exploitation, will be increased.

In this introductory chapter, I describe the frequency with which mixed species coloniality is found among herons in the Camargue, and examine the major population changes which have

occurred for each species. I then show the patterns of overlap in resource use between the different species pairs to identify the areas in which competition could potentially occur. Particular attention is given to overlap in breeding sites, feeding sites and food. This chapter provides a background for the more detailed studies of the Grey and Purple Heron, which form the major part of this thesis.

METHODS

Population Size.

Changes in the relative abundance of the six species of colonial heron which breed in the Camargue were examined from the results of nest censuses which have been carried out in most years since 1968. I used the results from only those colonies located within the delta or on the banks of the river Rhone, because detailed nest censuses were not always made for colonies outside the delta. No information was available on the number of non-breeding individuals of any species.

Nest censuses for the reed- and tree-nesting species require rather different methods. Any differences resulting from the two techniques would not mask interspecific effects as each of the six species is restricted to nesting in one habitat only. Details of the methods used to census the tree-nesting species were reported by Hafner (1977), and the same author kindly made available unpublished information for use here. The methods used for censusing the reed-nesting species are discussed in Chapter 2.

Assessment of Dietary overlap.

Interspecific overlap in the diet of the Camargue herons during the breeding season was measured by comparison of the types and sizes of prey that were fed to nestlings. Comparisons between species were made only with samples taken from chicks older than 10 days for the tree-nesters or 15 days for the reed-nesters (which have a longer nestling phase), because the diet of younger chicks is known to show both qualitative and quantitative differences in composition when compared with that of older chicks (Chapter 5). The food requirements of very young chicks are small, and will not contribute greatly to the energy demands made on the adults, nor therefore to any possible depletion of prey resources (one possible source of interspecific competition).

Food samples were collected from several colonies within the delta, and also from two colonies just outside the delta, whose adults used the delta as a major feeding area. Details of the techniques used for collecting and analysing the regurgitated food samples are reported in Chapter 5, and by Hafner(1977), and are not repeated here.

Dietary overlap in both prey type and prey size was calculated between species pairs, using Schoeners'(1968) formula:

$$R_{0} = 1 - \frac{1}{2} \sum |P_{ij} - P_{ik}|$$

where P_{ij} and P_{ik} are the intensities of utilisation of the 'i'th resource by the 'j'th and 'k'th species. In this study the

'intensity of utilisation' was measured as the percentage by dry weight of that size or type of prey in the diet. Of four overlap indices evaluated by Linton et al.(1981), only Schoeners' estimated overlap accurately for a wide range of real overlap values (7 - 85%). Values of his index range from zero, implying no overlap in resource use, to one, implying complete overlap. The data used for the calculation of overlap indices was collected from several colonies, in order to obtain sufficiently large samples for analysis. True measures of overlap could be obtained only by comparing the food intake of individuals feeding in the same place and at the same time. Such measurements were not possible, but it is clear that real overlap values between species will be larger than those obtained by grouping information from several different colonies.

The degree of specialisation in the types and sizes of prey taken by each species was calculated from the inverse of Simpsons' diversity measure (see Levins 1968):

$$B = 1 / \sum_{i=1}^N P_i^2$$

where P_i is the proportion by dry weight of the prey type class, or size class, i in the sample. Values of B can range from $1/N$ to N (the number of categories), low values indicating greatest specialisation (lowest diversity). Each prey type was theoretically available to any of the species, whereas certain sizes of prey which were consumed by the large species were "unavailable" to the smaller species, on mechanical grounds. 'Prey size diversity' measures were therefore corrected by dividing B by the number of size-classes that each species could

consume. I assumed that no heron or egret species could consume a prey from a class greater than the largest size-class that was recorded in the samples from that species. Ideally, the degree of specialisation should be measured in relation to the relative proportions of the different prey types or size-classes available to the predator (Feinsinger et al. 1981). These proportions could not be measured adequately, since availability was impossible to measure. The resulting values can thus be examined relative to other species, but are not absolute.

Information on the biometrical differences between the six colonial species was collected to aid the interpretation of ecological differences. Few data were available from live individuals, and I therefore took measurements from museum skins collected from Mediterranean breeding areas.

RESULTS AND DISCUSSION.

Species Composition and Distribution of the Colonies.

Nesting colonies are places not only in which birds breed, but also from which they exploit the food resources of the surrounding feeding habitats. They are thus centres for potential intra- and interspecific competition (Ashmole 1963, Burger 1981). The opportunity for severe interspecific competition will be greatest among those species which breed together in mixed-species colonies, if resources run short.

The six species of colonial heron which breed in the Camargue are divided into two groups by their choice of nesting habitat. The

two largest species, the Grey Heron and the Purple Heron, breed exclusively in reedbeds, while the four smaller species, Little Egret, Night Heron, Squacco Heron and Cattle Egret, all nest in trees. There is no overlap in nesting habitat between these groups, even though Grey Herons normally nest in woods in northern Europe (Cramp and Simmons 1977). Occasional nests of this species are found in Tamarix bushes in the Camargue, but these are usually within reedbeds.

The majority of pairs of each species breed in large mixed-species colonies, with between one to three other species (Table 1.1). For the tree-nesting species, those colonies containing only three species normally lacked Squacco Herons, while those containing only two species lacked both Squacco Herons and Cattle Egrets. The distribution of both tree and reedbed heronries between 1979 and 1982 is shown in Figure 1.1.

Population Changes.

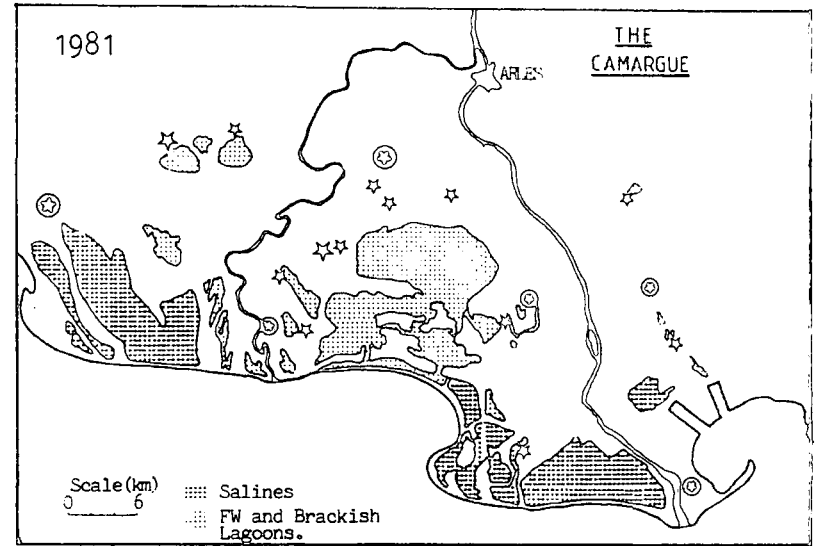
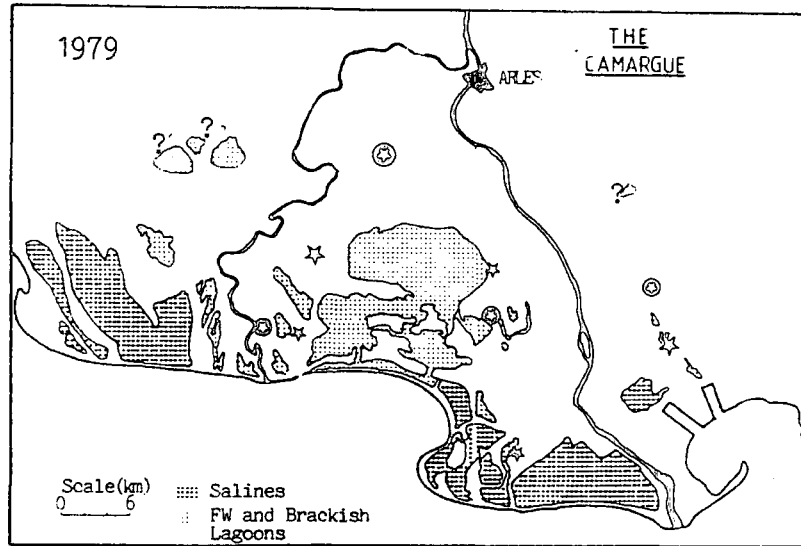
Changes in the sizes of the breeding populations of Ardeidae which have occurred within the Camargue delta since 1968, are summarised in Figure 1.2. The significance of long-term changes were examined by linear regression of log population size on year. Marked changes in abundance are apparent for three species during this period. Two, the Cattle Egret and the Grey Heron, have established major breeding populations in the area since the censuses began. Although the former species was recorded in France as a vagrant as early as 1825, the first successful breeding was not proved until 1969, when two pairs bred in the

TABLE 1.1.

Percentage of nesting pairs, and number of colonies (in parentheses) of Camargue herons in 1980 which occurred in monospecific colonies, and in colonies with one, two or three other species. Colonies to the west of Montpellier are excluded from the analyses.

	NUMBER OF SPECIES IN THE COLONY				TOTAL NUMBER OF PAIRS
	1	2	3	4	
Grey Heron	3.9%(3)	96.1%(2)	-	-	438
Purple Heron	36.2%(2)	63.8%(3)	-	-	1056
Little Egret	-	10.8%(2)	19.6%(1)	69.6%(2)	945
Night Heron	-	11.1%(2)	42.5%(1)	46.5%(2)	424
Cattle Egret	-	-	16.0%(1)	84.0%(2)	438
Squacco Heron	-	-	-	100.0%(2)	65

Figure 1.1. The distribution of tree- and reed-nesting heron colonies in the Camargue, from 1979 to 1982.



⊙ = Tree-nesting colony.(large symbol > 500 pairs).

☆ = Reed-nesting colony.(large symbol > 200 pairs).

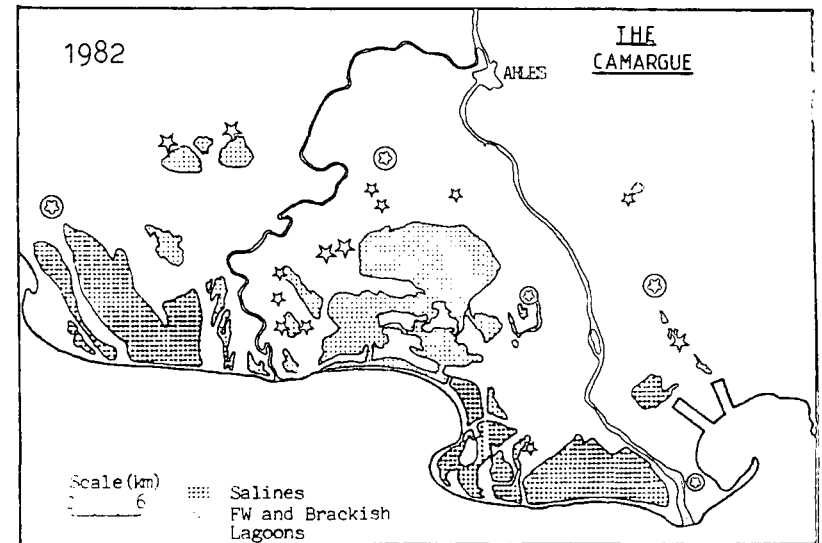
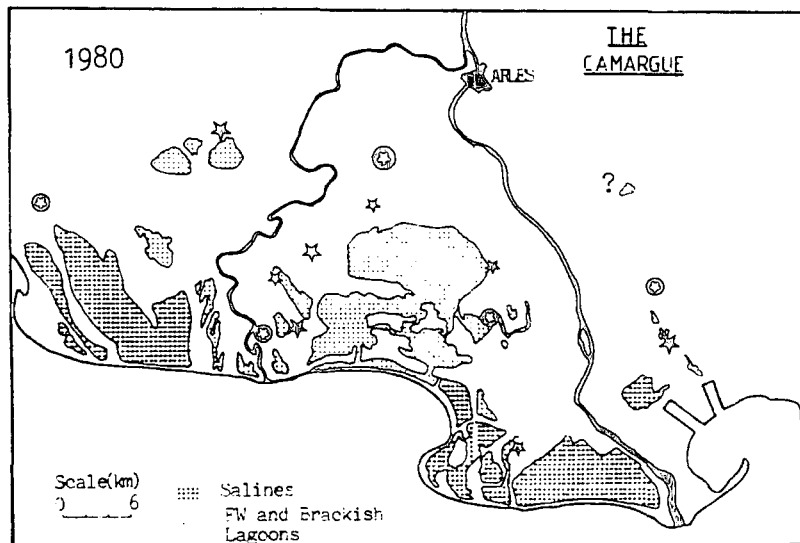
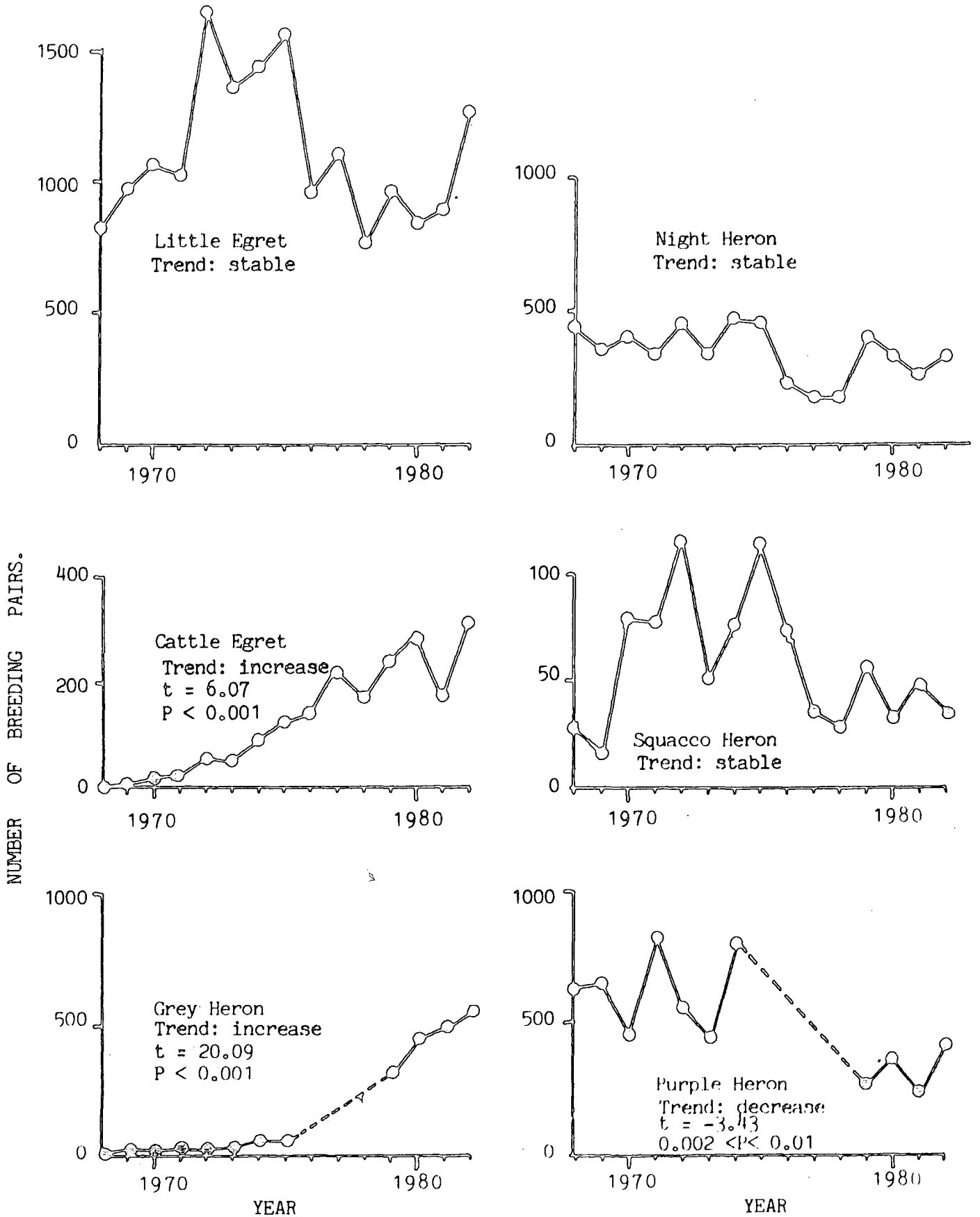


Figure 1.2. Number of nesting pairs of colonial Ardeidae breeding in the Camargue, 1968-82 (Includes only those colonies located within the delta or on the banks of the river Rhone.). Trend analysis calculated by linear regression of log population level, against year.



Camargue(Hafner 1970). The growth of this population has been followed closely(Hafner 1975, Bredin 1983), and in 1982 a total of 468 pairs bred in the Camargue and environs, with 423 pairs within the delta. Cattle Egrets are partial migrants in Camargue, with a small proportion of the breeding population remaining each winter.

The first successful breeding of Grey Herons in the Camargue occurred in 1964(Blondel 1965). There was a rapid development of a substantial breeding population(Walmsley 1975), and in 1982 a total of 614 pairs were censused in and around the Camargue, making Grey Herons the second most numerous of the breeding Ardeidae, after the Little Egret. The population continues to expand, particularly in areas outside the delta. Small numbers of Grey Herons winter in the Camargue.

Populations of the remaining four colonial species have been present in the Camargue for at least the last 50 years, and probably much longer, although the documentation is poor. Hafner(1975) summarises the historical information for the Night Heron, Little Egret and Squacco Heron. Results of more recent annual censuses are given in Hafner et al. 1979, 1980, 1982 and 1984. All three species are primarily summer migrants to the Camargue, although small numbers of Little Egrets also overwinter. Populations of the Little Egret and Squacco Heron have both fluctuated considerably, while the numbers of Night Herons have been rather more stable. No significant long-term trends are apparent for any of these three species.

The Purple Heron is the only species whose breeding population has declined significantly within the delta since 1968 ($t = -3.43$, $0.002 < P < 0.01$). This species is a summer migrant to the Camargue. Censuses of the Purple Heron have revealed large annual fluctuations in population size, with the average population for 1968-74 being 48% higher than in the years 1979-82. A more detailed examination of this decline is presented in Chapter 2.

Feeding habitats.

No quantitative studies were made on the relative utilisation of different feeding habitat types by the six species, yet this may be an important component of their ecological similarity. I have thus made a qualitative assessment, drawn from the results of surveys of habitat use (Hafner 1977 and Voisin 1978) by the tree-nesting species and personal observations of Grey and Purple Herons (Table 1.2). Seven major habitat types can be recognised: salines, brackish marshes, temporary and permanent freshwater marshes, ricefields, canals/ditches and dry ground. The implications of overlap in the usage of these habitats is described below.

Biometrics.

Morphological similarity has frequently been used to infer ecological similarity between species (eg. Ricklefs and Travis 1980). Although there are some experimental examples of the mechanisms which provide such links (eg. Kear 1962), this approach may not be valid for some groups of species (eg. Wiens and

Table 1.2. Qualitative assessment of usage of different feeding habitat types by the six species of colonial heron in the Camargue, during the breeding season.

	BRACKISH		FWM		CANALS/		DRY
	SALINES	MARSHES	TEMP.	PERM.	RICEFIELDS	DITCHES	GROUND
Grey Heron		***	***	***		***	*
Purple Heron			**	***	*	***	*
Little Egret	***	***	***	**	***	*	
Night Heron		***	***	***	*	***	
Squacco Heron				***	***	***	
Cattle Egret			**		*		***

Key.

- *** Major feeding habitat.
- ** common feeding habitat.
- * occasional observations only.
- FWM Fresh-water marshes.

Rotenberry 1981). For the Ardeidae, two parameters have been shown to be related to the use of feeding resources, namely bill structure and leg length, the former related to prey handling ability and the latter to wading depth (Kushlan 1978, Mock and Mock 1980). In addition, Burger and Trout (1979) suggested that body size may play an important role in the structuring of heron communities, particularly at nesting sites, through the outcome of aggressive encounters.

Measures of bill length, depth and width alone did not account adequately for interspecific differences in bill size and shape. I have therefore combined the three measures to give an estimate of bill volume:

$$\text{Bill Volume (cc)} = \frac{\pi}{3} \frac{a \cdot b \cdot c}{1000}$$

where a) = Bill length (mm)
 b) = Bill Depth (mm)
 c) = Bill Width (mm)

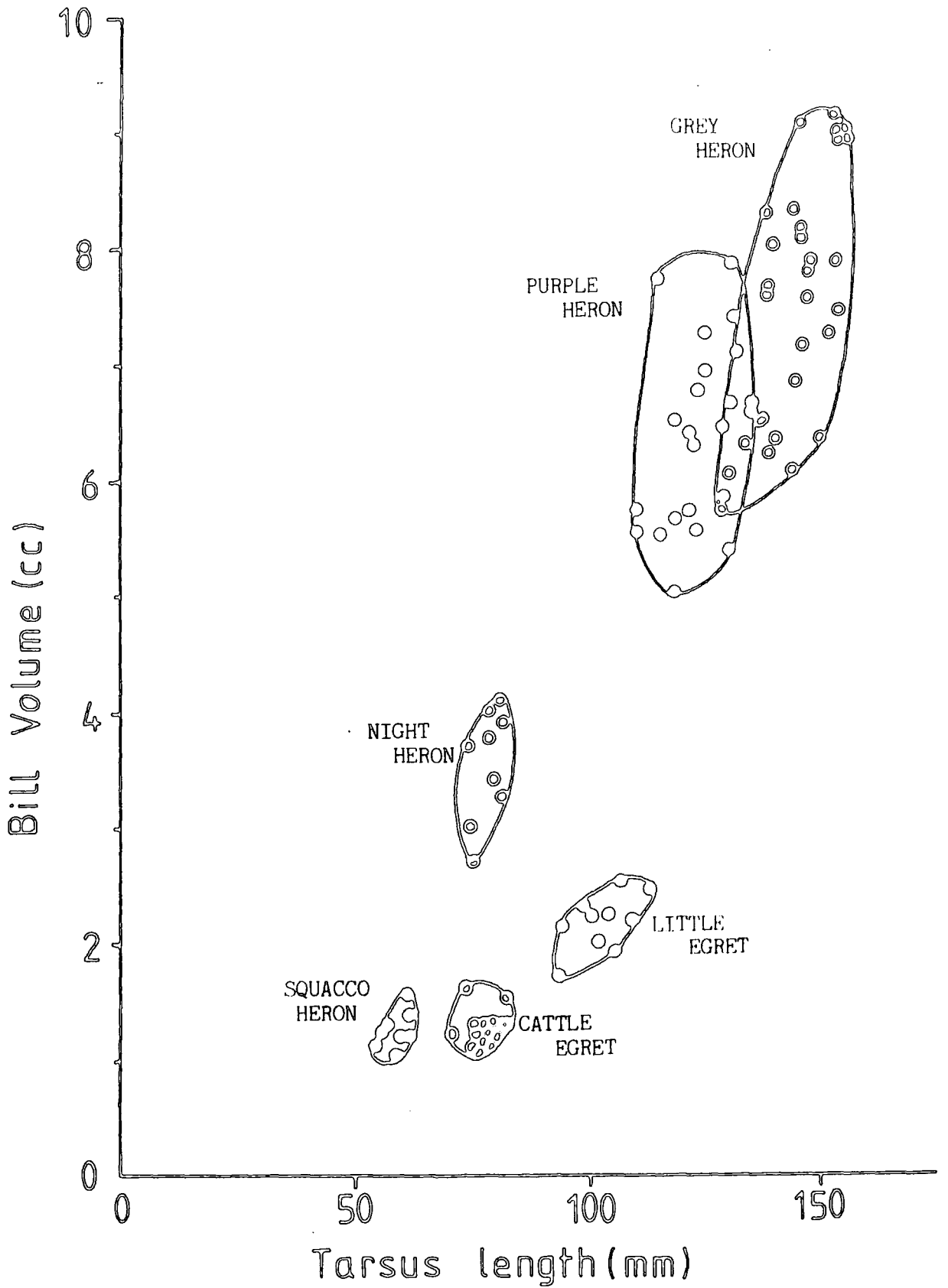
The relationship between bill volume and tarsus length for the six colonial Ardeidae which breed in the Camargue is shown in Figure 1.3. All six species have rather discrete biometrical characteristics, although each shows overlap with at least one other species in one of the parameters measured. Cattle Egrets, the only species to exploit a unique feeding habitat, dry ground, overlap extensively with both Squacco Herons (bill size) and Night Herons (tarsus length). The remaining three smallest species (Squacco Heron, Night Heron and Little Egret), all of which exploit freshwater marshes as a major feeding habitat, show no overlap in biometrics. The two largest species (Grey and Purple Heron) which also feed predominantly in freshwater habitats are the only species to overlap directly in both bill size and tarsus length.

Figure 1.3. Morphological differences between the Camargue Ardeidae. Data were collected from museum skins only. Bill volume is calculated as the volume of a cone with an ellipsoid base. Thus,

$$\text{Bill Volume (cc)} = \frac{\pi}{3} \frac{a \cdot b \cdot c}{1000} \quad \text{where } \begin{array}{l} a) = \text{Bill length (mm)} \\ b) = \text{Bill Depth (mm)} \\ c) = \text{Bill Width (mm)} \end{array}$$

NB. Each symbol refers to one individual.

Figure 1.3.



Thus, inference from biometrical similarity suggests that the five heron and egret species which feed in the freshwater marshes of the Camargue might occupy relatively discrete feeding niches. Only Grey and Purple Herons, the two largest species, demonstrate extensive overlap. Variation in bill volume is very large for both species, and clearly some individuals will overlap far more than others. The role that such variation might play in reducing intra-specific competition would certainly merit further study.

Dietary Composition and Overlap.

A wide spectrum of prey types was recorded in the diet of Camargue herons during the breeding season (Table 1.3), although each species tended to be more or less restricted in the number and types which it consumed.

Grey Herons were the most specialized, feeding almost entirely on fish, particularly Carp and Eels, which were taken mainly from areas of open water in freshwater and brackish marshes. Purple Herons took a far wider variety of prey types, although fish still accounted for 82% of the diet. The composition of the diet, and personal observations indicate that they feed mainly in freshwater areas but with more closed vegetation than used by Grey Herons. Such areas included ditches and ricefields. Aspects of the diet and mechanisms of prey selection of these two heron species are treated in further detail in Chapter 5.

Table 1.3.

Dietary composition(% by dry weight) of colonial herons which breed in the Camargue. Data were collected from the regurgitates of old nestlings(see methods for details). The various categories were defined by those prey representing at least 2.0% of the diet of any single species. All other prey categories were grouped as either 'other Vertebrates' or 'other Invertebrates'.

	Grey Heron	Purple Heron	Little Egret	Night Heron	Squacco Heron	Cattle Egret
A. anguilla	40.1	37.1	5.3	43.9	-	-
Cyprinus carpio	45.9	17.0	7.8	13.5	2.0	-
Mugil spp.	10.3	13.8	2.4	-	-	-
Lepomis gibbosus	0.7	3.3	1.9	4.0	-	-
R.rutilus	1.6	3.4	-	12.0	-	-
Abramis brama	-	6.5	-	-	-	-
Gambusia affinis	-	1.3	20.1	0.2	0.1	-
A.alburnus	-	-	-	4.3	-	-
Pomatoschistus microps	-	-	2.2	-	-	-
Rana ridibunda	-	4.1	1.3	3.1	53.2	24.9
Bird spp.	-	0.5	-	2.5	-	-
Lizard spp.	-	6.5	0.6	-	-	0.9
Other Vertebrates	1.2	4.5	4.0	1.3	0.4	1.6
Arachnida	-	-	0.1	-	0.4	2.3
Crustacea	0.1	-	10.6	0.3	0.5	0.1
Odonata imagos	-	0.2	9.9	-	4.0	9.3
Odonata larvae	-	-	0.1	0.1	0.3	6.5
Coleoptera larvae	-	0.5	28.7	14.5	14.6	2.9
Diptera imagos	-	0.1	2.1	-	0.5	1.0
Diptera larvae	-	-	0.2	0.1	2.0	0.8
Orthoptera	-	1.2	0.6	-	20.9	47.1
Other Invertebrates	-	-	2.5	0.2	1.2	2.5
Niche Breadth (B)	2.61	4.99	6.37	3.98	2.85	3.34

Frogs, Orthoptera and aquatic Coleoptera larvae formed the bulk of the diet of Squacco Herons making it the most specialised in diet of the four tree-nesting species. Such specialisation may result from the relatively predictable conditions offered by the permanent marshes and ricefields in which Squacco Herons are usually found (Hafner et al. 1982). Cattle Egrets were also specialised, most of their foraging occurring on terrestrial habitats (Bredin 1983). The main components of their diet were Frogs, Orthoptera, Dipteran imagos and Coleopteran larvae. A broader spectrum of prey was taken by Night Herons which forage both by night and by day, in mainly freshwater areas (Watmough 1978). Their diet included a large proportion of fish, particularly Eels, and also many Coleopteran larvae. Little Egrets took the widest range of prey of all the colonial herons, and fed in the greatest diversity of habitats - ricefields, freshwater marshes, brackish marshes and saline lagoons (Hafner et al. 1982). Their diet included many species of fish and aquatic invertebrates.

Overlap values were calculated for each species pair and varied from as much as 69% overlap between Grey Heron and Purple Heron, to as little as 1% between the prey types taken by Grey Herons and Cattle Egrets (Table 1.4). The three species pairs which showed greatest overlap, Grey Heron/Purple Heron, Purple Heron/Night Heron, Grey Heron/Night Heron, comprised the predominantly piscivorous species. Much of the overlap in each case could be explained by the proportions of Eels and Carp in the diet. These three species all forage in rather similar

Table 1.4. Prey type overlap between the colonial Ardeidae breeding in the Camargue(see Methods for details of calculations). Values were calculated from the prey type categories listed in Table 1.3.

	Grey Heron	Purple Heron	Little Egret	Night Heron	Squacco Heron	Cattle Egret
Grey Heron	1.000	-	-	-	-	-
Purple Heron	0.685	1.000	-	-	-	-
Little Egret	0.174	0.258	1.000	-	-	-
Night Heron	0.573	0.629	0.328	1.000	-	-
Squacco Heron	0.025	0.085	0.254	0.208	1.000	-
Cattle Egret	0.014	0.086	0.202	0.078	0.564	1.000

habitat types, although the Purple Heron prefers more closed vegetation than the other species, while the Night Heron is restricted to shallower water by its shorter legs (Figure 1.3). A large proportion of the foraging of the last-named species also occurs by night (Watmough 1978). The only other species pair to demonstrate an overlap in prey types of greater than 50% was Cattle Egret/Squacco Heron. The biological significance of this similarity must be negligible, because these species exploit entirely different habitats, and are thus unlikely to interact either directly or indirectly through prey depletion.

Examination of the distributions of prey sizes taken by each species (Figure 1.4) reveals some interesting features. Firstly, the modal and maximum prey size is clearly related to the bill size for each species (cf. Figure 1.3). Large-billed species can thus consume a greater range of prey sizes than the smaller-billed species. The prey size distributions of the three largest species, Grey Heron, Purple Heron and Night Heron all show a clear positive skew, implying that they are selectively taking large prey, and at least the two largest species are almost entirely avoiding the smaller prey classes taken by the other three species. The Grey Heron thus has the potential of taking the widest range of sizes of prey, and yet is the most specialised of all.

The three smallest species (Little Egret, Cattle Egret and Squacco Heron) overlap greatly in the size distributions of prey

Figure 1.4. Size distributions of prey in the diet of six species of colonial heron in the Camargue, during the breeding season. Data are taken from regurgitated food samples collected from nestlings in 1980, excluding those from very young chicks (see text). Values of B and B_{corr} indicate size-specialisation (see text for methods).

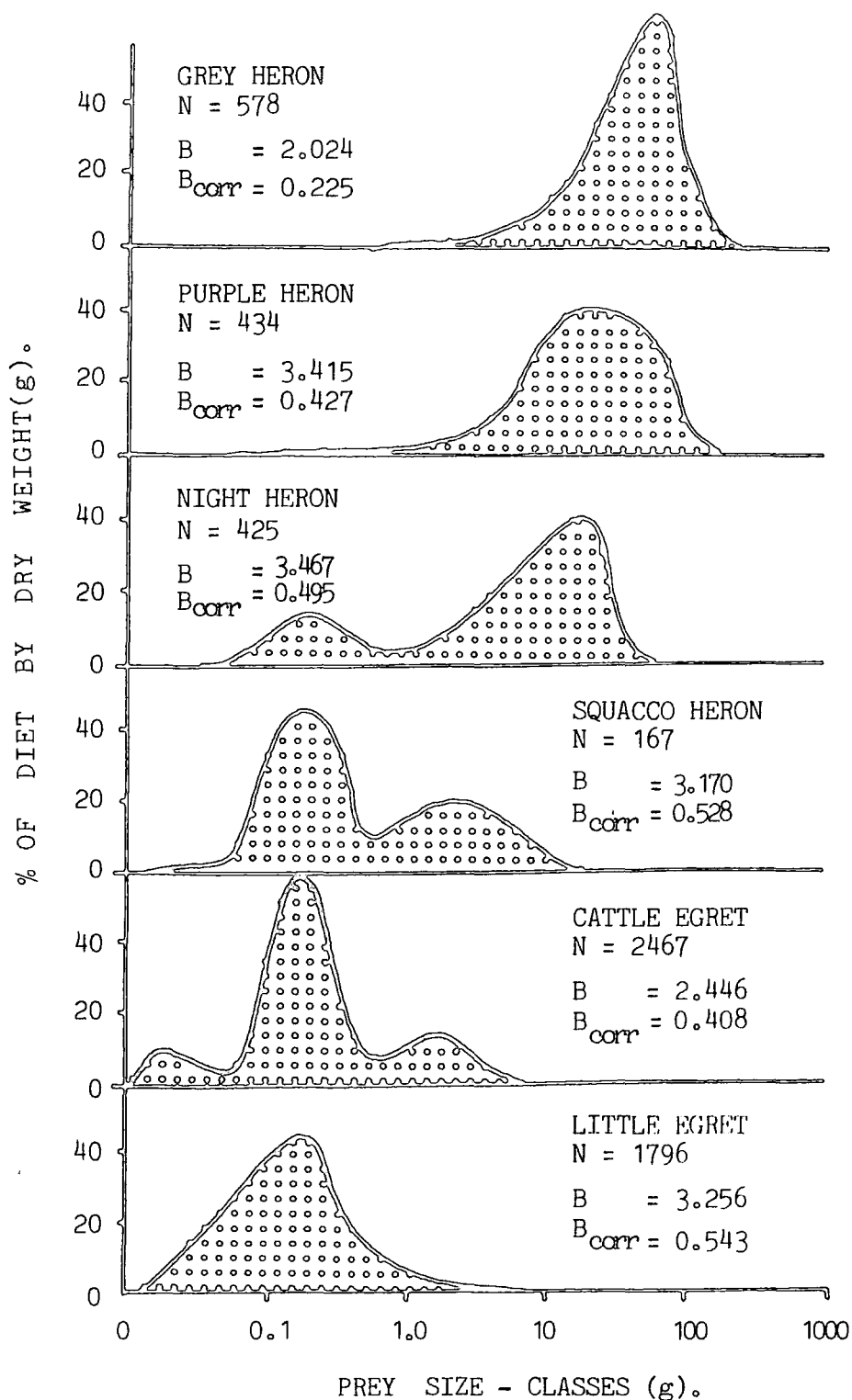


Table 1.5. Prey size overlap between the colonial Ardeidae breeding in the Camargue (see Methods for details of calculations). Values were calculated from the percentages of prey by dry weight divided into size classes on a logarithmic scale, using Schoeners' (1968) formula.

	Grey Heron	Purple Heron	Little Egret	Night Heron	Squacco Heron	Cattle Egret
Grey Heron	1.000	-	-	-	-	-
Purple Heron	0.621	1.000	-	-	-	-
Little Egret	0.034	0.126	1.000	-	-	-
Night Heron	0.316	0.690	0.281	1.000	-	-
Squacco Heron	0.066	0.278	0.653	0.465	1.000	-
Cattle Egret	0.025	0.132	0.708	0.319	0.775	1.000

taken (Table 1.5), but not much in prey type. The larger species (Grey Heron, Night Heron and Purple Heron) overlapped greatly in both prey type and prey size. This was particularly true for Grey Heron/Purple Heron and Purple Heron/Night Heron. All other overlaps between species pairs had relatively low values.

CONCLUSIONS.

There have recently been dramatic changes in the relative abundance of the six species of colonial heron which breed in the Camargue. These can be explained largely by the establishment and expansion of breeding populations of Grey Herons and Cattle Egrets and a simultaneous decline in the numbers of Purple Herons.

Although Cattle Egrets have increased as Purple Herons have declined, the egrets are ecologically very distinct from the herons, and are unlikely to have been responsible for the observed population decline. In contrast, Grey Herons overlap to a large degree with Purple Herons, both in morphology, breeding sites, prey types and size-classes of prey. More detailed analyses of the possible effects of this overlap are presented in Chapter 2 to examine whether competition from the expanding Grey Heron population could be held responsible for the decline in Purple Herons.

CHAPTER TWO

The Distribution and Abundance of Reed-nesting Herons in the Camargue.

INTRODUCTION

From studies of morphological and ecological overlap described in Chapter 1, I concluded that the greatest potential for interspecific competition in the breeding community of Camargue Ardeidae occurred between the Purple and Grey Heron. Indeed, the gross patterns of population change in the numbers of these two species breeding in the area support this possibility, since the Purple Heron has declined in numbers at the same time as the Grey Heron has become established and dramatically increased. In this Chapter, I examine the factors which might limit the numbers of the two species which breed in the Camargue, and consider whether evidence from detailed counts at individual colonies supports the competition hypothesis.

Monitoring the absolute size of bird populations may not always be possible, and frequently only indirect methods can be used. However, breeding populations of the larger colonial birds can often be assessed accurately in a particular area, and an extensive literature exists, treating the techniques and problems relating to specific groups (eg. Gulls and Skuas: Kadlec and Drury 1968, Furness 1977, Ferns and Mudge 1981. Tree-nesting herons: Fasola and Barbieri 1975, Hafner 1977, Kushlan 1979). Problems may arise either because colonies are so large that absolute

counts, by eye, are not possible, or because, being vulnerable to predation, they are often sited in inaccessible places: on isolated islands, sea-cliffs, tall trees, or in reedbeds. The choice of an appropriate census method depends on the habitat and characteristics of the species (crypticity, nesting density, vulnerability to predation, etc). Reed-nesting herons present particular problems for census work, and methods devised for counting Purple and Grey Herons in Camargue are discussed below.

The results of the counts available to date are used to formulate proposals for the continued monitoring of reed-nesting heron populations in the Camargue. In addition, the findings permit the recommendation of specific management procedures, aimed at conserving the remaining colonies of breeding Purple Herons.

METHODS.

Technical difficulties arise in the accurate census of reed-nesting herons in Camargue because:

- (a) Nests are built well below the tops of the reeds, and are thus concealed from ground observers outside the colony.
- (b) Penetration of reedbeds on foot is hindered by the high density of reeds, deep water and mud. It is not possible to maintain accurate transects when searching for low densities of nests over a wide surface area.
- (c) Predation of nests by Marsh Harriers Circus aeruginosus may be increased if a colony suffers disturbance.

Three methods have been used for the census of reed-nesting herons in the Camargue and other regions: ground counts, aerial

surveys, and estimates of colony size from the activity of foraging adults at the colony. Monitoring the breeding population of herons in a region requires that all colonies are located and counted accurately, because regional trends in population size may not be reflected in the trends at a particular colony (see below, c.f. also Den Held 1981).

Colonies were found by visiting all suitable reedbeds during the breeding season (March/July). The characteristic calls and behaviour of breeding adults are easily detected from the ground, while observations of the regular "traffic" of foraging adults from a suitable breeding habitat to nearby feeding grounds also aids location (Walmsley 1973). Colonies are readily visible from the air (Plate 1), and can be rapidly located and counted over a large area.

The estimation of colony size from the activity of foraging adults was used to census the Camargue heronries in 1964 only (Williams 1965). The technique assumes a relationship between the observed frequency of feeding flights from a colony, and the absolute number of nests in that colony. The relationship must be calibrated by making absolute counts of at least one colony. This was not done for the Camargue counts, and the 1964 results must be considered highly uncertain, as the measures of feeding flight activity were not controlled for any of the environmental variables shown recently by Erwin and Ogden (1979) to significantly affect this activity. The results for 1964 were therefore excluded from any analyses.

Ground counts were used to census the heronries in 1963 and 1968-1975. Colonies were visited twice during each breeding season to locate as many of the nests and ring as many of the chicks as possible (Walmsley 1975). Teams of ringers worked slowly through each colony, and few nests were missed. The count at each colony was taken as the total of all nests within the colony which had been recorded to contain eggs or chicks, or show signs of successful breeding such as the presence of white droppings on the nests. (Nests constructed at the beginning of the season, which are not later occupied, are rapidly demolished by other adults stealing the reeds).

Aerial counting techniques were developed in 1979, and used during the main study period (1980-1982). Flights were made on two dates in each year, to coincide with the periods of optimal visibility of Grey and Purple Heron nests, respectively. This period occurs when most of the nests in each colony contain nestlings, but before any young have fledged. During the nestling period, the vegetation around the nest is broken down making the nest, which is whitened by excreta, very visible from the air. After fledging, reed growth rapidly conceals the position of the nests. The timing of the census flights is thus critical.

Censuses were carried out on the following dates :

1979	15th May	20th June
1980	7th May	28th June
1981	5th May	2nd July
1982	10th May	2nd July

Precise dates were determined by the availability of pilot and aircraft, and particularly by weather conditions. Strong winds precluded flights, and also bent reeds over the nests, reducing their visibility from the air. Calm conditions, with strong sunlight to maximise the contrast between occupied nests and reeds, were considered ideal.

A single-engine monoplane was used for the counts, carrying two observers plus the pilot. One observer directed the pilot, and concentrated on photographing the colonies, while the second made supplementary photographs, and recorded detailed observations on each site visited. These included the exact location of the colony, species present, vegetation and signs of habitat management.

All areas of suitable breeding habitat along the Mediterranean coast of France were visited, each flight lasting from 3-4 hours. Reedbeds were surveyed from 600 feet. On location of a colony, altitude was increased slightly before the aircraft was banked steeply over the colony to allow vertical photographs of the nests. Disturbance at the colonies was minimal, and adult herons could be seen standing by their nests on many of the photographs. Kushlan (1979) concluded that aircraft had equally little effect on colonies of tree-nesting herons in Florida. Photographs were made on colour transparency film, to be later projected onto white paper to accurately mark and count each nest. A sample photograph is shown on Plate 1. Species identification of

Plate 1. Aerial photograph of a Grey Heron colony in the Camargue (Les Bruns, in 1980), showing the appearance of occupied nests in reedbeds. Counts of the number of pairs in large colonies were carried out by piecing together numerous such photographs, covering the entire colony.

Plate 2. Aerial photograph of the Grand Mar. This used to be an area with extensive reedbeds, supporting up to 320 pairs of Purple Herons. Recent intensification of habitat management for wildfowling has removed much of the reed, leaving only fringes as shelter for the duck. No pairs of Purple Herons can now breed in this area.

individual nests was readily achieved as they differ markedly in size and form.

Comparability of Ground and Aerial Counts.

It is most unlikely that any reedbed colonies were missed by the use of either technique. One instance of Grey Herons (3 nests) nesting in Tamarix bushes away from reedbeds was noted, and it is possible that a very few similar occurrences were unrecorded.

Grey Heron nests are more robust than those of Purple Herons, and are also constructed earlier in the season, before major reed growth has occurred. They are thus very visible, and aerial counts reflect accurately the number of occupied nests. Comparison of ground and aerial counts for this species in several colonies where the positions of nests were accurately known, revealed identical results from the two methods. It was very difficult to locate all the Grey Heron nests in large reedbeds from the ground because they were widely dispersed. Ground counts were used to census this species in Camargue only when the total numbers present were still small. They were normally associated with Purple Heron colonies, and I have confidence that the counts from 1964-75 accurately reflected the true size of the breeding population.

Purple Heron nests are smaller, and must be counted later than those of Grey Herons, when the reeds are more fully grown. Their nesting dispersion is very compact and thus most nests are easily located during ground counts. Occasional colonies, located in

very tall reed, were difficult to count accurately from the air, and for such colonies supplementary ground counts were made and included in the results (eg at Couvin in 1979 and Mas Neuf in 1982 - locations shown in Figure 2.1).

RESULTS

Purple and Grey Herons were the only Ardeidae to form colonies in the reedbeds of the Camargue, during this study. In 1964, a small colony of Little Egrets, Night Herons and Squacco Herons occurred in a reedbed in association with Grey and Purple Herons (Blondel 1965), but this has not since been recorded.

The two-dimensional nature of reedbeds, as opposed to three-dimensional woodland heronries may result in colonies extending over considerable areas of reeds. For example, the colony at Les Bruns covered more than 30 hectares. Habitat discontinuities, such as canals, open water and patches of unsuitable reeds (see below) often resulted in colonies being divided into several subgroups of nests.

Habitat Characteristics of the Colonies.

Colonies were located in reedbeds of Phragmites australis only, although dense stands of Scirpus maritima and Typha angustifolia also occur. Not all reedbeds were suitable for the location of heronries, and detailed observations of their management patterns revealed the following characteristics to be important:

- Occupied reedbeds remained inundated throughout the breeding season, unless human interference with water levels

caused drying out to occur. In 1981, the main study colony at Couvin was artificially drained during the breeding season. Over 50 pairs of Grey Herons had begun nesting, but only one pair successfully reared a brood. All other pairs abandoned their nests or lost them to predators. Several nests were taken by ground predators, and at least one Fox Vulpes vulpes was observed in the colony. Purple Herons, which returned from their winter quarters just as the area was finally drying out in April, did not attempt to breed. (In the previous year, 109 pairs of Grey and 149 pairs of Purple Herons successfully nested at this site).

-Heronries occurred in stands of mature reed only. Reedbeds which had been broken down by heavy grazing, or degraded by repeated cutting, were not occupied. High densities of nesting herons in the same area of reeds in consecutive years also caused breakdown of reed-structure. Both species construct their nests in spring, from the dead reeds of the previous season, before major reedgrowth has occurred. Reedcutting or burning removes this material, and therefore prevents nesting unless undamaged areas remain.

-Herons are very sensitive to disturbance, particularly during colony establishment, and this may render sites unsuitable for breeding. All Camargue colonies occur on private hunting marshes, where disturbance during the summer is slight, unless habitat management occurs.

Distribution, Size and History of the Colonies.

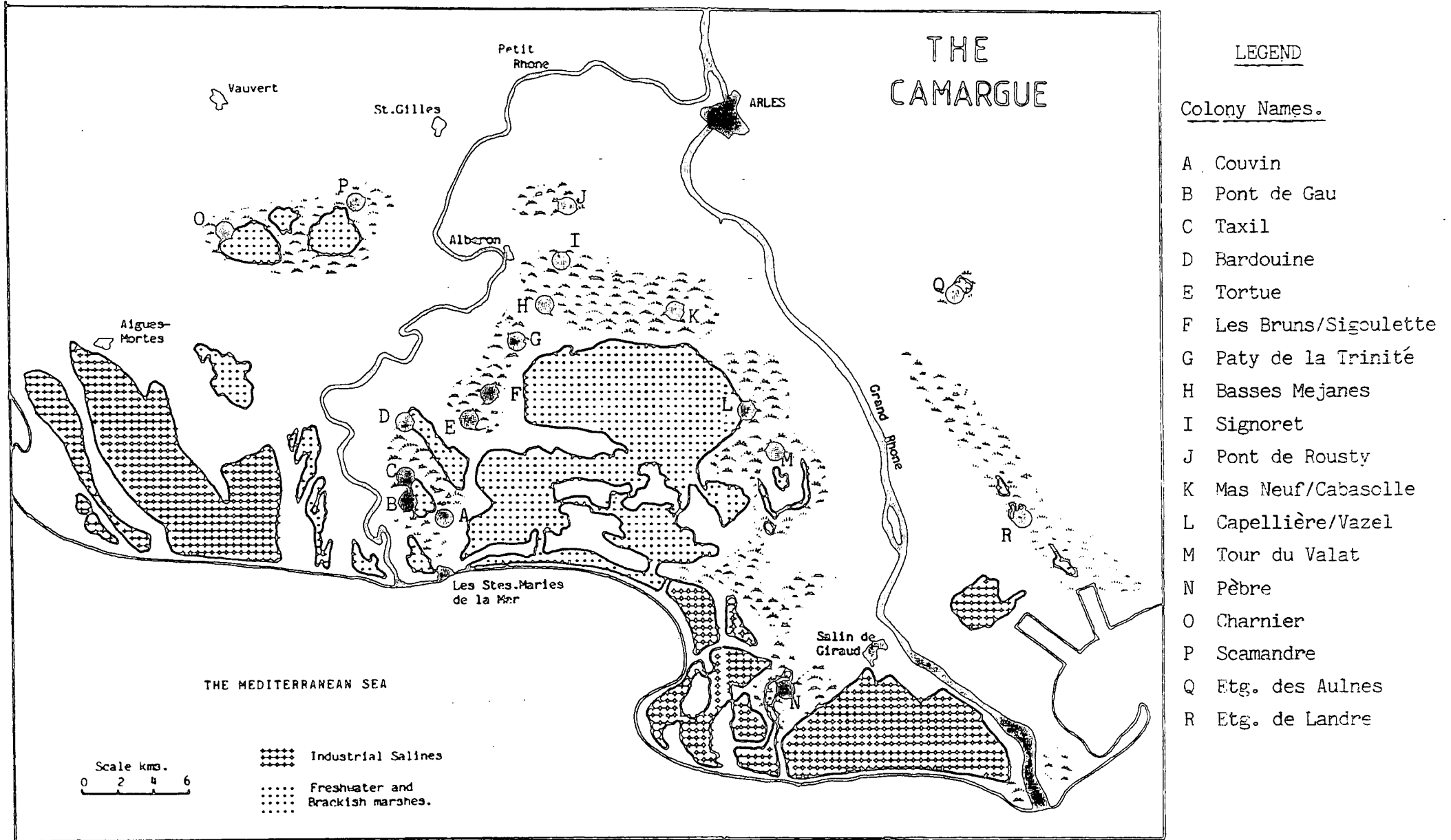
The habitat requirements for nesting restricted the location of colonies within the delta to the broad band of freshwater marshes which encircle the Etang de Vaccares and brackish marshes (Figure 2.1). Further colonies occurred to the East of the Camargue on the Plan du Bourg, and to the west at the Etangs de Scamandre and Charnier. A further four breeding localities were sited to the west of these, in marshes bordering the Mediterranean coast. The most distant was at the Etang de Capestang, 118 kms from the delta.

Grey Heron.

Grey Herons possibly bred in the Camargue at the start of the last century. Jaubert and Lapommeraye (1859) state that they were once sedentary in the Midi, but following reclamation of parts of the Camargue, they became only passage birds. From then, until the 1960s there were frequent records of wintering Grey Herons (Paris 1907, Van Oordt and Tjittes 1933, Mayaud 1936), but very few of summering birds and no suggestion of breeding. Grey Herons are conspicuous, and are of economic interest in fish-farming areas (Hafner and Moser 1980), and breeding attempts would therefore be unlikely to go unrecorded.

The first three nests were found in 1964, among a colony of Purple Herons, to the west of the Vaccares (Blondel 1965). Since then, the growth of the breeding population has been followed closely (Walmsley 1975, and this study). Growth has been exponential (Figure 2.2), and in 1982 a total of 614 pairs

Figure 2.1. The distribution and names of all Purple and Grey Heron colonies located in the Camargue, since 1963.

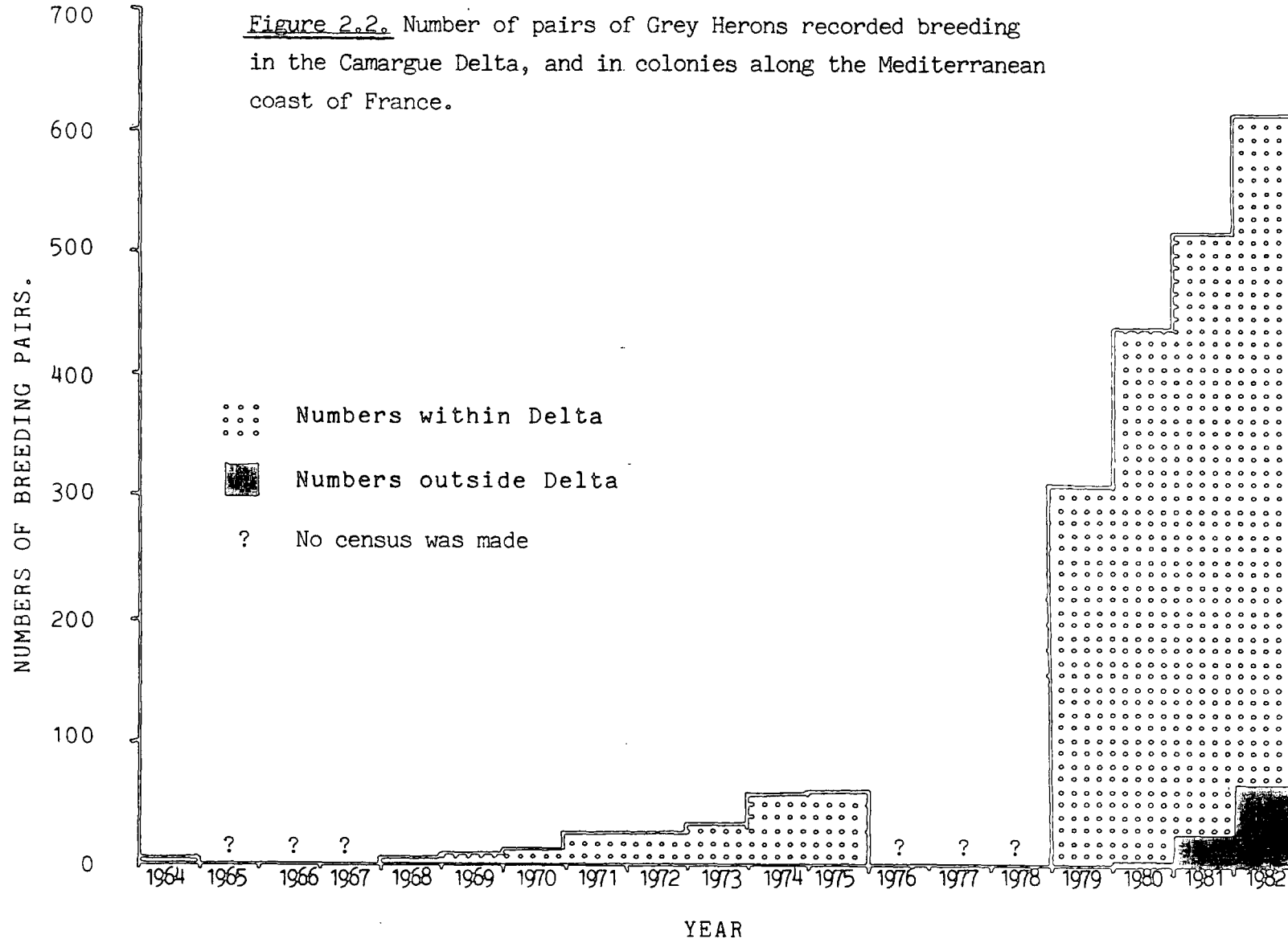


LEGEND

Colony Names.

- A Couvin
- B Pont de Gau
- C Taxil
- D Bardouine
- E Tortue
- F Les Bruns/Sigoulette
- G Paty de la Trinité
- H Basses Mejanes
- I Signoret
- J Pont de Rousty
- K Mas Neuf/Cabasolle
- L Capellière/Vazel
- M Tour du Valat
- N Pèbre
- O Charnier
- P Scamandre
- Q Etg. des Aulnes
- R Etg. de Landre

Figure 2.2. Number of pairs of Grey Herons recorded breeding in the Camargue Delta, and in colonies along the Mediterranean coast of France.



occurred in sixteen breeding sites (Table 2.1). Solitary nests were occasionally found, whilst the largest colony contained 438 pairs.

The occupation of new breeding sites has occurred radially away from the site where the first nucleus of nests was recorded (Figure 2.3), and the most distant breeding site now lies 118 kms to the west. This may indicate that the pioneer breeders occupied the optimal sites first, and that less suitable sites were used only as the first sites became saturated.

The expansion of the breeding population within the delta appears to be slowing (Figure 2.2.), as recent increases in the total population have occurred largely at localities outside the delta. This may suggest a saturation of the sites within the delta. Two reedbeds outside the delta at which Grey Herons have recently started to breed, (Etangs de Scamandre and Landre), apparently offer suitable conditions for the development of large colonies, and it is here that future increases in the total population are likely to occur.

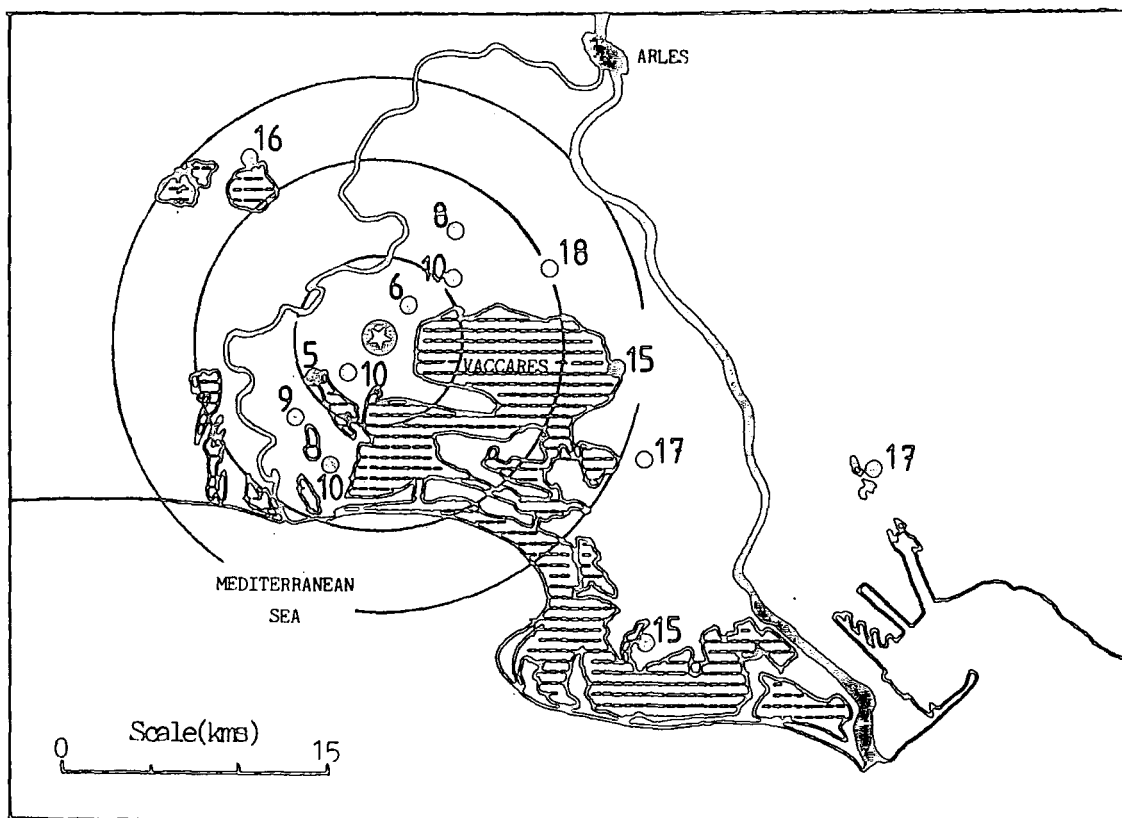
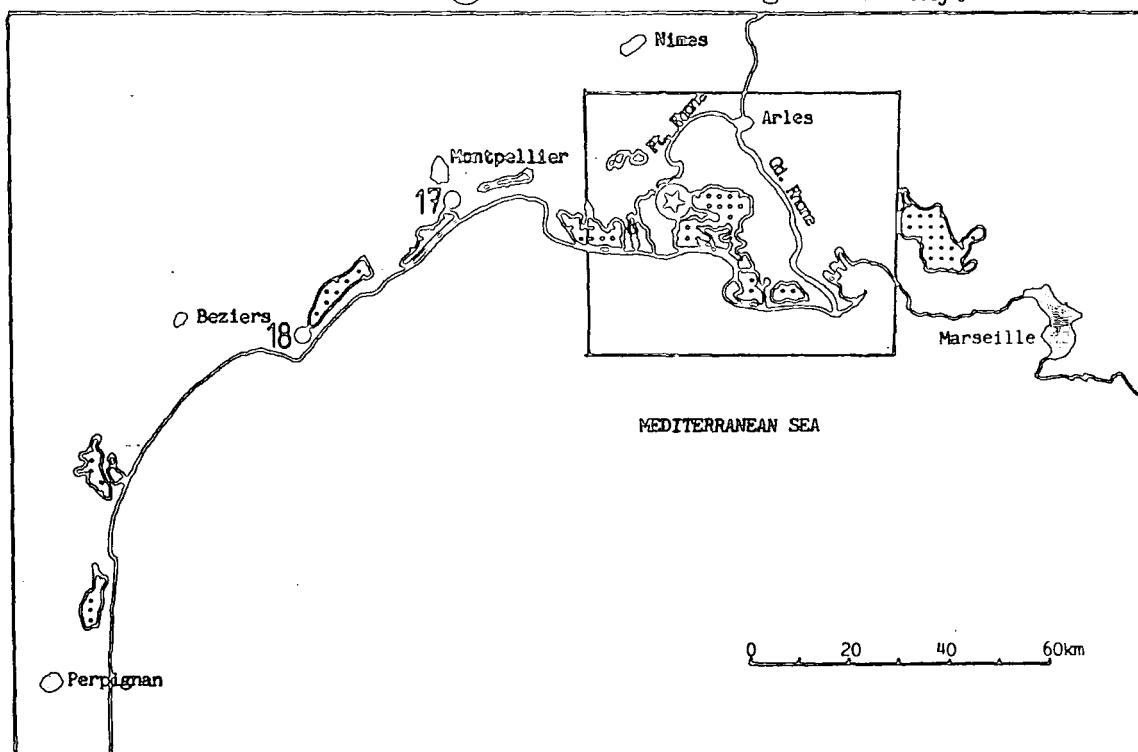
Purple Heron.

The first record of Purple Herons breeding in the Camargue, is of a single nest in the Marais de la Belugue in 1924 (Gibert 1924). There is no reason to believe that they were not present before this date, since only six years later, Hughes (1930) recorded a colony of 200 pairs in the Grand Mar. Geroudet (1939) stated that the species was rare in the Camargue in 1938 due to an absence of

Table 2.1.

LOCALITY	1964	1968	1969	1970	1971	1972	1973	1974	1975	1979	1980	1981	1982
Les Bruns	3	3	6	8	22	22	30	29	58	260	311	438	390
Consécaniere	-	-	2	3	3	2	-	3	-	-	7	11	14
Paty de la Trinité	-	-	-	1	-	-	-	-	1	-	-	10	78
Signoret	-	-	-	-	-	1	-	-	-	-	-	-	-
Taxil	-	-	-	-	-	-	2	2	-	-	-	-	-
Baisse de la Tortue	-	-	-	-	-	-	-	19	-	-	-	-	-
Basses Mejanès	-	-	-	-	-	-	-	2	-	-	-	-	-
Couvin	-	-	-	-	-	-	-	2	-	45	109	1	40
Pèbre	-	-	-	-	-	-	-	-	-	2	4	29	20
La Capellière	-	-	-	-	-	-	-	-	-	1	6	-	-
Tour du Valat	-	-	-	-	-	-	-	-	-	-	-	3	-
Mas Neuf	-	-	-	-	-	-	-	-	-	-	-	-	8
TOTAL(Delta)	3	3	8	12	25	25	32	57	59	308	437	492	550
Seamandre	-	-	-	-	-	-	-	-	-	-	1	21	50
Landre	-	-	-	-	-	-	-	-	-	-	-	2	11
Estagnol	-	-	-	-	-	-	-	-	-	-	-	-	1
Bagnas	-	-	-	-	-	-	-	-	-	-	-	-	2
TOTAL(out of Delta)	-	-	-	-	-	-	-	-	-	-	1	23	64
GRAND TOTAL	3	3	8	12	25	25	32	57	59	308	438	515	614

Figure 2.3. The sequential occupation of new breeding sites by Grey Herons along the Mediterranean coast of France. Numbers show the interval (years) between the first breeding record, and the occupation of that colony. ⊛ = location of original colony.



reeds. The available information remains very sparse until the first census was made in 1963 (Williams 1965), although occasional records of colonies were made in the interim period (Yeates 1948, Fragnière 1950). The information collected from exhaustive counts of the colonies between 1968 and 1982 is shown in Table 2.2.

Four Purple Heron colonies occurred to the west of the Camargue, at the Etangs de Vendre, Bagnas, Estagnol and Capestang. These were located and censused only in the years when aerial techniques were available. A total of between 165 and 507 pairs were recorded in the three years. Records of probable breeding at these sites in 1974 and 1977, suggested fewer pairs to be present (S.N.P.N. 1974, 1975, 1977).

In and around the Camargue, where a longer series of counts were available, colonies have been found in three main areas:

1. NW of the delta.

Two very large colonies were located in the extensive reedbeds of the Etangs de Scamandre and Charnier. These two colonies held 381, 462 and 726 pairs in 1980, 1981 and 1982 respectively. Similarly, Williams (1965) recorded the presence of very large colonies at these sites in 1963 and 1964, and a further colony at Sablon, in 1963 only. These colonies were not censused in the intervening years.

2. E of the delta.

A large colony occurred in the Dépression du Vigueirat, at the Etang de Landre, in each year (max. 300 pairs). Williams (1965) recorded a colony of 250 pairs at this site in 1963, and a

Table 2.2.

LOCALITY	1968	1969	1970	1971	1972	1973	1974	1979	1980	1981	1982
Couvin	200	250	140	160	100	-	80	120	149	-	-
Taxil	140	140	130	25	-	100	110	-	-	-	108
Bardouine	-	100	50	80	10	-	20	-	-	-	-
Les Bruns	75	100	?	150	100	70	65	160	144	110	-
Paty de la Trinité	-	-	50	-	-	16	60	-	-	8	140
Rousty	-	-	-	-	-	-	-	-	-	9	21
Signoret	90	-	-	250	250	40	200	-	82	42	-
Basses Mejanes	-	-	-	-	-	150	120	-	-	-	15
Cabassolle	50	-	-	30	-	-	-	-	-	71	-
Capellière/Vazel	40	35	80	120	120	70	150	5	-	-	-
Tour du Valat	30	35	26	10	-	10	-	-	-	-	-
Pèbre	10	-	-	-	-	-	-	-	-	-	-
Mas Neuf	-	-	-	-	-	-	-	-	-	-	118
Pont de Gau	-	-	-	-	-	-	-	-	-	-	8
TOTAL(Delta)	635	660	476	825	580	456	805	285	375	240	402
Landre	?	?	?	?	?	?	?	200	300	174	213
Etg. des Aulnes	?	?	?	?	?	?	?	?	?	14	18
Scamandre	?	?	?	?	?	?	?	?	381	182	380
Charnier	?	?	?	?	?	?	?	?	-	280	346
Vendre	?	?	?	?	?	?	?	?	118	64	178
Bagnas	?	?	?	?	?	?	?	?	63	37	104
Estagnol	?	?	?	?	?	?	4	?	39	24	62
Capestang	?	?	?	?	?	?	?	?	?	40	163
TOTAL(out of Delta)	?	?	?	?	?	?	4+	200+	901+	815	1464
GRAND TOTAL	635+	660+	476+	825+	580+	456+	809+	485+	1276+	1055	1866

further two large colonies in 1964. A further small colony which had previously been noted by Bigot et al. (1980), was located at the Etang des Aulnes (max. 18 pairs). Again these colonies were not censused in the intervening years.

3. Within the Delta.

Colonies were located in the broad band of freshwater marshes which encircle the Etang de Vaccares, and saline lagoons (Figure 2.1). The pattern of occupation of these colonies has been complex, individual sites being occupied and subsequently abandoned at irregular intervals. A minimum of 18 sites have been used since 1968, although the maximum used in any one year was nine. In each census year between 1968 and 1975 there were four to seven colonies of 50 or more pairs, whilst from 1979-1982, the maximum number was three.

- Marshes north of Stes. Maries. (Couvin, Taxil, Pont de Gau).

Over 100 pairs were present in every year of census (max. 250), except in 1980 when no pairs bred following the complete but temporary drainage of the area for hunting management.

- Marshes west of the Vaccares. (Sigoulette, Les Bruns, Paty de la Trinité, Bardouine). Between 75 and 160 pairs occurred in every census year. All nested in one colony in some years; alternatively in three small colonies.

- Marshes north of the Vaccares. (Rousty, Signoret, Basses Méjanes, Cabasolle, Mas Neuf). The distribution of colonies and number of pairs was extremely unpredictable: maximum of 320 pairs in two colonies; minimum nil.

- Marshes east of the Vaccares. (Capellière, Tour du Vazel,

Tour du Valat, Pèbre). Maximum of 150 pairs present until 1974; 5 in 1979; none since.

Estimations of the total numbers of Purple Herons breeding on the French Mediterranean coast can be made only for the years of this study. Summation of all the colonies described gives totals of 1276, 1067 and 1874 pairs for the years 1980, 1981 and 1982 respectively. Evidence from the censuswork of Williams (1965) suggests that the population was of a similar order of magnitude in the early 1960s, although rather larger numbers may have been breeding in the delta.

DISCUSSION

The contrasting patterns of dramatic increase of the Grey Heron and slow decline of the Purple Heron populations within the delta imply that the size of the breeding populations of these two species are clearly not determined by the same factors. Possible factors fall into two groups: those which act on the herons during the non-breeding season (whilst most or all are absent from the Camargue), and those which act while the herons are breeding in the Camargue.

Grey Heron.

The continuing increase of the breeding Grey Heron population in the Camargue, implies that this species has not yet become resource limited. The remarkable rate of increase suggests that feeding conditions in the Camargue are extremely favourable for Grey Herons, a fact supported by the diet studies reported in

Chapter 5. Populations of Grey Herons have been expanding in many areas of Europe (Blok and Wattel 1978, Fasola et al. 1981, Marion 1980, Pic 1980, Vicente 1974), in part a result of improved bird protection laws in those countries where herons were previously heavily shot. This is supported by evidence from areas with many fish farms, where populations may still be in decline as a result of shooting (Lipsberg 1981, Meyer 1981).

If human interference was the factor inhibiting Grey Herons from nesting in the Camargue until 1964, then there may have existed an 'empty niche' for this species, ever since nesting stopped in the middle of the last century (Jaubert and Lapommeraye 1859). The presence of a regular wintering population suggests that the ability of individuals to disperse from other breeding areas was not the factor limiting breeding. There is some evidence (Figure 2.2) that the number of pairs breeding within the delta is beginning to reach a plateau level, while the population is maintaining its growth in colonies at increasing distances from the Camargue (Figure 2.3). The cause of this stabilisation may be a lack of suitable breeding sites for colonies. This will be discussed in depth for Purple Herons, below.

Purple Heron.

The breeding population of Purple Herons within the Camargue delta has declined over the last 18 years. However, there has been no evidence of a similar decline in the size of colonies adjacent to the delta over the same period. Year-to-year fluctuations in total population size in Camargue, and in the

size of individual colonies have been large and complex. In years when total population size increased, some colonies were abandoned. Conversely, new colonies were formed in years when the total population decreased. These findings suggest that at least one of the factors which determine the overall size of the breeding population in the Camargue delta may act differentially on birds from different colonies. As birds from the different colonies most probably winter together (principally in West Africa (van der Kooij 1976)) it is likely that they will be affected similarly by any factors operative during the non-breeding season. Consequently, the factor(s) acting differentially on different colonies must operate during the breeding season. The most likely factor(s) are local variations in food availability, availability of breeding habitat, and competition.

1. Competition between Grey and Purple Herons.

Grey and Purple Herons are morphologically very similar (Chapter 1, Figure 1.3), breed together in the same habitats, and show a broad overlap in the types and sizes of prey which they feed to their nestlings during the breeding season in the Camargue (Chapter 1, Tables 1.4 and 1.5). They are thus potential competitors. A significant negative correlation exists between the numbers of breeding pairs of the two species censused between 1968 and 1982 within the delta ($r = -0.720$, $P < 0.05$), although this need not imply any causal relationship. Indeed, a similar correlation exists between Purple Heron and Cattle Egret ($r = -0.652$, $P < 0.05$). These two species are morphologically very

dissimilar, breed and feed in different habitats, and show almost no overlap in the prey they feed to their nestlings.

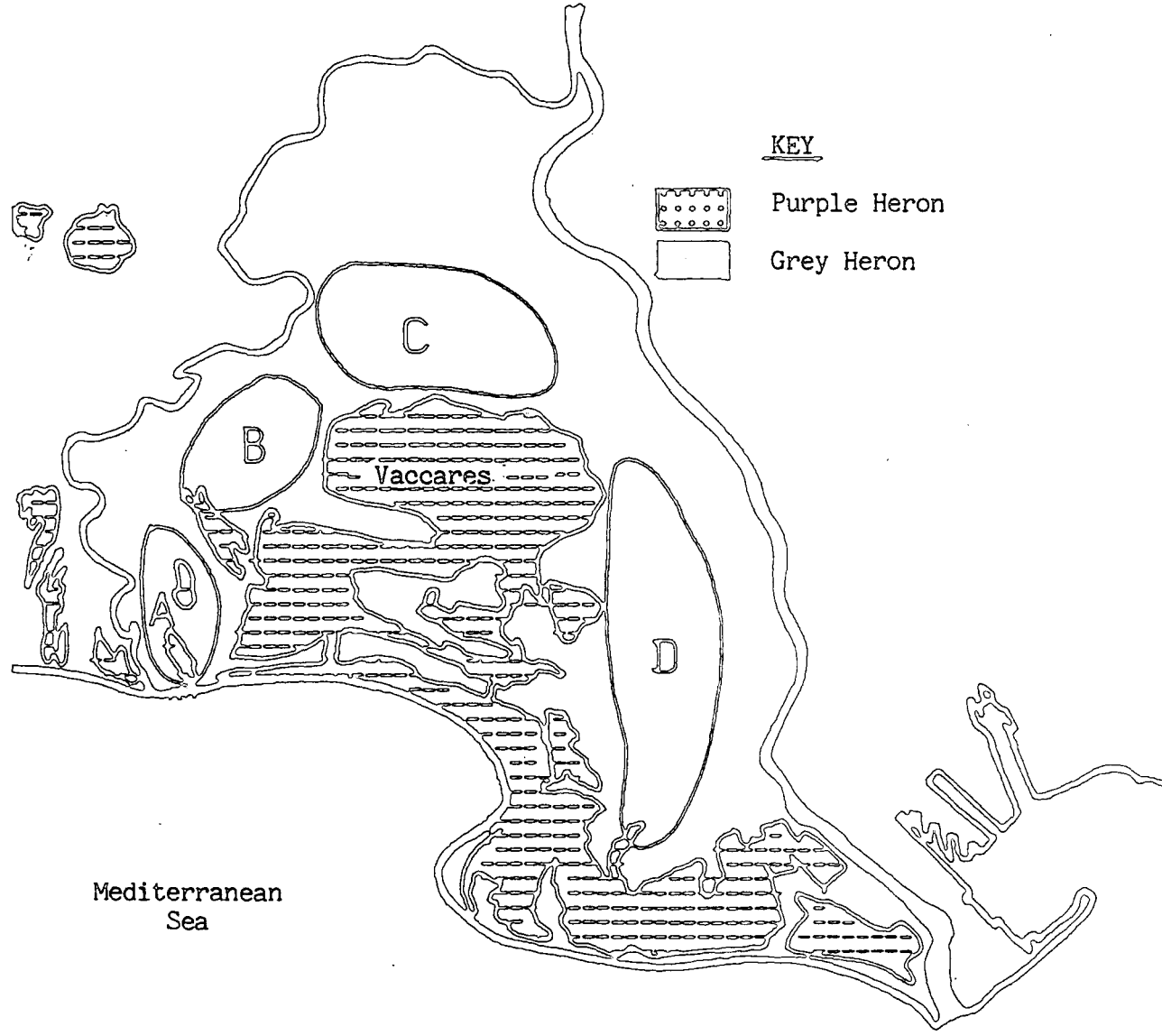
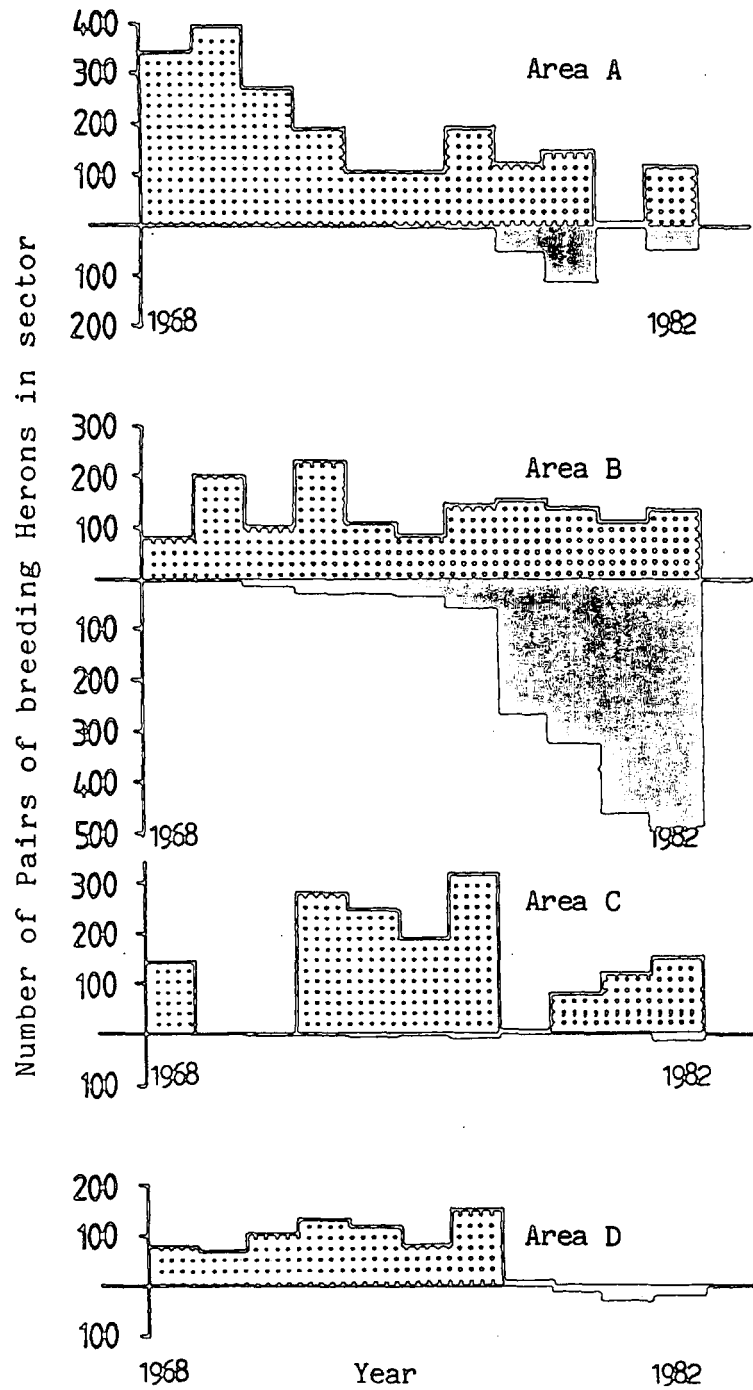
Evidence from fluctuations in the numbers of pairs of Grey and Purple Herons at individual colonies do not support the competition hypothesis. Firstly, the Grey Heron population is expanding steadily, yet occupation of particular sites by Purple Herons varies from year to year. Secondly, the greatest effects would be predicted in those areas where the increase in Grey Herons had been greatest. No such effect exists (Figure 2.4). In the marshes to the west and south of the Etang de Vaccares, where the main increase of Grey Herons has occurred, no decline of the Purple Heron population is apparent. In contrast, all breeding colonies of Purple Herons to the east of the Etang de Vaccarès have disappeared, although the Grey Heron population here has remained very small. Thus, it is unlikely that competition with Grey Herons during the breeding season has been responsible for the observed changes in the size of the Purple Heron population.

2. Availability of Breeding and Feeding Habitat.

Climatic effects on the quantity of available food and/or breeding and feeding habitats could not act locally enough to account for the year-to-year fluctuations in the numbers of pairs observed within each colony. In contrast, human-induced habitat changes have been widespread. Although 23% of the Camargue is protected under reserve status, all reedbed heronries in the region are located on private marshes which are managed intensively for wildfowling. Large unbroken reedbeds are not used

FIGURE 2.4. Year by year comparisons of the numbers of pairs of Grey and Purple Herons breeding in different parts of the Camargue Delta. The patterns suggest that competition with Grey Herons during the breeding season has not been important in bringing about the observed decline in breeding Purple Herons. Data are presented for the years 1968-74 and 1979-82 inclusive.

FIGURE 2.4.



by wildfowl, and many formerly extensive reedbeds are now intensively managed to ensure large surfaces of open water. Plate 2 shows an area of the Grand Mar where this has occurred, and no suitable heron breeding habitat remains. This site previously supported up to 300 pairs of breeding Purple Herons. The following reedbed management techniques were observed in the Camargue during this study:

1. Reed-cutting and burning. The commercial exploitation of reeds occurred at several breeding sites. Reeds were cut and removed during the non-breeding season. In smaller reedbeds where commercial exploitation was not economic, the reed was usually removed by burning. Both heron species construct their nests from dead reedstems, before spring reedgrowth occurs. They are thus unable to nest in areas of reedbed which have been either cut or burned in the previous winter.

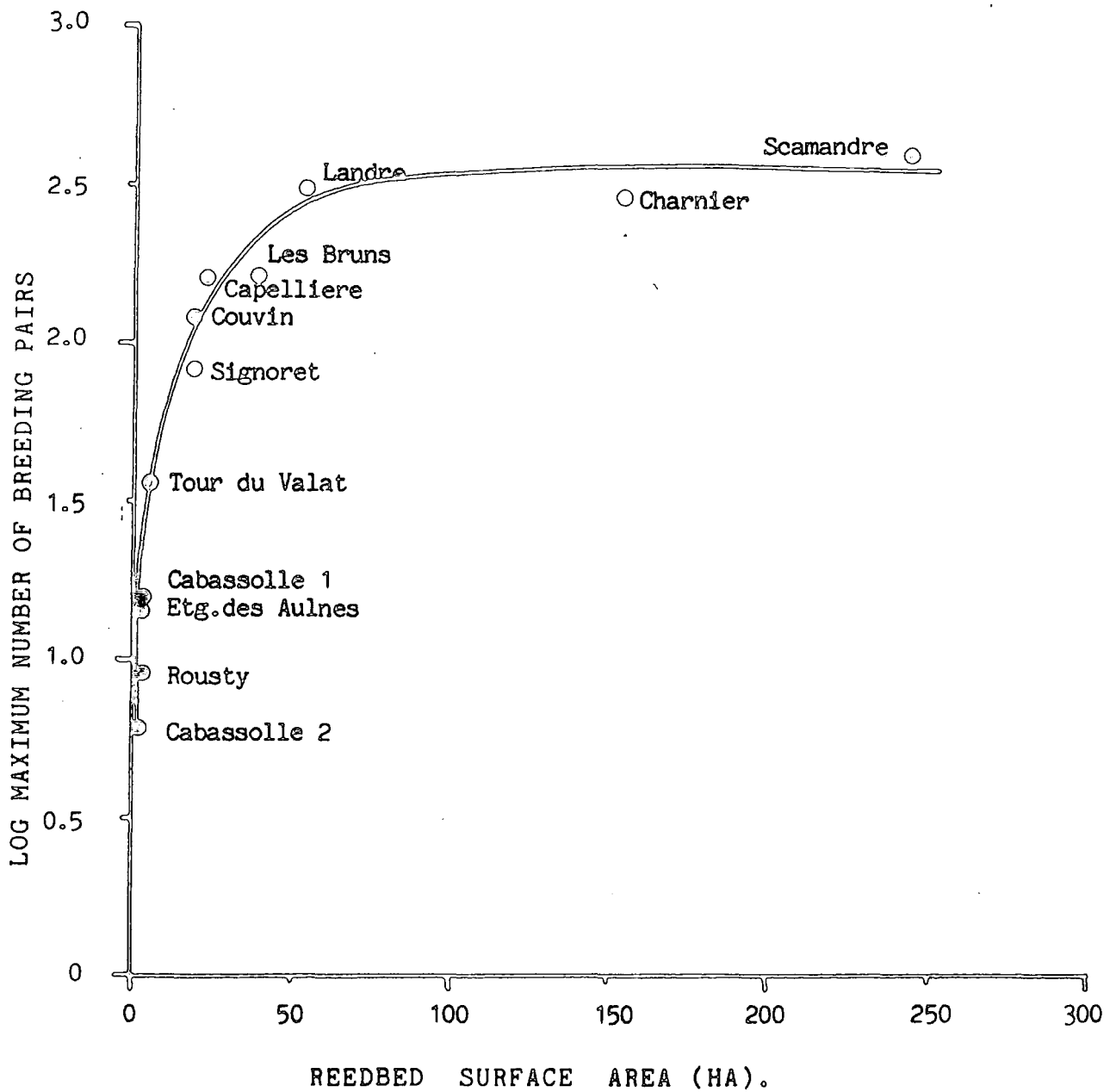
2. Drainage. Another common wildfowl management technique, allowing oxygenation of the substrates, and access to the marshes by cattle, is to temporarily drain the hunting marshes and associated reedbeds in the summer months. This prevents both breeding and feeding by herons. Drainage normally begins in March, but may not be complete until June in wet summers. Breeding may thus be well advanced before the effects of drainage are felt, and the complete nesting failure of a colony may result. This was observed at several sites during the course of the study, but most dramatically at one of my main study colonies, at Couvin in 1981 (see above).

3. Grazing. Overgrazing, by cattle and horses, is an important factor in reducing suitable breeding habitat, and has increased

dramatically during the last 10 years (Dr L. Hoffmann pers.comm.). This was observed both in flooded marshes, and in sites which had been drained specifically to allow easier access for cattle.

The observed management practices have tended to replace closed reedbed with more open waterbodies. Thus, during the period of the decline, the amount of feeding habitat available has probably increased (Purple Herons do not feed in closed reedbeds), whilst the availability of breeding sites has been drastically reduced. It is therefore unlikely that loss of feeding habitat has been responsible for the decline. An important question is whether the reduction in number and size of reedbeds could actually limit the number of Purple Herons breeding in the Camargue. In each year of study, all areas of suitable reedbed greater than 10ha., excepting those adjacent to another major colony, were occupied by breeding herons. Figure 2.5 shows the relationship between reedbed surface area and the maximum number of nesting pairs of Purple Herons in each reedbed. The shape of the curve implies that in reedbeds of less than ca. 30-40ha., colony size was limited by the available surface area of reeds. In reedbeds larger than this, some other factor (presumably food availability -see Chapter 3) sets an upper limit to the size of the colonies. Within the delta, there were no reedbeds larger than 40 ha., whereas there were three outside the delta (Scamandre, Charnier and Landre). In these latter colonies, extensive reedcutting did not affect colony size, because the colony simply shifted between years to suitable parts of the reedbed. In the smaller reedbeds

Figure 2.5. Effect of reedbed surface area on the size of Purple Heron colonies. Data are for the maximum number of pairs recorded in each colony, for the period when reedbed surface area was known (from aerial photographs or maps). The line was fitted by eye.



where such shifts were not possible, extensive management inhibited nesting. An important question is whether members of these colonies fail to breed, or move to other areas and breed successfully. No colour-ringing studies have been undertaken as yet to examine this. However, it appears that the numbers of Purple Herons which breed within the Camargue delta (at least in some years) are limited by the size, and particularly the number of suitable breeding sites.

The pattern described for colonies within the Camargue delta contrasts strongly with the situation recently described for the Dutch breeding population of Purple Herons. Here, the size of the individual breeding colonies fluctuate in parallel (Den Held and Den Held 1976), suggesting that the same factor is acting on all the colonies. Den Held (1981) demonstrated that the numbers of pairs returning to breed each year in these colonies was related to rainfall in the wintering areas of West Africa. Following winters of drought in these areas, fewer pairs returned to breed in the Dutch colonies, while larger numbers returned following winters of good rainfall. Recently, this hypothesis has been supported by data from ringing recoveries (Cavé 1983), which showed that the survival rate of the Dutch after-first-year birds was related to drought in the Sahel area. The survival of first-year birds did not show this relationship, because many of them die before reaching their main winter quarters.

Analyses of European ringing data (Van der Kooij 1976) showed that the populations of Dutch and Camargue breeding Purple Herons

both winter in the same area of West Africa, as do the Camargue populations of Squacco and Night Herons. Using information from the Camargue, Den Held (1981) showed the same relationship between winter drought and the subsequent size of the breeding populations of Squacco and Night Herons, but he could not demonstrate the relationship for Purple Herons. In the results described above, I offer an alternative hypothesis: that the availability of breeding habitat in the Camargue limits the breeding Purple Heron population below that level set by winter mortality. Thus, while the number of Purple Herons which seek to breed in the Camargue each year may be limited by winter mortality, the proportion of these birds which can install in colonies within the delta is limited by the availability of suitable nesting habitat. It is possible that the importance of winter mortality may be more clearly seen when the Mediterranean population of Purple Herons is considered as a whole. However, available data are, as yet, inadequate to permit a meaningful analysis.

In the next chapter, I continue my examination of the factors limiting population size in Purple Herons, particularly of the factors which limit the size of individual colonies in areas where suitable breeding habitat is superabundant.

CHAPTER THREE

The Foraging Ecology and Behaviour of Colonial Purple Herons.

INTRODUCTION.

Some Purple Heron colonies in the Camargue are limited in size by the availability of sufficient area of suitable habitat for breeding, whereas others are limited by some other factor or factors (see Chapter 2). A crucial question for the management and conservation of heron populations, in this and other breeding areas, is whether birds which are prevented from breeding at one site through habitat loss, are able to join another colony and breed successfully. Alternatively, would the Camargue be able to support the same number of breeding pairs as it does now if there was only one site (unlimited in area of reeds) in which the herons could breed? If not, what is the mechanism which limits the size of a colony? In this chapter, I attempt to answer some of these questions by focussing on limitations imposed by food gathering.

During the breeding season, birds which rear nidicolous young become obligate Central Place Foragers (sensu Orians and Pearson 1979). They go out to forage from the nest, and must return to this fixed central place at intervals, with food for the nestlings. The way in which individuals might maximise their rates of food acquisition and delivery to the nest are similar to those predicted from traditional optimal foraging theory (eg. see MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977). However, Central Place Foragers also incur the additional costs of travelling between the central place and the feeding grounds.

This is costly both in time and energy. One way in which birds might minimise these costs is to defend exclusive territories around their nest during the breeding season, and thus ensure unique access to local resources, at a time when limitations of both time and energy may be crucial to successful reproduction. In many species, the size of territories during the breeding season is related to food abundance. They are often smaller where food is abundant than where it is scarce(eg. Kluiver 1951, Cody and Cody 1972). A review of the role of territoriality in controlling access to food resources is given by Davies(1980).

Many birds which rear nidicolous young, including Purple Herons, are also colonial breeders. The economics of coloniality as opposed to alternative strategies are complex, and for herons have been reviewed by Burger (1981). In species in which it occurs, the benefits of coloniality to the fitness of the individual are assumed to be greater than the costs incurred from such behaviour. One particular cost associated with coloniality is the means by which the individuals within the colony must partition the available food resources around the colony, for in this situation individuals cannot defend an exclusive area around the central place. If resource levels remain stable, the greater the number of birds in the colony, the greater is the potential competition between those birds for the available food. Only by foraging at increasing distances from the colony can individuals gain access to unexploited food resources (unless already exploited by members of an adjacent colony),but by doing so they will incur the additional costs of extra travel time. One

prediction of Central Place Foraging theory is that these costs can be minimised by bringing back larger prey loads as distance to the feeding sites increases, and this has been supported by field evidence in Wheatears Oenanthe oenanthe (Carlson and Moreno 1981, Brooke 1981). I examine this and other predictions in relation to measures of the foraging effort of adult Purple Herons.

In areas where the size of the breeding population is not limited by a lack of breeding habitat, there is strong evidence that the size and dispersion of heron colonies is related to the food resources around the colony. Both Lack (1954) and Braaksma and Bruyns (1950) independently demonstrated that Grey Heron colonies were larger near rivers and lakes, than in areas with only small tributaries or canals. Similarly, Fasola and Barbieri (1978) showed that the density of mixed-species colonies of herons and egrets in northern Italy increased with the percentage of land used for ricefields (a major feeding habitat). Also, Burger (1981) demonstrated a significant correlation between the size of heronries in New Jersey and the length of shoreline available in the surrounding marshes. There is little information to suggest the mechanism by which such a relationship might occur, although it seems most unlikely that individuals are able to directly assess the availability of food resources around a colony in relation to their own numbers (sensu Wynne-Edwards 1962). A more plausible explanation might be that they are able to measure the availability of food resources indirectly, through such cues as the level of interference competition on the feeding grounds. In

this chapter, I provide evidence for a mechanism by which such relationships might be explained.

METHODS.

The foraging activity of Purple Herons was studied at the colony of the Etang de Landre (Figure 3.1), which is located on the Plan du Bourg 10km north of the mouth of the Grand Rhone. This colony has been occupied for many years, and contained 174 and 213 pairs in 1981 and 1982 respectively. It was chosen for study because:

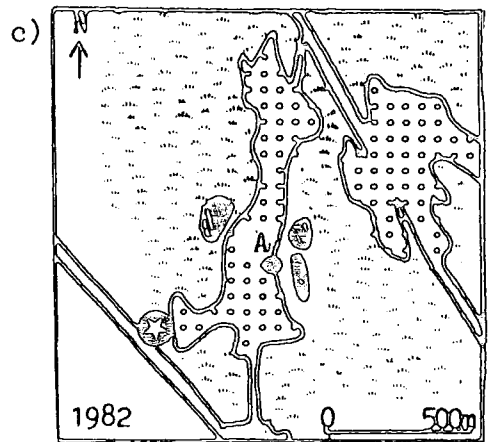
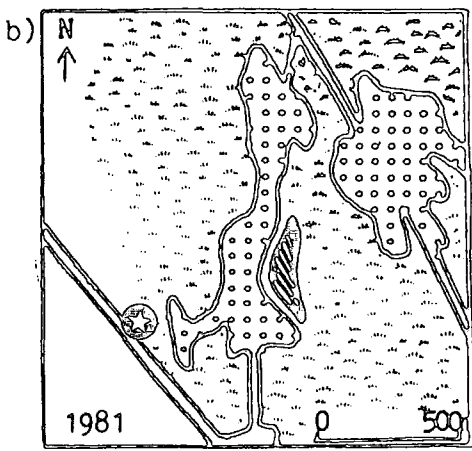
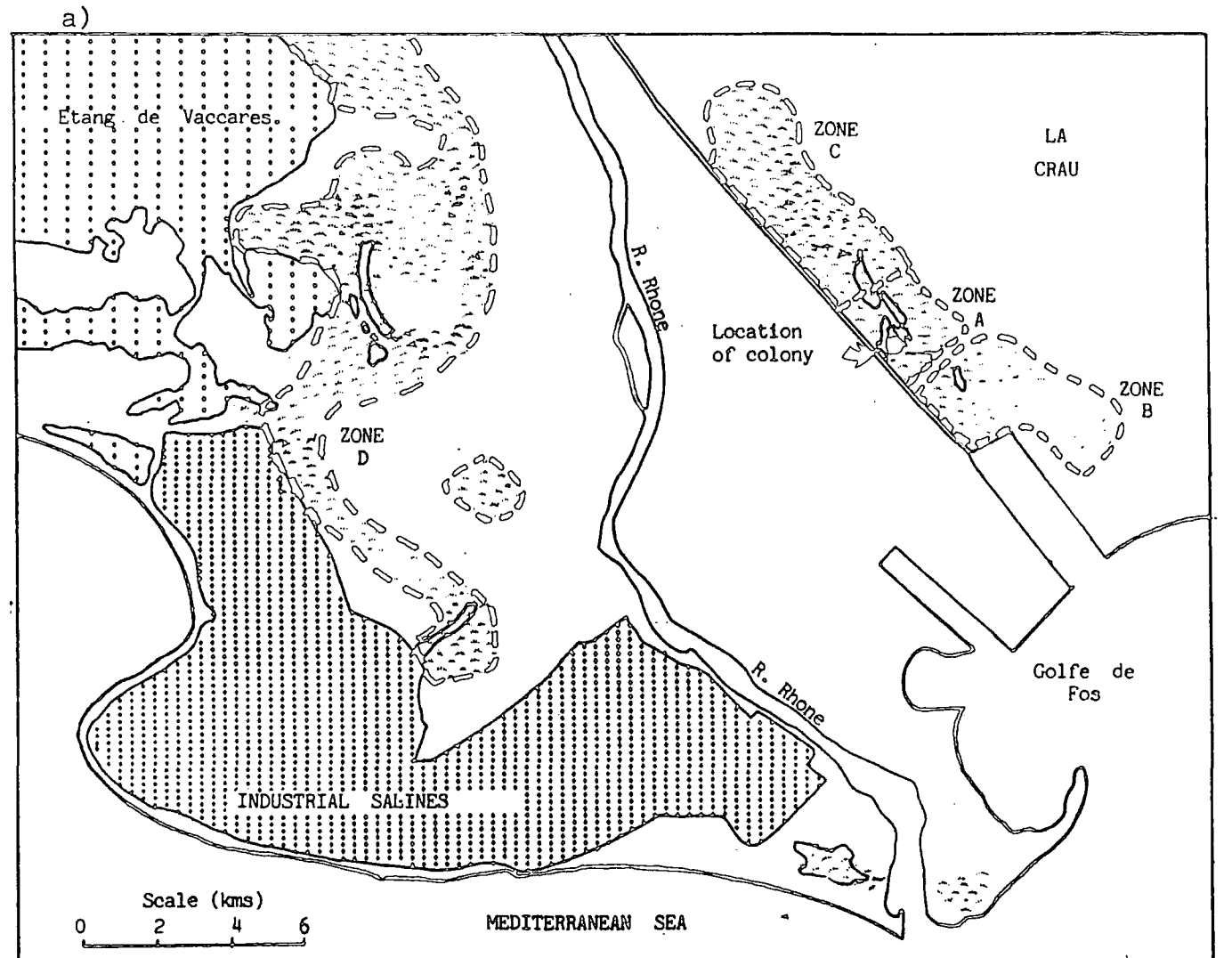
- 1). The number of nesting pairs was not limited by the availability of suitable nesting habitat.
- 2). Areas of feeding habitat around the colony were limited and distinct. Destinations of foraging adults departing from the colony could therefore be assigned to specific areas.
- 3). Access to the colony was good. Departure of foraging adults could be observed from a raised vantage point 500m from the colony. The colony could be approached closely by boat, and the reedbed was penetrable on foot.
- 4). The colony was on a well-guarded wildfowl hunting property, free from disturbance in spring and summer. No habitat management occurred in the vicinity of the nests.
- 5). The colony contained very few pairs of Grey Herons, a species which overlaps greatly with the Purple Heron in its ecological requirements, and might have competed for food resources or feeding localities.

Figure 3.1. Location of the study colony at the Etang de Landre:

- a) showing relationship with surrounding feeding areas (A - D).
- b) and c) showing position of the observation point for monitoring foraging departures of adults, in 1981 and 1982, and the location of the tower-hide (1982 only).

⊙ Position for monitoring foraging departures.

A Location of tower-hide.



6). The next large Purple Heron colony was 23km away. Observations suggested that birds from these two colonies overlapped little in their use of the same feeding grounds.

Dawn to dusk observations of the foraging activity of adults at the study colony were made on 12 days in the 1981 and 32 days in the 1982 breeding season. Observations in both years were terminated in early July, with the approach of the hunting season. Assistance with the long observation periods was received in both years, particularly during the nestling phase of the breeding season (see Acknowledgements). Information was collected by two methods:

1. Observations of the Departures of Foraging Adults.

When adult Purple Herons depart on foraging trips from the colony, they fly directly to their feeding areas at heights of between 5-100 metres. They can thus be followed, using binoculars, for distances up to 5 km from the colony. The discrete nature of the available feeding areas around the study colony enabled the destination of each departure to be assigned accurately to a particular feeding zone.

Observations were made, from a raised vantage point 500m from the colony, of the frequency and destination of all foraging trips from the colony, at intervals of a few days throughout the breeding season. The timing of all departures was recorded to the nearest minute into a tape-recorder, with information on flocksize and destination (foraging zone). Departures around dawn

detected on the ground was 500-700m (compared with 5km in the air), because the habitats in which they both breed and feed have a swamping effect on signal strength. The information collected was therefore restricted to recordings of their attendance at the colony, plus regular monitoring of their departure directions. Because of the above limitations, the technique was not continued in 1982.

Access restrictions to the study colony were lifted in 1982, permitting intensive observations to be made at marked nests. The problem of observing heron activity at nests hidden by reeds was partly overcome by the use of a 4m high tower-hide. This was constructed on a floating raft of six 200 litre oil drums. The tower was positioned before the arrival of the first Purple Herons, in March 1982. The first pairs to return built their nests within 40m of the hide. Contents of these nearest nests were partially visible at the start of the breeding season, but became rapidly hidden by new reed growth. I selected 17 study nests near to the hide. These were marked with tall bamboos, individually colour-coded with plastic tape, visible from the observation tower. From breeding studies, reported in Chapter 4, it was known that no broods larger than four chicks ever survived to fledging. To ensure that the food demands of the broods in the study nests would be comparable, I adjusted the five study nests which contained only three chicks at hatching, by adding a fourth chick of the correct age, shortly after hatching.

and dusk could not always be recorded accurately because of the poor light and fog, and these periods have been excluded from the analyses.

Nocturnal activity at the colony was monitored on 4 nights in 1981 and 7 nights in 1982 (from the tower-hide). These observations included nights of both full and no moon. The level of activity was recorded both visually, with image intensifying binoculars, and acoustically by listening for the characteristic calls of adults returning to their nests with food for their young. In addition a certain amount of information was collected in 1981 from the nocturnal attendance at the colony of two radio-tagged breeding adults.

2. Observation of the Behaviour of Individual Herons.

It is very difficult to study the behaviour of breeding Purple Herons, because they both breed and feed in closed vegetation, and are extremely intolerant of human disturbance. Additionally, in the Camargue they fed at up to 15km from the colony and frequently on hunting properties where access was often restricted. No attempt was made to colour-mark breeding birds. Instead, seven breeding adults were captured in 1981 and equipped with radio-transmitters, to support the data already being collected from observations of arrivals and departures. Subsequent transmitter failures and nest-desertions meant that only three individuals gave information during the breeding season. The maximum range over which these birds could be

It was possible to recognise the adults from the study nests without marking them as individuals. Purple Herons are strictly monogamous, and the individuals visiting one nest could therefore confidently be assumed to be of the same pair. The individuals of several pairs could be separated by plumage differences, particularly the colour of their wing-coverts. It was known from the results of radio-tracking, and numerous other observations, that individuals were very faithful to particular feeding zones (see below). It was therefore possible to identify the individuals of a pair simply by observing their arrival and departure directions at visits to the nest. Of the 17 study nests observed, there were 6 for which the two members of the pair fed in the same zone, and could not therefore be separated. These birds were excluded from analyses in which it was necessary to identify the members of the pair.

Dawn to dusk observations were made to record the timing of all arrivals and departures at the study nests. For several individuals which fed in the local marshes, it was possible to plot their precise feeding destinations on a map, in relation to known landmarks. For individuals foraging further away, their feeding zones (see Figure 3.1) were recorded for as many foraging trips as possible.

RESULTS.

Use of Feeding Areas.

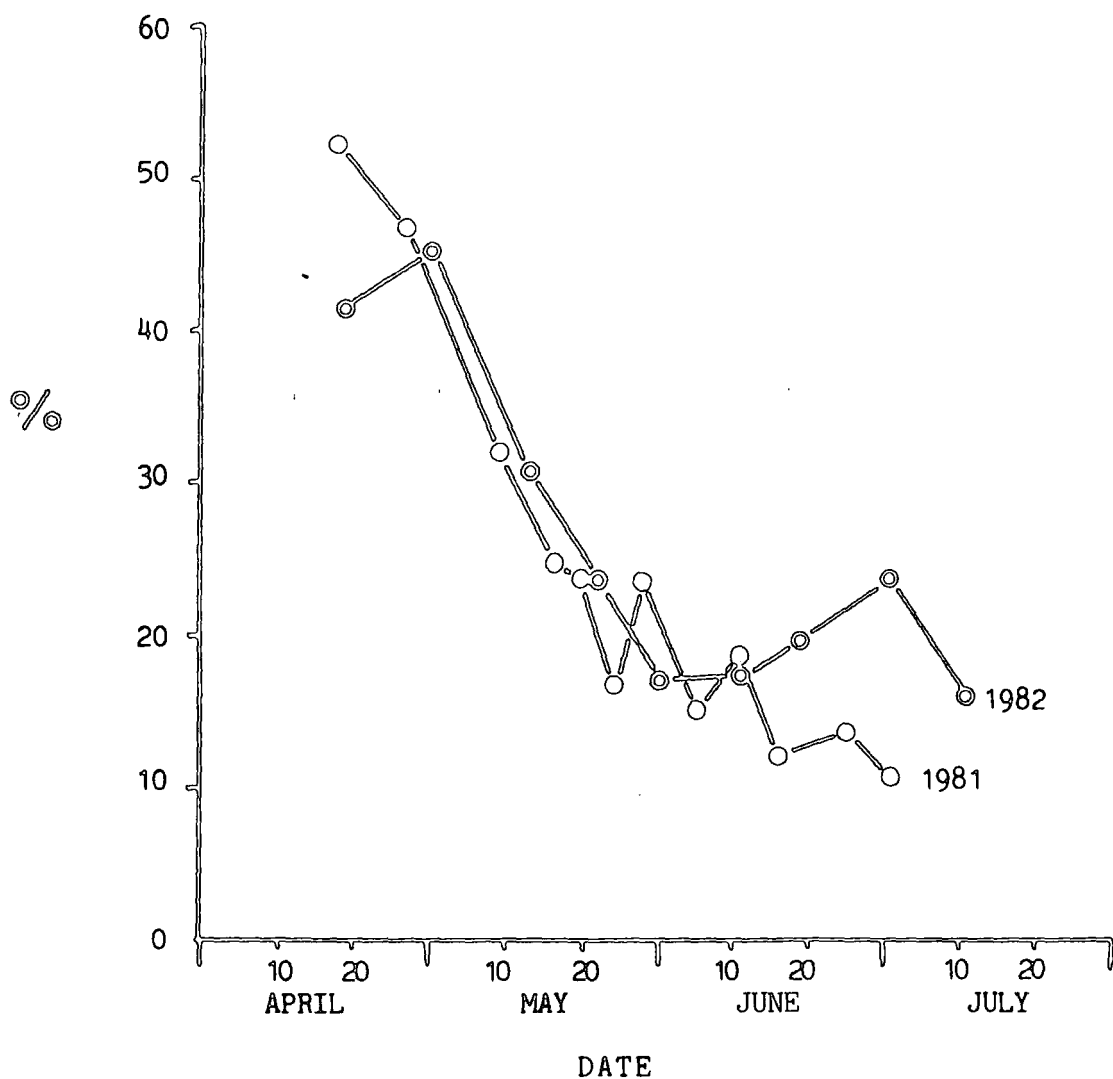
Breeding Purple Herons fed at distances from their nests of tens of metres to up to 15km from the colony. Suitable feeding grounds

at distances greater than this lay in one direction only(at the Grand Mar, ca 22km NW), and no herons were observed either departing in this direction or flying over observation points between the two areas. Diet studies, reported in Chapter Five, confirmed observations that the herons did not feed in the brackish lagoons of the Réserve Nationale of the Camargue which span a large surface area from 15 to 30km to the west of the colony.

The four discrete zones of feeding habitat used by herons from the study colony(Figure 3.1) were separated by large expanses of unsuitable habitats which were not used to any great extent by foraging herons. Within each zone, a complex patchwork of different feeding habitat types were available (temporary and permanent marshes, ditches, canals, etc.). It was not possible to measure the quantity or quality of available food resources in each zone, particularly as these may fluctuate rapidly in response to changes in water levels, temperature etc.. I have assumed that the relative opportunities for feeding offered by each zone remained approximately the same throughout the breeding season.

The relative usage of these four feeding areas by herons from the colony changed during the course of the breeding season. Similar patterns were observed in 1981 and 1982 (Figure 3.2). At the start of each season, approximately half the departures were to local feeding areas(less than 2km from the colony). As each season progressed, the proportion of departures to local feeding

Figure 3.2. Seasonal variations in the percentage of departures of Purple Herons from the colony to feeding grounds less than 2km from the colony. The data are based on the total number of departures observed during each day of observation.



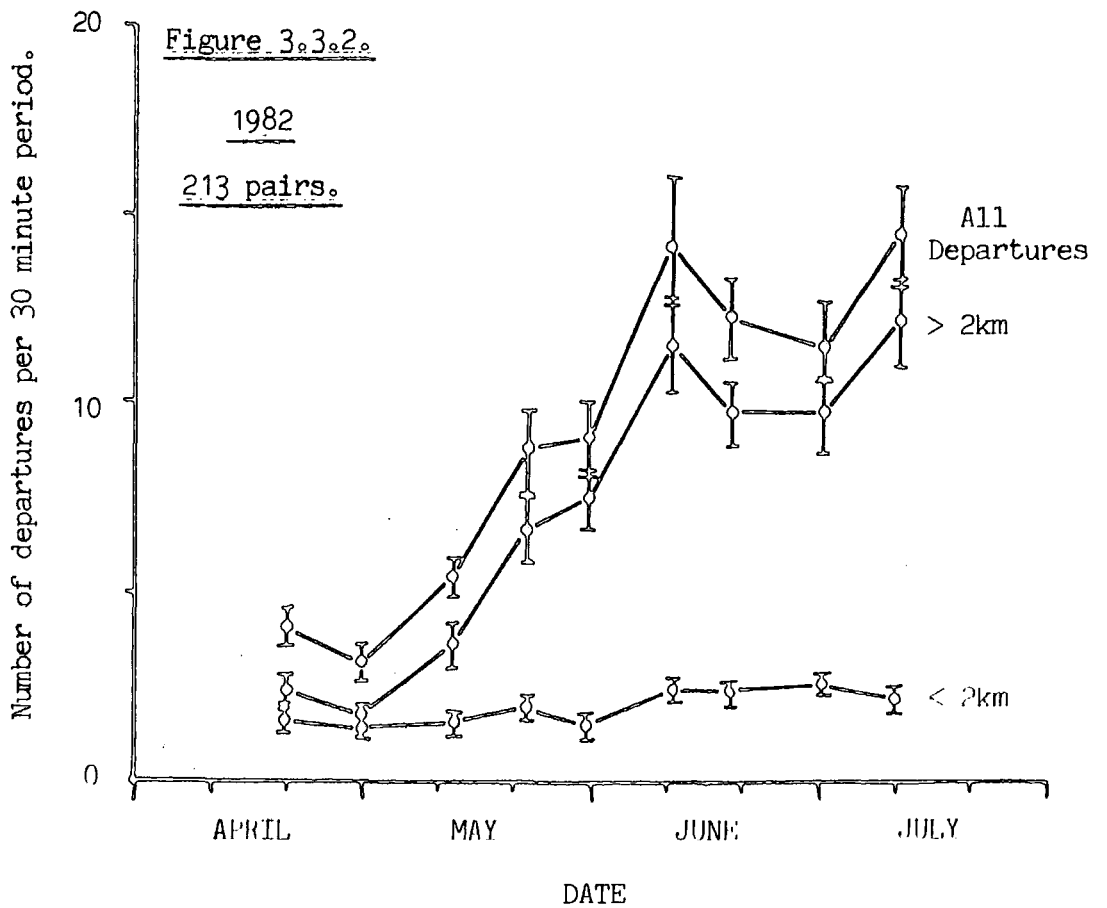
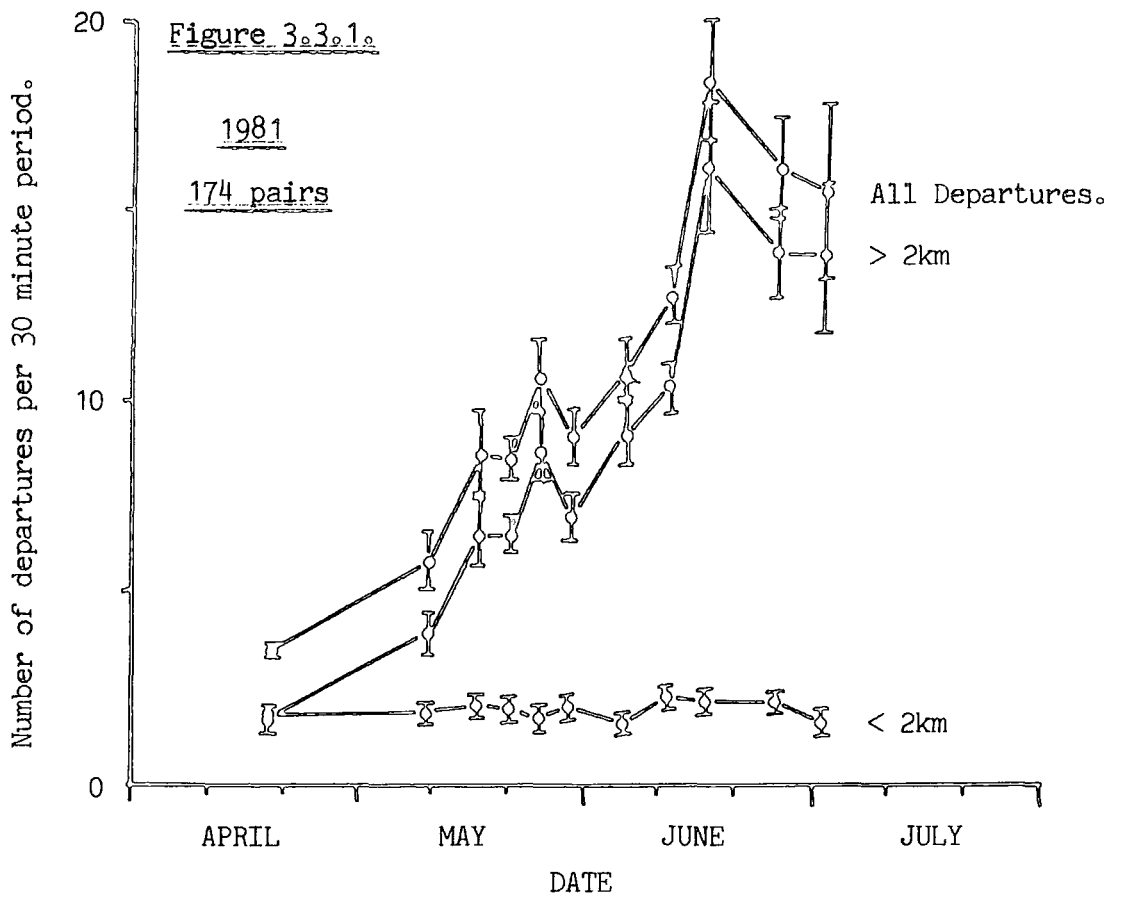
areas diminished, until in early to mid July only 10 - 15% of the departures were to these areas, while the majority of individuals went to feed at distances up to 15km away.

Examination of the absolute rates of departures to the different zones (Figures 3.3.1 and 3.3.2) helps to interpret this pattern. Again, there is very good agreement between the results from 1981 and 1982. At the start of the season in mid-April, the total rate of departures from the colony was low because few nests were occupied, and the incubating adults did not have to make frequent foraging trips to feed their nestlings. The rate then increased to a peak in mid-June, which was 3-4 times the rate in April. This corresponded with the period when the majority of nests contain young (Chapter 4). Despite this dramatic increase in the rate of all departures from the colony, the rate of departures to the local feeding areas remained constant from the beginning of May to July, in both years (1981: $t = 0.001$, $P > 0.10$; 1982: $t = 2.56$, $P > 0.05$). Thus, increases in the rate of all departures from the colony arose entirely from the increased rate of departures to the more distant feeding zones. Furthermore, although there were more pairs in 1982 than in 1981, there was no significant difference between the two years in the rates of departures to the local feeding areas ($t = 0.976$, $P > 0.10$). (NB. The peak rate of all departures in 1981 was higher than in 1982, despite the number of nesting pairs being lower. I believe this was due to a greater synchrony in nesting in the first year, which is indicated by the broader but lower peak in 1982). These findings suggest that the local feeding areas were filled at the beginning

Figure 3.3.1. Seasonal variations in the rate of departures of foraging Purple Herons from the colony of Landre to feeding areas at different distances from the colony, in 1981.

Figure 3.3.2. Seasonal variations in the rate of departures of foraging Purple Herons from the colony of Landre to feeding areas at different distances from the colony, in 1982.

Data for both years are presented as the mean (\pm 1 SE) number of departures to each zone per 30 minute observation period, for each day of observations. 'Near' feeding areas are defined as those less than 2km from the colony. 'Far' feeding areas are between 2km and 15km from the colony.



of the season to a level which was not exceeded either later in the season when the total number of individuals in the colony was far greater, or between years when colony size was different. An examination of the behaviour of individual birds helps to interpret this pattern.

Behaviour of Individual Birds.

Trial radio-telemetric studies in 1981 suggested that breeding adult Purple Herons were very faithful to individual foraging zones. Only three individuals gave adequate information, but during 73 foraging trips to observed destinations, all three birds remained faithful to their original foraging zone.

More detailed observations on a larger sample of individuals were collected in 1982 from the tower hide. In general, these observations supported those of 1981, namely that each bird showed a high degree of fidelity to a particular foraging area. However, three individuals of the 34 observed moved permanently from zone C, at a time when the marshes in that area were being artificially drained for hunting management purposes. Two of these moved to zone A, and a third to zone D; they then remained faithful to these zones. In addition, several instances were observed when individuals which normally fed in the more distant areas stopped to feed in the local marshes. Such birds would leave the colony on their normal flight path and suddenly drop into the local marshes, suggesting that they may have observed an empty feeding site while flying over. Individuals which normally

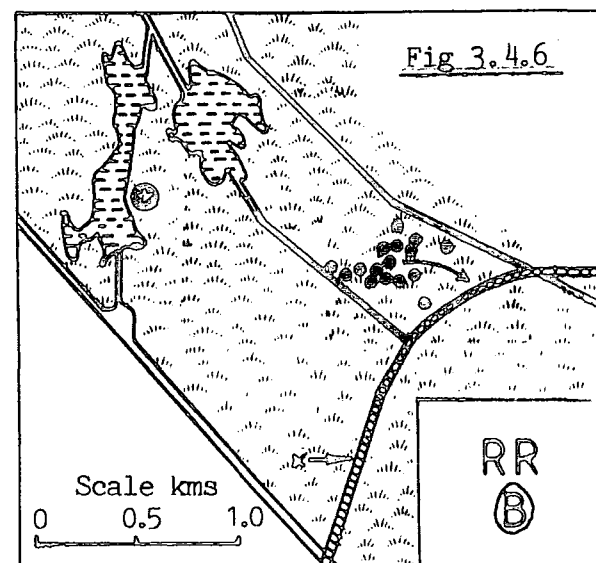
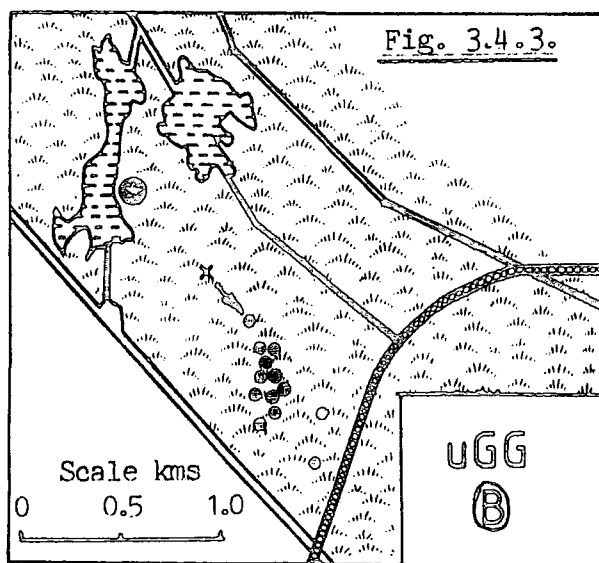
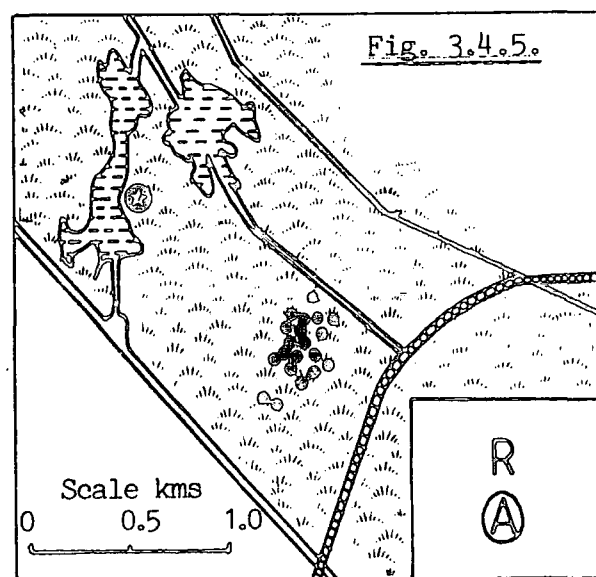
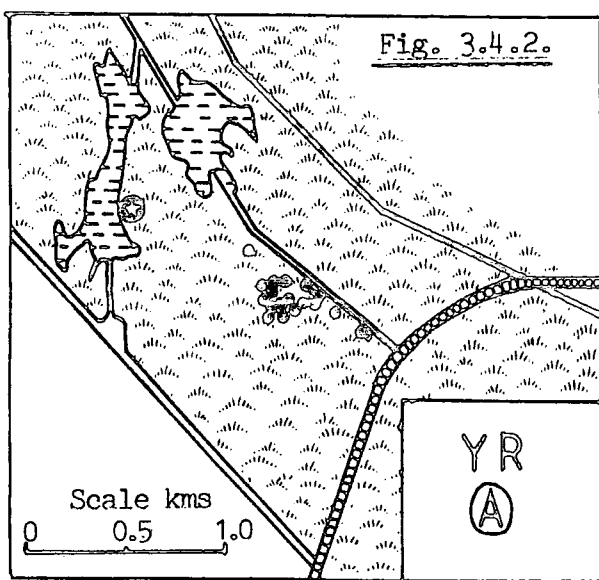
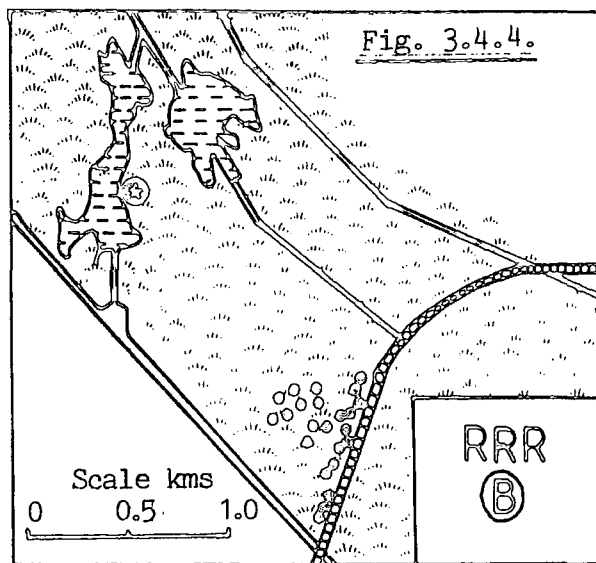
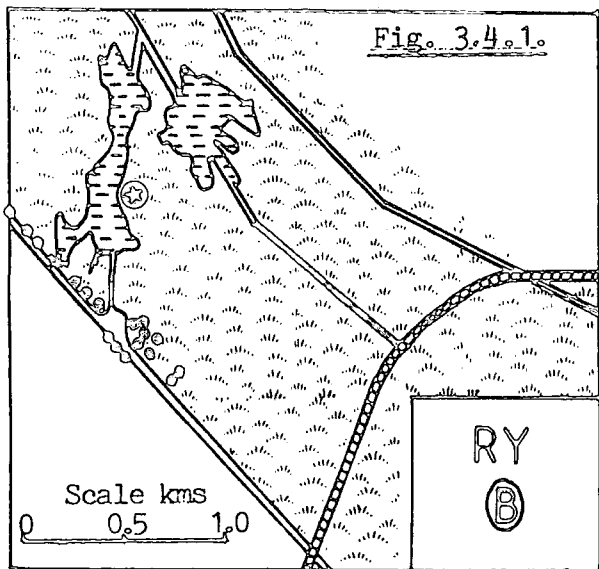
fed in the local marshes were never observed to fly to the more distant zones.

The precise feeding locations of six individuals which fed only in the local marshes were monitored throughout the nesting season. Records were made of their foraging flight destinations in relation to known landmarks, for large samples of foraging trips. The results of these observations (Figures 3.4.1 to 3.4.6) showed that not only were these individuals faithful to the local marshes, but also that they restricted their foraging to very limited areas within that zone. Several pieces of information strongly suggest that these individuals were defending feeding territories. Firstly, there was remarkably little overlap in the feeding sites visited by individual birds, despite these sites occupying a large proportion of the local marshes available to the south of the colony. (Some apparent overlap may have resulted from errors in estimating the precise landing position, but these were thought to exceed no more than a 50m radius around the true landing point). Secondly, a number of aggressive interactions between these birds were observed on their feeding grounds. On three occasions, an individual which attempted to land in an area slightly away from its normal foraging site was observed to be displaced and chased almost immediately by another individual, and eventually settled to feed in its normal area. On a fourth occasion, another individual was observed to displace and chase another Purple Heron out of its normal feeding area, when it returned to its feeding grounds from the colony.

Figures 3.4.1 to 3.4.6. Observed landing points of six individual Purple Herons which fed in the marshes near to the colony. Observations were for all departures seen from the tower, throughout the breeding season. Exact landing locations are plotted in relation to known landmarks (canals, bushes, pylons etc.). The position of the colony is shown by an asterisk. The symbols in the lower right hand corner are the nest code of the individual. The observations for individual YR Ⓐ were from an extra study nest, and were included in this Figure to boost the sample size. The data were not included in later sections, due to disturbance of this nest by myself.

Symbols

- Observed landing point; no interaction.
- x Observed landing point, followed by immediate displacement by another bird.
- ↘ Observed landing point, and aggressive interaction immediately observed to displace another individual from this site.



The two members of a pair did not share a feeding territory, nor necessarily feed in the same zone. Indeed, there was neither a positive nor a negative association between the zones used for feeding by the two birds. The observed frequency of feeding in the same zone was not significantly different from that expected if birds had been assigned randomly to pairs on the basis of the observed numbers occupying each feeding zone (Table 3.1). I never observed the partner of a bird, known to be holding a feeding territory, visit that territory.

Temporal Variations in Activity.

Nocturnal Behaviour.

Eleven nights were spent at the colony to examine the extent of nocturnal activity. No major activity was observed, and in contrast to the daylight hours the colony was very silent by night. The results of the observations are summarised in Table 3.2. It is concluded that Purple Herons do not normally feed their nestlings by night. The single observation of large grouped departures of fledging nestlings on 09.07.82 is not understood, but may have been related to the avoidance of predators.

Adult Purple Herons continued to depart from the colony until dusk (Figure 3.5), implying that at least some individuals were absent from the colony during the night. This was confirmed from a small amount of data collected for two breeding Purple Herons (not of the same pair) which had been equipped with radio-transmitters. Neither bird showed activity at the colony during the night, in accordance with other observations. However,

Table 3.1. Association between the feeding zones occupied by partners of breeding pairs at the study nests.

Observed Frequencies(pairs).

		Partner A				
		Feeding zones	A	B	C	
Partner B	A	1	-	-	-	N=17 pairs
	B	1	1	-	-	
	C	2	3	4	-	
	D	0	2	3	0	

Null Hypothesis: there is no association between the feeding zones occupied by the two members of a pair.

	Feeding Areas	
	Joint	Not joint
Observed	12	22
Expected	10.9	23.1
$(\text{Obs.} - \text{Exp.})^2 / \text{Exp.}$	0.11	0.05

$$\chi^2 = 0.16 \quad 0.95 > P > 0.05$$

Table 3.2. Summary of observations made of the nocturnal feeding activity of breeding Purple Herons at the colony of the Etang de Landre, in 1981 and 1982.

1981: Observations made from a raised observation point 500m from the colony, on a major flyway between colony and feeding grounds.

DATE	MOON	ACTIVITY
19/20.5.81	Full	No activity.
27/28.5.81	Quarter	No activity.
05/06.6.81	Half	No activity.
09/10.6.81	Quarter	No activity.
10/11.6.81	Quarter	No activity.
16/17.6.81	Full	No activity.
24/25.6.81	Quarter	No Activity.

1982: Observations made from the tower-hide.

18/19.5.82	None	Very little activity after nightfall, excepting a few calls from roosting birds. None observed in flight.
25/26.5.82	New	Birds arriving for up to 25 minutes after dusk. A single possible feed at 0043, and some noise from other sectors. No birds seen in flight.
08/09.6.82	Full	Almost no activity, except for a single definite departure at 0203 to zone D, and another possible departure at 0350.
09/10.7.82	Half	Last birds into colony 15 minutes after last light. Silence until 0105 when many chicks started calling and flying. Flock of 5 departed to NE. 0125, 3-5 more chicks depart. 0135, 8 chicks seen together. Nothing more until dawn. A possible feed at 0130?

each spent a number of nights away from the colony. Examination of the number of nights when these birds were either absent throughout the night, or absent after dusk or before dawn (Table 3.3), suggest that the members of each pair share equally the number of nights spent at the colony while incubating or guarding young chicks. When the chicks became old enough to be left unguarded, a significantly higher proportion of nights was spent away from the colony (Both individuals combined: $\chi^2 = 4.072$, $0.01 < P < 0.05$). No conclusive evidence was obtained as to whether birds absent from the colony at night were foraging, or simply roosting elsewhere.

Diurnal Patterns of Activity.

Adult Purple Herons were active at the colony throughout the daylight hours, from shortly before dawn to just after dusk (Figure 3.5). The daily pattern of departures was characterised by a peak at dawn, when a large proportion of the individuals which had roosted at the colony departed for the feeding grounds, followed by a relatively constant number of departures throughout the day. Observation of individual nests during the incubation phase, showed that changeovers of the adults occurred one, two or three times daily, with a modal frequency of once per day (71% of the nest-days observed during this period ($n=63$)). Thus, both adults shared equally in incubation. Changeovers of the members of each pair on the nest occurred mainly during the middle of the day, with few in the early morning or late evening (Figure 3.6). During the changeovers, the two adults spent on average only 18.7 ± 1.3 seconds together at the nest ($n=43$ timed changeovers),

Table 3.3. Nocturnal attendance at the colony by two radio-tagged adult Purple Herons, from different nests, showing the percentage of observed nights(N) in which the two individuals were present in the colony.

	Channel 14 (fed in Zone B)	Channel 15 (Fed in Zone D)	Both
Incubation and Guarding Phase(Chicks < 25 days old)	66.7(15)	37.5(16)	51.6(31)
Chicks unguarded (>25 days old)	22.2(9)	22.2(9)	22.2(18)

Figure 3.5. Diurnal activity patterns of adult Purple Herons at a breeding colony. Figures show the percentage of the daily foraging departures from the colony in each half hour period, throughout the day, on four different days.

19.04.82 Incubating nests only; no chicks in colony.

20 & 28.05.81 The majority of nests contain young chicks, but some are still incubating.

11.06.81 All nests now have chicks; some very large.

Figure 3.5.

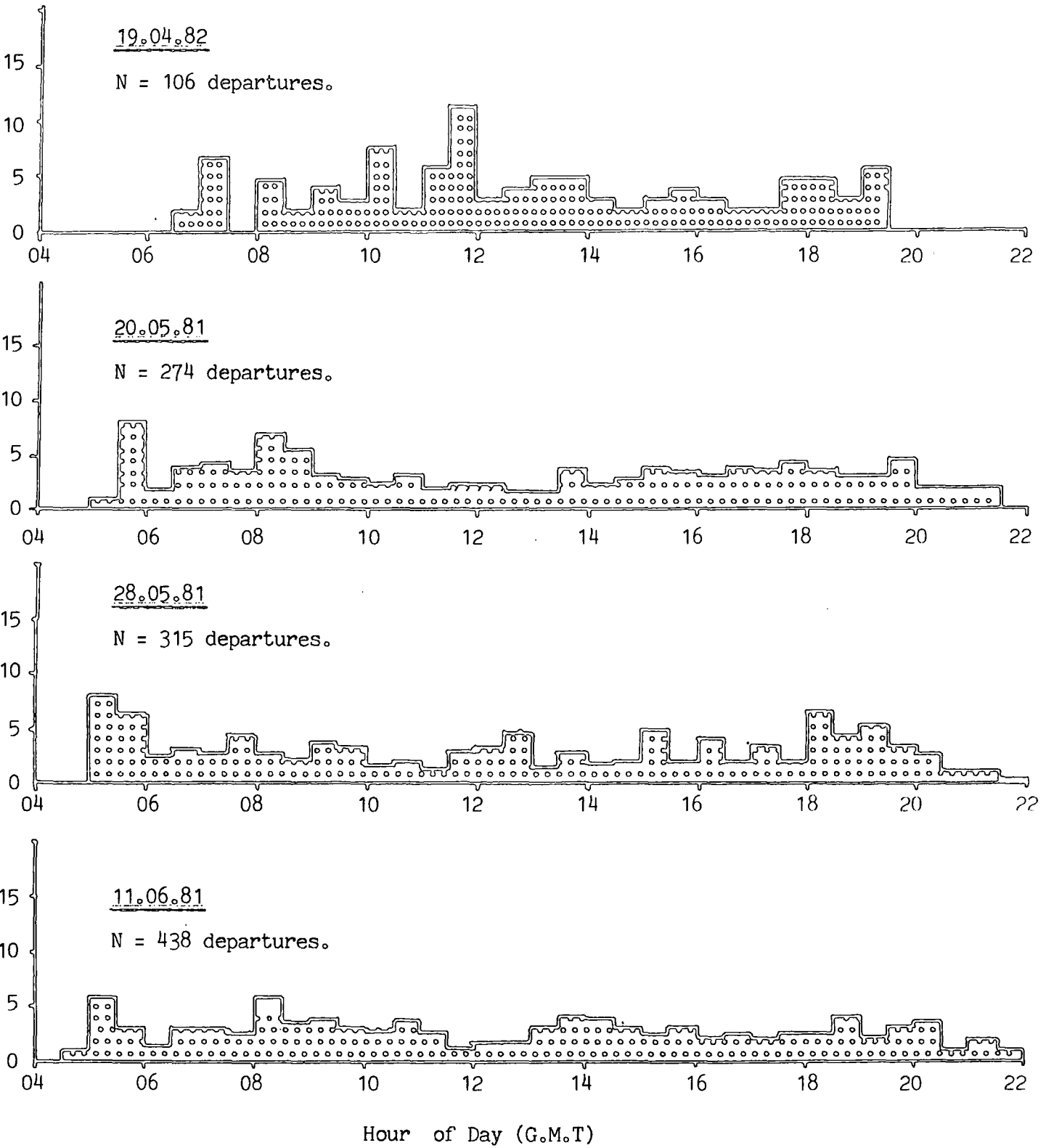
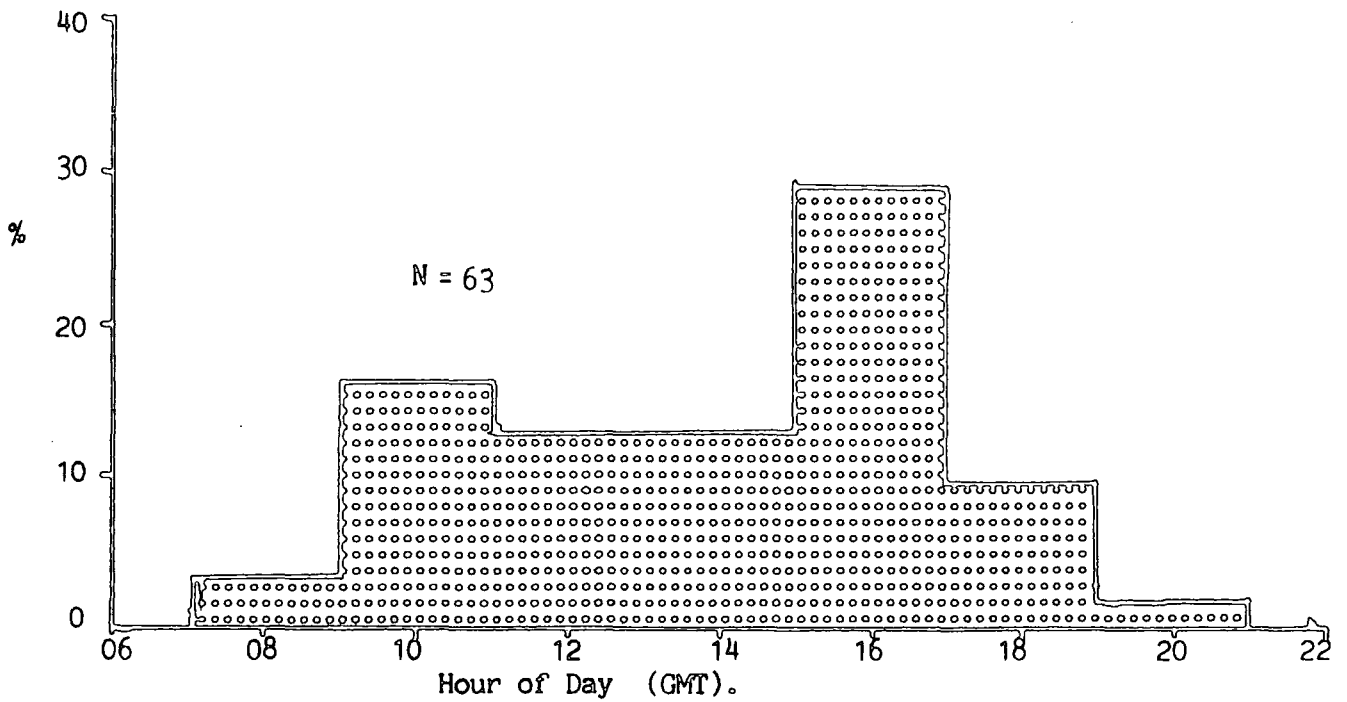


Figure 3.6.

Daily timing of Changeovers at the nest during the incubation period for adult Purple Herons breeding in the Camargue, in 1982. Data were collected for the 17 study nests at the colony of the Etang de Landre.



before the relieved bird left the colony. From hatching, until the chicks were ca. 20 days old, they were guarded by one adult always, with changeovers occurring regularly throughout the day, as the adults returned to feed the brood. From the end of the chick-guarding phase until fledging (ca. 45-55 days), both adults fed the nestlings.

Duration of Foraging Trips.

From the observation tower, 218 foraging trips were recorded for which the identity of the adult and its destination and time spent on the feeding grounds were known. The latter was calculated as the time interval between the departure from and return to the nest, minus the time required to fly the round trip from colony to feeding grounds. I measured flightspeeds under calm conditions by timing individuals on flight-paths between two known points. Purple Herons flew at an average ground speed of 44 km/hr, with no significant differences between outward and return journeys ($t = 0.91$, $P > 0.05$). I assumed that each adult flew to the centre of its known foraging zone. For zones A, B, C and D these distances were 1.1 km, 3.4 km, 4.5 km and 13.5 km, respectively. The estimated flying times to the nearest minute were thus 3, 9, 12 and 37 minutes for the round trip.

I could not measure the total number of foraging trips made by an adult in a day, since the first departures and last arrivals occurred before dawn and after dusk respectively, at which times they were not visible. Instead, I have examined the duration of individual foraging trips.

Round-trip times ranged from 72 to 746 minutes. The mean time spent on the feeding grounds per foraging trip for adults feeding in the four feeding zones, and for four age-classes of nestlings are shown in Table 3.4. The four age-classes relate to the early and late guarding phases (only one adult foraging), and the early and late post-guarding phases (both adults foraging). The time spent on the feeding areas per foraging trip varied significantly with the age of the brood for adults feeding at two of the four feeding zones (A and C). This followed a pattern related to the increasing food demands of the brood, and the release of the second adult for foraging at the end of the guarding phase. A similar pattern was observed for the two remaining feeding zones (B and D), although the differences were not statistically significant. Adults spent longest on the feeding areas when the food requirements of their brood were lowest (ie. just after hatching), and least time just before the end of the guarding phase, when despite the high food requirements of the brood, only one adult could forage at a time. In the early post-guarding phase, there was a temporary increase in the average duration of each foraging trip as both adults collected food simultaneously, followed by a reduction again as the chicks grew older.

There was no significant variation in the time spent feeding per foraging trip by birds feeding at different distances from the colony, except for those feeding very young chicks. For this group, significantly longer was spent on the feeding grounds by those feeding far from the colony than by those feeding nearby

Table 3.4. Time spent on the feeding grounds, per foraging trip, by adult Purple Herons while feeding nestlings. Data are the mean values (minutes) \pm 1 SE (N) for four age classes of chicks, for adults feeding in each of the four foraging zones.

ZONE	Age of nestlings (days)				
	1-10	11-20	21-30	>30	
A	187.8 \pm 50.2(14)	152.1 \pm 29.8(26)	209.2 \pm 40.2(27)	194.7 \pm 40.6(23)	*
B	223.8 \pm 67.4(11)	174.3 \pm 46.5(14)	186.8 \pm 48.3(15)	187.7 \pm 76.6(6)	ns
C	267.6 \pm 61.4(19)	169.1 \pm 36.0(22)	248.8 \pm 82.9(9)	246.3 \pm 142.4(3)	**
D	338.2 \pm 138.0(6)	188.9 \pm 56.9(11)	254.1 \pm 89.8(8)	175.8 \pm 87.9(4)	ns
Excluding travel time	*	ns	ns	ns	

Note: Asterisks denote the level of significance when the respective groups are analysed for heterogeneity by a one-way ANOVA. Thus, * = 0.01 < P < 0.05
 ** = 0.001 < P < 0.01
 *** = P < 0.001

Significance of diffs. with travel time included. ** * ** ns

(Table 3.4). For adults feeding broods over 20 days old, time spent on the feeding areas was correlated with the time spent feeding the chicks on return to the nest ($r = 0.248$, $0.01 < P < 0.05$), indicating that longer feeding bouts, on average, resulted in larger prey loads being delivered to the nest. There were significant differences in the time spent feeding chicks at the nest for adults feeding in the four zones (One-way ANOVA: $F = 3.376$, $DF = 3,64$, $0.01 < P < 0.05$). The mean values for zones A, B, C and D were 136.7, 128.8, 110.3 and 213.9 seconds. Thus, there was some indirect evidence that birds visiting the most distant feeding sites were bringing back larger prey loads to their nests.

Comparison of the duration of entire foraging trips (ie. including travel time) for birds feeding at different distances, indicated that those feeding a long way from the colony made significantly longer trips than those feeding near to the colony. This was true for birds foraging for the three youngest age-classes of chicks (Table 3.4), but not for those with the oldest chicks where the sample was small.

DISCUSSION

a) Occurrence of Territoriality.

Although the individual adult Purple Herons studied were all faithful to particular feeding zones, it was not known whether each defended an exclusive feeding territory. Detailed observations were made only for those individuals feeding

adjacent to the colony, all of which were found to defend long-term feeding territories. However, there was evidence to suggest that these were preferred feeding areas, so that although it may have been advantageous to defend feeding territories here, it may not have been so on areas more distant from the colony.

The local feeding zones were composed largely of permanent marshes, which offer predictable water levels and food supplies atypical of the temporary marshes which cover much of the Camargue. The latter marshes are exploited to a lesser degree by foraging Purple Herons, which may not necessarily defend feeding territories on such habitats. Similarly, Krebs(1974) showed that Great Blue Herons Ardea herodias defended feeding territories on inland canals and marshes, whereas they fed in loose aggregations on the ephemeral food supplies provided by tidal habitats. There are several other reports of species in which only a part of the population defends feeding territories eg. Pied Wagtails Motacilla alba(Davies 1976, 1981), Grey Plovers Pluvialis squatarola (Townshend et al. 1984) and Grey Herons (Marion 1984). The need for measures of the costs and benefits of territoriality, as opposed to alternative strategies, is discussed in a review of the subject, by Davies(1980).

Why Defend Feeding Territories?

The occupation of long-term feeding territories by Purple Herons implies that they contain a resource worthy of defence. Such resources could be mates, food, or access to food(ie. feeding places).

The members of a pair did not share or even visit each other's territories, which strongly implies that territorial defence is not related to the acquisition of mates. Food resources (predominantly fish - see Chapter 5), were extremely abundant throughout the breeding season in the permanent marshes surrounding the colony, and it seems most unlikely that this could have been a limited resource. In contrast, the number of sites from which the herons could gain access to food was limited by the extensive areas of water deeper than their maximum wading depth. Although no data were collected, I observed that the individuals feeding on the lagoon in front of the colony tended to visit adjacent feeding sites (shallow water on the margin of the lake) successively, in a manner very reminiscent of the patch use by feeding Pied Wagtails reported by Davies (1976). In that example, the territorial wagtails visited riverbank feeding sites and temporarily depleted the prey resources therein; these resources then re-accumulated before the bird again visited that site. Dugan (in prep.) has reported very similar use of 'foraging circuits by Little Egrets in Camargue. The same mechanism may also work for territorial Purple Herons, whereby a bird feeding at a particular site would cause local depletion of available prey, either through eating them, or through scaring them into deeper water where they would be inaccessible. In their study of the feeding ecology of the Goliath Heron Ardea goliath, Mock and Mock (1980) reported a very similar use of feeding sites - in this case floating mats of Potamogeton. By defending and using such sites successively, the birds ensured a higher rate of food

intake than if sharing such sites with other individuals, or by visiting sites randomly. If this hypothesis were correct, it would explain why the individuals of a pair do not defend the same territory. This aspect requires further investigation.

What limits colony size?

Colonies which are not limited in size by the availability of adequate breeding habitat, must be limited in size by some other factor. Thus, Coulson and Dixon (1979) reported that colonies of Kittiwakes Rissa tridactyla did not grow in the manner expected of an expanding population, but that the rate of increase became progressively less as the colony increased in size. For the Purple Herons, there was little evidence that more pairs bred in such colonies in years when many other colony sites had been destroyed, at which time there must presumably have been a large surplus of potential breeders in the area. The evidence for other species of heron, from regions where most colonies were limited in size by factors other than a lack of suitable breeding habitat, strongly points to food resources (or access to them) as a key factor (Lack 1954, Braaksma and Bruyns 1960, Fasola and Barbieri 1978, Burger 1981). Similarly, Ashmole (1963) concluded that competition for food during the breeding season could regulate the size of tropical seabird breeding colonies.

The results presented in this chapter provide strong evidence for a mechanism for the density-dependent regulation of colony size in Purple Herons. The feeding areas adjacent to the colony became

filled at the start of the breeding season, to a level which was not exceeded later in the season even though the number of individuals feeding from the colony was far greater. Secondly, there was no difference in the use of the near areas between 1981 and 1982, despite the increased number of pairs breeding in 1982.

Increases in the number of departures from the colony later in the season were explained entirely by a higher proportion of birds feeding in more distant zones. Thus, during the course of each season, individuals joining the colony became increasingly less likely to find feeding places near to the colony, and therefore incurred the extra cost of travel time related to feeding in the more distant areas. There is little evidence for similar mechanisms among other colonial species, although Evans(1982) reported that foraging Black-billed Gulls Larus bulleri used feeding sites efficiently by foraging at sites close to the colony, when these were available.

Foraging Trips, Parental Effort and the costs of Foraging at long distances from the colony.

All observations related to nests containing either four or five chicks. Since no broods greater than four chicks were ever observed to survive to fledging(Chapter Four), I have assumed that the adult herons at the study nests were collecting food at or near their optimal working capacity(sensu Royama 1966). Indeed, the herons continued foraging for their nestlings throughout the day, spending little or none of the daylight period at the colony, except when guarding chicks. Other maintenance activities, such as resting or preening, apparently

occurred either while on the feeding areas, or at night. This contrasts with some other colonial species, such as Shags Phalacrocorax aristotelis (Pearson 1968), and Common Terns Sterna hirundo (Courtney and Blokpoel 1980) which may spend a large proportion of the daylight hours loafing at the colony.

Purple Herons did not feed their chicks by night, and clearly the demands of their brood had to be met during the available hours of daylight (max. 18 hours). These demands were further restricted by the need for broods younger than ca. 20 days old to be guarded both day and night by one parent. The average duration of foraging trips varied with the age of the brood (Table 3.4.), in a pattern related to changes in the food demands of the brood per adult foraging. Trips were shortest when food demands on the adults were highest, implying that they could increase their food delivery rates to the nest by an increase in foraging effort. The shortest foraging trips were recorded when the brood was aged 11-20 days old, at which time only one adult was foraging. This must therefore represent a potential bottleneck period in the breeding cycle at which time overall breeding success may be determined (see Chapter 4). Galbraith (1983) reported similar conclusions for Kittiwakes Rissa tridactyla, and suggested that the degree to which adults were prepared to leave their broods unguarded was related to the difficulty experienced in feeding their brood. In this species, temporary desertion of the brood by both adults occurred at night, when the chance of predation by Herring Gulls Larus argentatus was slight. Nest-predation of reed-nesting herons by Marsh Harriers is common, and adults are

therefore unable to desert their nests by day, until the chicks are able to leave their nests to hide in the reeds. Heat stress in young chicks, from direct exposure to the sun, must also be a severe problem requiring the adults to shade them at the nest. Chicks older than 20 days can leave their nests to hide in the reeds from predators and gain shade from the sun. Since adults do not feed their chicks by night, the option of temporary desertion, seen in the Kittiwake, is not available to Purple Herons. Following the end of the guarding phase, joint parental feeding effort doubles the potential food delivery rate of the adults to the brood. A slight increase in the time spent feeding per foraging trip was observed in this period, suggesting a temporary release in parental foraging effort.

Flight is metabolically the most expensive activity that an adult Purple Heron is likely to undertake while rearing nestlings. Tinbergen, in Drent and Daan (1980), showed that daily variations in body weight of adult Starlings Sturnus vulgaris foraging for nestlings were negatively correlated with the number of hours per day spent in flight. Thus, at least a part of the energetic cost of flight was born by the adults themselves. Over longer periods, the adults must maintain their own body condition, and the cost must then be born to a large extent by the brood, in terms of the reduced rate of food delivery by the adults to the nest. I have shown that adult Purple Herons are faithful to particular feeding areas, but that these may range in distance from 200m to as much as 15km from the colony. There must be flight-costs associated with foraging in these more distant areas. Such costs can be

divided into those related to the greater energy expenditure resulting from the increased proportion of each day spent flying, and those related to the loss of feeding time which must be spent in flight.

Using data from Table 3.4 for chicks aged 11-20 days (the greatest bottleneck period for the adults), and assuming an 18 hour day available for foraging and equal sized preyloads (see below) from the different foraging areas, I estimate that if both adults are feeding in the same zone, then the daily average number of food deliveries to the nest will be 7,6,6 and 5, for birds in zones A,B,C and D respectively. Thus, not only will birds feeding in zone D incur 12 times the energetic flight-costs of those feeding in zone A, but they will also deliver almost 30% less prey to their nests.

One way in which the adults might reduce the costs of feeding in the more distant areas, assuming that time for feeding is limited, is to fly faster than those birds feeding at the nearer sites. Marion (1984) suggested differences in average flight-speed between individual Grey Herons (not necessarily related to the distance at which they were feeding from the colony), but his observations are difficult to interpret since measures were made under a wide range of wind conditions. I found no difference in flight-speeds of birds when comparing their outward and return trips, but did not make the critical measures of the same bird flying to different distance feeding zones. However, even if birds feeding in zone D were to fly twice as

fast as those feeding in zone A, they would still take six times as long to make the journey, and their flight costs would also be much higher. Increases in flight speed are therefore unlikely to alter significantly the findings.

Another way by which the birds could reduce the costs of foraging in more distant areas is by bringing back larger prey loads, as predicted by the theory of Central Place Foraging (Orians and Pearson 1979). Experimental evidence has supported this prediction for Wheatears (Carlson and Moreno 1981, Brooke 1981). For Purple Herons, I was only able to assess indirectly the size of individual prey loads. Firstly, the time spent feeding per foraging trip did not differ significantly for the birds feeding on the four feeding zones, except when feeding very young chicks (Table 3.4.), at which time the ability of the adults to deliver food to the nest was presumably not limited. However, there were significant differences in the time spent at the nest feeding chicks for adults feeding in the four zones. Thus, there is weak evidence only that birds using more distant feeding zones are delivering larger food-loads to their nests per foraging trip. Further measures of the size of preyloads brought back to the nest, using nestbalances, are required to elucidate the importance of such variations in minimising the costs of distant feeding.

Although, on average, the near feeding areas were occupied earlier than those further away, some individuals chose to forage at distant sites from the very start of the season. Any

advantages gained by foraging in these more distant areas have not yet been considered. Firstly, there may be some very good feeding sites in these areas where the increased costs of extra travel time are outweighed by the increased food intake rates. Secondly, interference competition from other individuals would be expected to decrease with distance from the colony, particularly since there were no other large colonies within 25km of Landre. In an analogous situation, Pienkowski and Evans (1983) demonstrated that breeding Shelduck Tadorna tadorna had higher breeding success in low density areas than in high density areas, because of reduced interference.

The results reported in this chapter, particularly regarding the costs of foraging at long distances from the colony, immediately raise the question of why Purple Herons breed in colonies. Such costs would be minimised by adopting the strategy of breeding in the centre of their feeding territory. Purple Herons could not do this however, since being large and conspicuous they are very vulnerable to ground predators. Thus, they must choose safe places in which to nest, which are inevitably in short supply. Nesting together also gives the additional protection against predators afforded by coloniality (Patterson 1965). Burger(1981) discusses the evolution of coloniality in Ciconiiformes, and concludes that the two main factors contributing to coloniality relate to predation and resource utilisation. Clearly the former is important while it seems unlikely that coloniality has evolved, in Purple Herons, for the exploitation of (food) resources, as indicated by the costs outlined in this chapter. 1

observed no indication of any advantages relating to information transfer between individuals concerning the location of food resources, since individuals fed singly and restricted their foraging to exclusive feeding territories which were occupied throughout the breeding season. Thus, coloniality seems to have evolved in Purple Herons to reduce the probability of nest predation, an important source of nesting mortality(see Chapter 4). The dispersion and large size of colonies in the Camargue may be suboptimal because the availability of suitable breeding sites is limited(see Chapter 2). In support of this, Tomlinson(1974) found that on Lake Mcilwaine, Rhodesia (2630ha.) which had extensive areas of suitable nesting habitat, there were 8 colonies totalling 65 nests, ranging in size from 2 to 19 pairs. A similar dispersion of colonies was noted in La Brenne (Trotignon 1982), an area with numerous ponds and reedbeds, where a total of 148-156 pairs were dispersed over 21 different breeding sites.

An important area for further research and for testing the hypotheses presented in this chapter would be to make direct measures of the costs of foraging in the different zones, by using nest-balances, and to relate these costs to overall reproductive output. I was unable to do this because of the small sample of nests under observation. Any effects were confounded by the contribution that both adults were making to the brood, since they did not necessarily feed in the same zone.

CHAPTER FOUR.

The Breeding Biology of Purple Herons in the Camargue, with particular reference to Seasonal Effects, and mechanisms of Brood Reduction.

INTRODUCTION.

In the previous chapter, I examined foraging costs associated with colonial breeding in Purple Herons. I suggested that these costs may set an upper limit to the size of a colony, because intraspecific competition prevents some birds using the resources in the surrounding feeding areas, so that they have to fly further, lose time for feeding and expend more energy in flight. Early breeders were shown to gain better feeding areas than late breeders, and it was argued that this would enable them to have higher food delivery rates to the nest. In this chapter I summarise the breeding biology of Purple Herons and examine seasonal trends in breeding success. Particular emphasis is placed on the breeding strategies adopted by Purple Herons which maximise breeding success under a limited food supply which may also vary both seasonally and regionally.

Lack(1954,1966) argued that the factor limiting reproductive output in many nidicolous birds was the rate at which the adults could provide food for their young. His view (Lack 1968) that many characteristics of the biology of a species, such as laying date, clutch-size and nestling growth rate, had evolved so that birds, on average, produce the greatest possible number of

surviving young, is now generally accepted (Drent and Daan 1980). In the Purple Heron, the date of the first egg and the size of the clutch are determined some five weeks before the food requirements of the brood begin to peak. In the unpredictable environment of Mediterranean freshwater marshes, a simple adjustment of clutch-size is unlikely to enable them to optimise their brood-size to the feeding conditions prevalent during the nestling phase. Some later adjustment of brood-size is therefore required. Such mechanisms have been reviewed by O'Connor (1978). In general, an asymmetry is set up in the brood such that a competitive hierarchy develops between the chicks, ensuring that at least some chicks gain adequate food. This mechanism for brood-size optimisation is known as the Brood Reduction Hypothesis (Lack 1954, O'Connor 1978). The initial asymmetry may be determined either by a staggered hatching of the brood, or by egg-size differences which result in differences in chick size at hatching (Bryant 1978, Warham 1974). Experimental evidence from the Laughing Gull Larus atricilla has shown that brood reduction works through feeding hierarchies between siblings (Hahn 1981).

Despite the conservation interest in wetland bird populations in western Europe, surprisingly little is known of the basic biology of the Purple Heron. Tomlinson (1974 and 1975) described aspects of chick growth and development of Purple Herons breeding at Lake McIlwaine, Rhodesia, whilst Kral and Figala (1966) describe aspects of the breeding biology of this species in Hungary. There have been no major studies from western Europe. Information on the timing of the breeding season, principal sources of

mortality, growth and survival of chicks are provided in this chapter. These have particular relevance to the timing and nature of management practices on both the breeding and feeding areas of Purple Herons in the Camargue, to be discussed in the final chapter of this thesis.

METHODS OF DATA COLLECTION AND ANALYSIS.

A major aim of studying the reproductive biology of the Purple Heron was to examine seasonal effects which might be associated with the costs of coloniality discussed in Chapter three. It was not possible to visit nests on a daily basis, both because of access restrictions (limited to a maximum of one visit per week on most hunting properties) and because of the potential disturbance to the colony which would result from more frequent visits (eg. see Tremblay and Ellison, 1979). In addition, access permission to colonies on some hunting properties was terminated on the approach of the hunting season, before heron breeding was complete.

All nests found were marked with numbered tags (tied to the reeds below the nest) on the first visit for which either eggs or young were present. The contents of such nests were recorded on all subsequent visits. Nests were located by walking transects across the shortest axis of the colony, working slowly up the longest axis to minimise disturbance to nests already visited. Because of the density and height of reeds it was not always possible to relocate all marked nests on each visit, particularly

if they were very dispersed. Thus, some of the nest histories are fragmentary only.

In 1979 and 1980, nest contents were monitored at the colony of Couvin, during the collection of regurgitated food samples reported in Chapter 5. In 1981, this colony was destroyed by drainage and no observations were collected. In 1982, I collected comparative information from the colonies of Landre and Mas Neuf, which included studies of the growth and survival of individually ringed nestlings.

Duration and timing of the breeding season.

Because nests were not visited daily, the initiation dates of most clutches were not observed directly. The laying dates of first eggs were therefore back-calculated from the date when the age of the clutch or the brood was first known. I assumed from the studies of Tomlinson (1975), Kral and Figala(1966) and my own observations, that Purple Herons laid eggs, on average, at intervals of two days, had an average incubation period of 26 days, and that incubation commenced as soon as the first egg was laid. Most nests could be 'aged' before hatching had finished, but for those which were first found at a stage later than this, I estimated the age of the brood from the age of the oldest nestling(see Appendix 3 for details). For the purpose of analysis, the data have been grouped into ten day periods. Only those colonies which were visited regularly throughout the breeding season were included in the analyses.

Clutch-size, egg-size and size of chicks at hatching.

Clutch size was analysed from those nests which showed either the same number of eggs on two consecutive visits (separated by at least four days), or those which were visited once during incubation and subsequently after hatching when the number of chicks present on the second visit did not exceed the number of eggs recorded on the first. Unhatched eggs were normally left on the nest, whilst partial losses of clutches to predators were rare in comparison to total losses (see below). Measures of clutch size should therefore be accurate.

Egg dimensions (length and breadth) were measured for all clutches discovered before hatching, at the colonies of Landre and Mas Neuf, in 1982. Each egg was numbered with a non-toxic marker pen, and wherever possible I noted the subsequent order of hatching of the eggs, and which chick came from which egg. For a small sample of eggs which were discovered just after hatching (ie damp chick, with numbered shell still in the nest), I was able to measure the hatching weight of the chicks. Analyses of egg-size all refer to egg volume, which was calculated from the egg dimensions by the formula:

$$\text{Volume} = K_V L B^2$$

where L=length, B=Breadth and K_V (a shape constant)=0.507. Hoyt (1979) measured values of K_V for a number of species and found that intraspecific variation was nearly as great as interspecific variation. Therefore an average value of $K_V=0.507$ can be used for the eggs of most species.

Nestling growth and development.

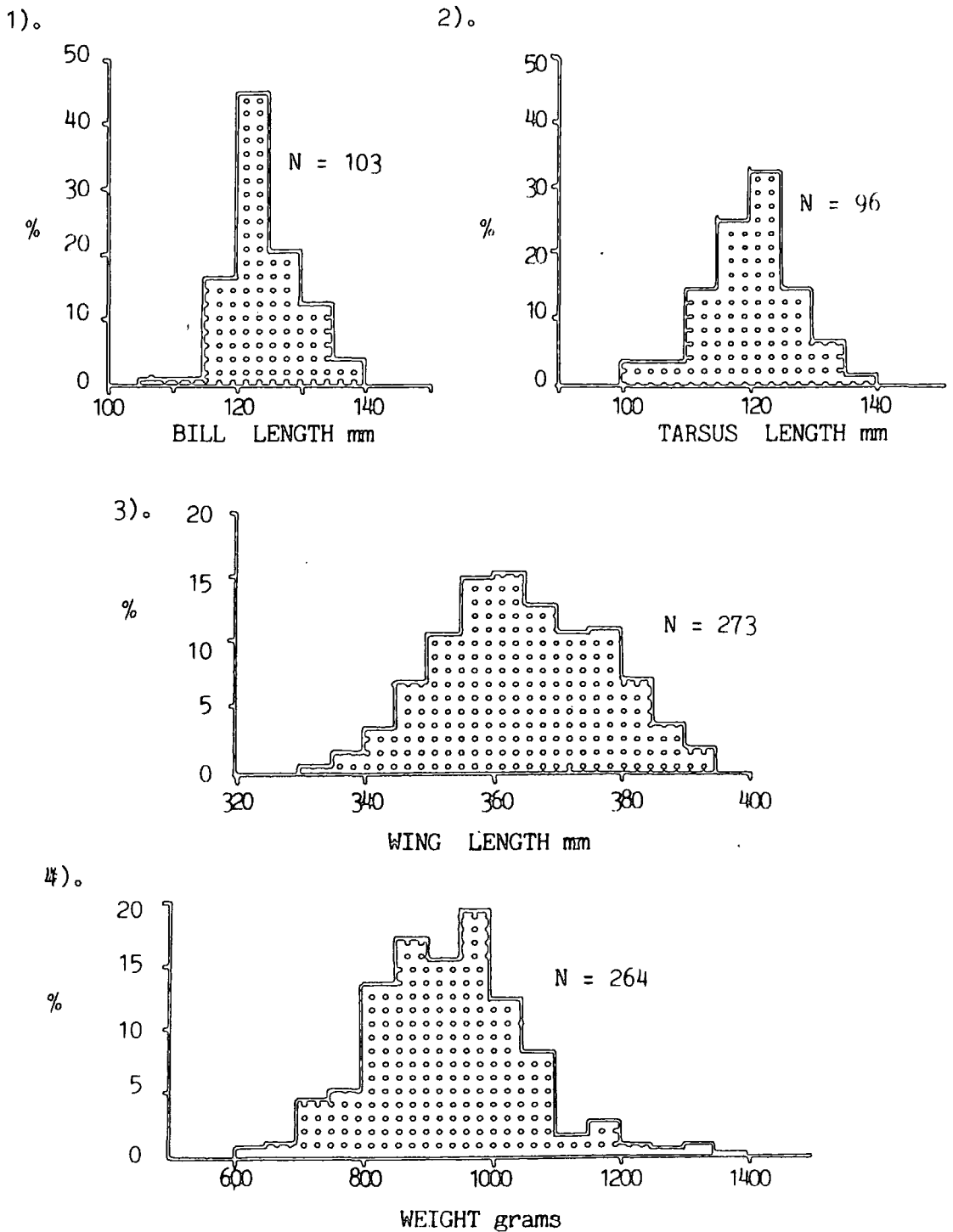
It was not possible to determine the sex of the Purple Heron nestlings which were measured for the analyses described below. Some herons show a degree of sexual size-dimorphism as adults (eg. see measures of museum specimens in Cramp and Simmons 1977), which might have confounded analyses of nestling growth rates. Examination of the frequency distributions of Bill length, tarsus length, wing length and weight of adult Purple Herons which had been captured during the breeding season in the Camargue as part of a general ringing program, gave no evidence of bimodality (Figures 4.1.1 to 4.1.4.). I have therefore assumed that any differences in growth rates of male and female nestlings would be small.

The following measurements were taken for all chicks:

1. Bill length (mm). Length of the upper mandible, from bill-tip to the start of feathering at the base of bill.
2. Tarsus length (mm).
3. Wing length (mm). Maximum chord.
4. Weight (g). Measured by suspending nestlings in a plastic bag from a Pesola balance (300g or 1000g balances were used to give the most accurate measurement for a given chick).

Individual nestlings were assigned a rank (A - D) on the basis of their order of hatching. All were ringed to allow individual recognition.

Figure 4.1. Frequency distributions of bill length, tarsus length and weight for adult Purple Herons captured in the Camargue between 1953 and 1982. Measurements were extracted from Tour du Valat ringing schedules. The unimodal patterns for all measurements indicate that there are not large differences in size between the two sexes.



Nesting Success.

Mayfield (1961) recognised two major difficulties associated with most field-studies of nesting success. Firstly, nests are frequently not found at the start of egg-laying, but more usually some time during the incubation or early nestling periods. Such nests are already 'survivors' and thus losses may be greatly underestimated since those occurring earlier will not have been recorded. Secondly, individual nests are rarely followed through from laying to fledging, resulting in many fragmentary nest-histories. Such data are often discarded from analyses, both wasting valuable information and biasing estimation of losses.

To overcome these problems, Mayfield (1961, 1975) developed a technique which can be used to estimate nest success both from nests which were not found at the start of laying, and from those which were not followed through to fledging. This is done by calculating losses only for the period when the nest was under observation (=exposure). Thus, a single nest under observation for 20 days has the same exposure as four nests under observation for 5 days each. Losses and exposure are calculated separately for the incubation and fledging periods. Losses occurring between two visits are assumed to have occurred half-way between the visits. The daily mortality rate (m) can then be estimated for each of these periods by dividing the number of losses in the period by the exposure. The daily survival rate (s) is simply $(1 - m)$. To calculate the probability of the nest or the nest contents surviving over a certain period (t), such as the incubation period, the appropriate daily survival rate is raised to the power ' t '.

Although Mayfield's original technique made great advances in the analysis of nesting success, it suffered from several drawbacks. Firstly, there was no statistical measure of the reliability of his estimators. Secondly, the technique assumes a constant mortality rate between periods (Green 1977) - an assumption which could not be tested. Thirdly, the assumption that nests which disappeared between two visits were lost half-way between the two cannot be valid, since this depends on both 's' and 't'. A mathematical reappraisal of the Mayfield method and its limitations has been made recently by Johnson (1979). He has derived the standard error of the Mayfield estimator, which allows both calculation of confidence limits and the examination of differences in survival rates between periods. He also replaced Mayfield's 'mid-point assumption' by the 'Mayfield 40% method', which assumes that any mortality which was not observed directly, should be scored as having occurred at the 40% interval between the last visit before the mortality and the visit when the mortality was first noticed. The main conclusion of his study was that, with these improvements, the Mayfield method was both robust and far easier to calculate than other methods, though these gave very similar results.

For Purple Herons, the problems recognized by Mayfield were apparent. Therefore, the survival of entire nests was calculated for the incubation and nestling periods separately, using the Mayfield 40% method and Johnson's (1979) method for calculating the standard error of the estimate. This analysis scores the losses of entire nest contents, and not partial losses. I

therefore examined these partial losses using the same method, but based on egg-days and chick-days of exposure, rather than nest-days. Chicks leave their nests well before fledging, and I was unable to follow their survival throughout the nestling phase. I thus measured survival until day 16 only, this being the earliest age at which a chick was ever observed to leave the nest. Although this can give only a minimum estimate for mortality, no other published figures are available (Cramp and Simmons 1977).

RESULTS

The details of breeding biology reported below are based on records from 336 Purple Heron nests, distributed as follows:

Couvin	1979	125 nests.
Couvin	1980	79 nests.
Landre	1982	65 nests.
Mas Neuf	1982	67 nests.

together with incomplete data from Landre 1981 and Les Bruns 1981.

Duration and timing of the Breeding Season.

Figure 4.2 shows the pattern of clutch initiation dates for Purple Herons (data for all colonies and years combined). Of 267 nests for which the clutch initiation date was known, 96.3% were started in April and May, with a pronounced peak in the last 20 days of April. No clutches were started in June. Table 4.1 summarises the results from individual colonies in the years studied. Within a year, the first clutches were on closely similar dates in different colonies (3 and 4 days difference). The median date of laying in 1982 was also similar at Landre and Mas Neuf. However, the differences between years were often greater (maximum difference = 16 days), even when comparing the first-egg dates at the same colony (1 and 14 days difference).

Clutch size, egg size and size of chicks at hatching.

Clutches varied in size from 2 to 5 eggs inclusive, with clutches of 3 and 4 eggs accounting for 90.5% of those observed (Table

Figure 4.2. Seasonal distribution of first-egg laying dates for Purple Herons breeding in the Camargue. All data combined(see text for methods).

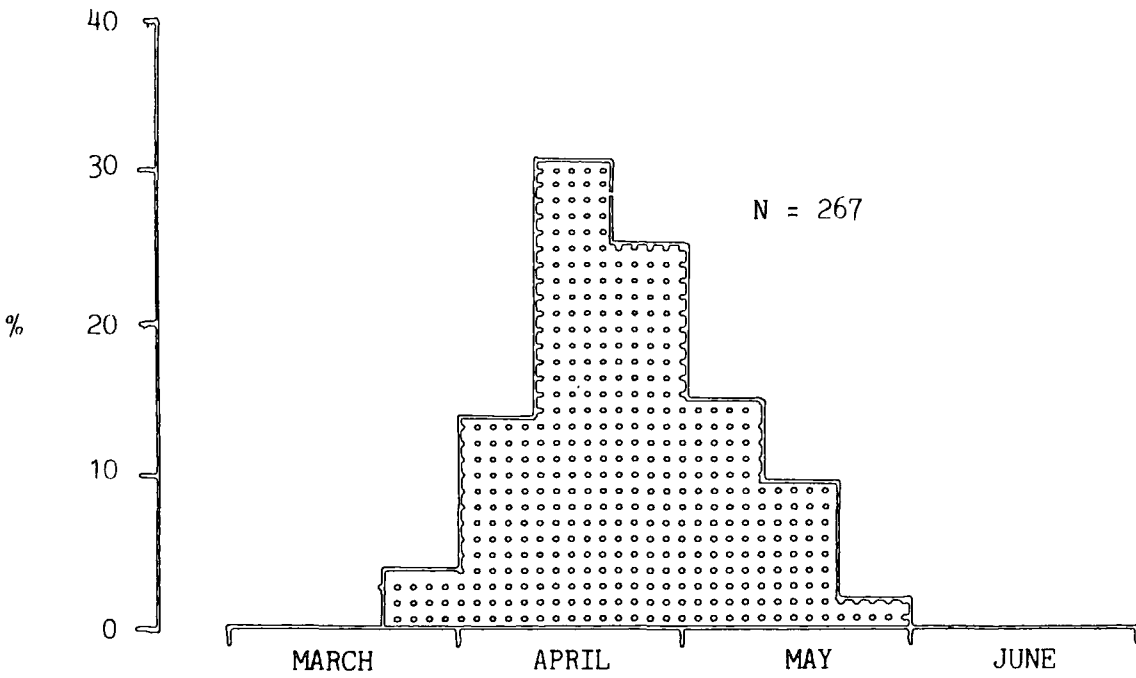


Table 4.1. Clutch-initiation dates of Purple Herons breeding in the Camargue, for different colonies and years. See text for method.

YEAR	COLONY	No.nests observed	Median laying date	Laying date of first clutch	Laying date of last clutch
1979	Couvin	93	20.04.79	28.03.79	25.05.79
1980	Couvin	59	27.04.80	11.04.80	20.05.80
1981	Landre*	65	--	10.04.81	31.05.81
1981	Les Bruns*	76	--	13.04.81	27.05.81
1982	Landre	51	22.04.82	09.04.82	10.05.82
1982	Mas Neuf	64	23.04.82	05.04.82	19.05.82

* Incomplete coverage, therefore median not calculated.

4.2). The average clutch size for all the data combined (N=242 clutches) was 3.48 ± 0.66 (1 SD) eggs. This compares closely with average clutch sizes for the Camargue of 3.3 in 1957 and 3.6 in 1963 (Williams 1965). Thus, annual differences in mean clutch size are small, and there have not been marked changes over the last 20 years. There was a significant decline in clutch-size with laying date (One-way ANOVA: $F=4.122$, Dfs 4,237, $P<0.01$) from an average of 3.75 eggs per clutch at the start of the season, to 3.14 at the end (Table 4.2).

The average calculated volume of 257 Purple Heron eggs, measured at the colonies of Landre and Mas Neuf in 1982, was 45.8 ± 3.6 (1 SD) cc. Variations in egg volume were not significantly greater between clutches than within clutches (4 egg clutches: $F = 1.314$; 3 and 156 d.f.; $P>0.05$. 3 egg clutches: $F = 1.499$; 2 and 162 d.f.; $P>0.05$). The smallest egg in a clutch was usually the last, and always amongst the last two to hatch, in both 3 and 4 egg clutches (Table 4.3). I could detect no significant correlations between clutch-initiation date and any of the following parameters: volume of smallest egg in clutch, range(max. - min.) in volume of eggs in clutch or mean egg volume in clutch, for either 3 or 4 egg clutches (both colonies combined). There was, however, a significant negative correlation ($0.01 < P < 0.05$) between the size of the largest egg in the clutch and laying date, for clutches of 3 eggs, but not for clutches of 4 eggs. There is thus weak evidence only, for any seasonal trend in egg-size.

Table 4.2 Seasonal Variations in the Clutch Size of Purple Herons Breeding in the Camargue.

PERIOD	CLUTCH SIZE				Mean	1SD	(N)
	2	3	4	5			
16-31 March	-	2	6	-	3.75	0.16	(8)
01-15 April	2	18	18	6	3.63	0.12	(44)
16-30 April	1	49	49	6	3.57	0.06	(105)
01-15 May	4	46	18	3	3.28	0.07	(71)
16-31 May	1	10	3	-	3.14	0.14	(14)
TOTALS	8	125	94	15	3.48	0.66	(242)

Null Hypothesis: There are no significant differences in clutch-size with season.

ONE-WAY ANOVA F = 4.122 D.F. 4,237

P < 0.01

Null Hypothesis Rejected.

TABLE 4.3. Size of egg, within the clutch, of the last egg to hatch. Figures show the number and percentage of clutches observed in which the last egg to hatch was either the largest, middle or smallest in the clutch.

Clutch-size 3 eggs.

	EGG SIZE			N
	largest	Middle	Smallest	
No.	-	1	17	18
%	-	5.6	94.4	

Clutch-size 4 eggs.

	Largest	EGG SIZE		Smallest	N
		2nd largest	2nd smallest		
No.	-	-	3	15	18
%	-	-	16.7	83.3	

The weight of Purple Heron nestlings at hatching, ranged from 21-46g with a mean of 36.3g (s.d.=4.8, N=30). Hatching weight was strongly correlated with egg volume ($r = 0.80$, $P < 0.001$) by the equation:

$$\text{Hatching weight(g)} = 0.86 \times \text{Egg Volume(cc)} - 2.74$$

Thus, the patterns observed in egg-size will occur also in chick-size at hatching.

Nestling Growth and Development.

The patterns of nestling growth in relation to age for 'A' chicks, are shown in Figure 4.3. Asymptote values could not be obtained, since chicks leave their nests at around 20 days, to hide in the reeds from potential predators. Rates of growth of Bill length, Tarsus length and Weight all approximate linearity from day 4 until at least day 24, whilst wing length development does not become linear until day 7. In the analyses reported below, I have examined nestling growth using rates calculated for individual nestlings during this linear phase (4-24 days old). Measures were always calculated over the greatest possible interval, and I rejected any values based on an interval of four days or less.

The mean rates of weight gain of chicks at the two study colonies are shown in Table 4.4 (Chicks which died were excluded from the analysis). There were no significant differences in the rates of weight gain between chicks of the same rank in the two colonies, and I have therefore combined these data in further analyses.

FIGURES 4.3.1 to 4.3.4.

Patterns of growth in nestling Purple Herons in the Camargue. Data are presented for the top-ranking nestlings from the colonies of Landre and Mas Neuf combined(all brood sizes).

- 4.3.1. Weight (grams).
- 4.3.2. Wing Length (mm).
- 4.3.3. Tarsus Length (mm).
- 4.3.4. Bill Length (mm)

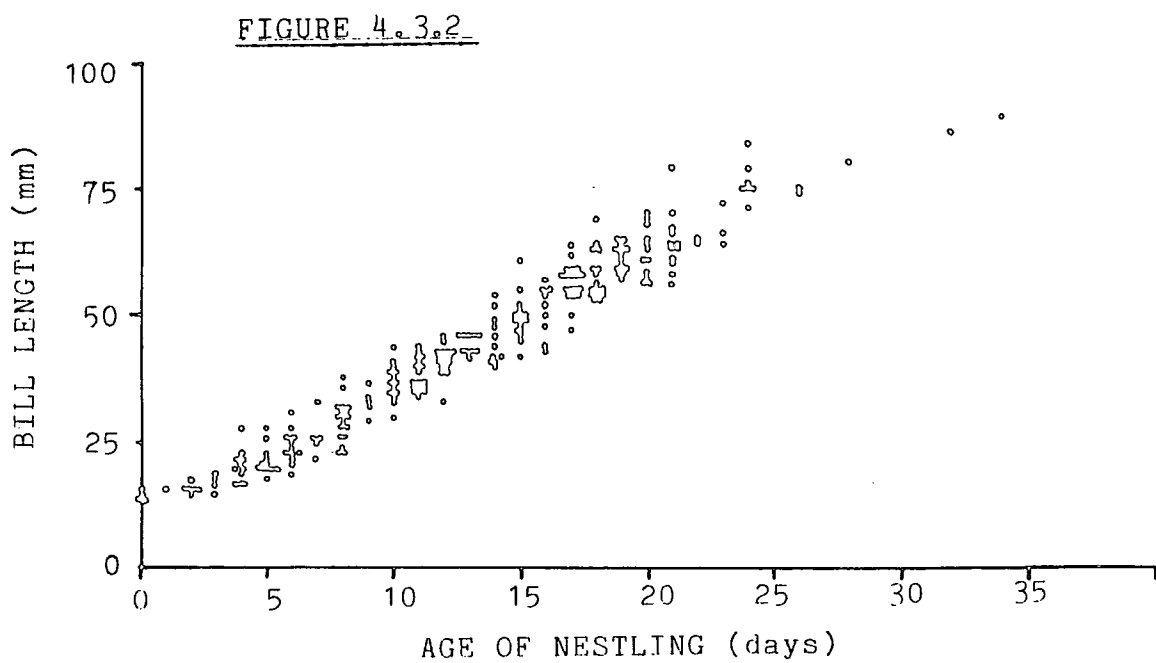
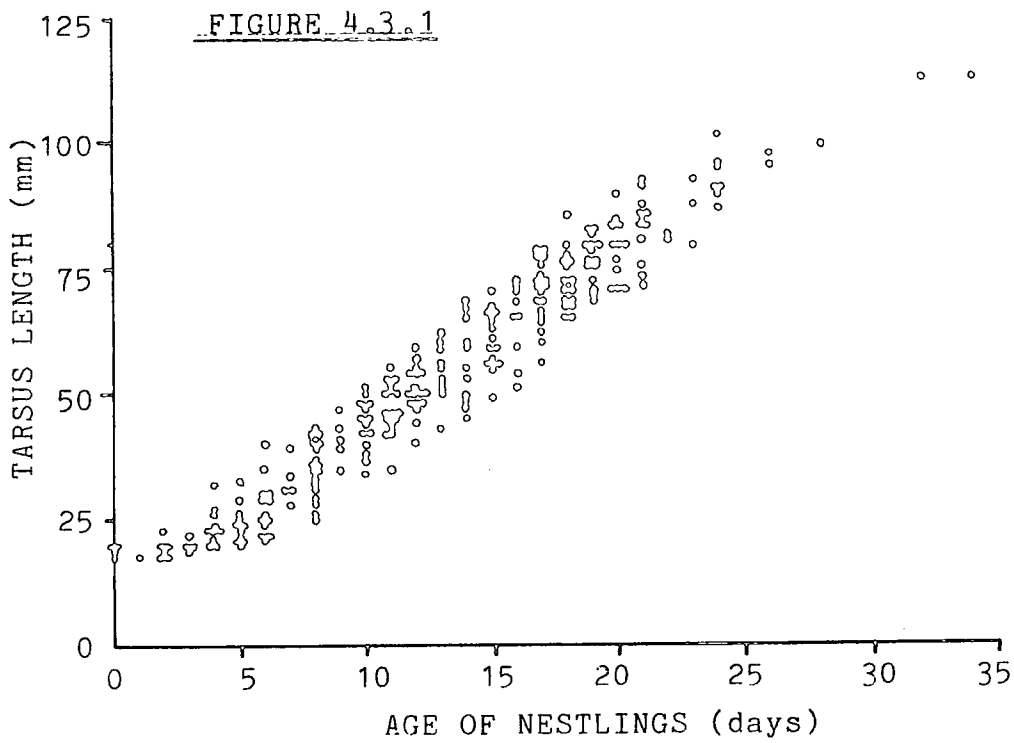


FIGURE 4.3.3

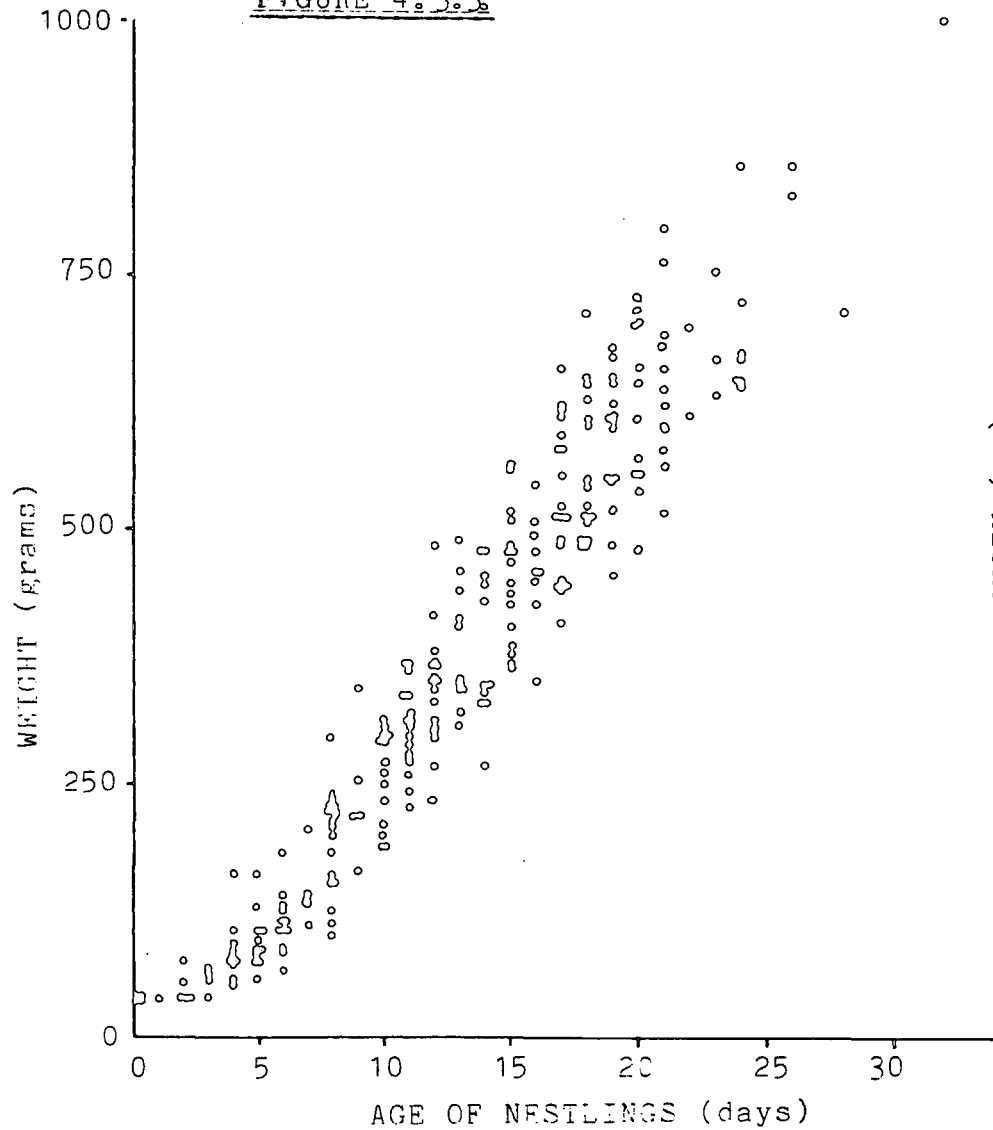


FIGURE 4.3.4

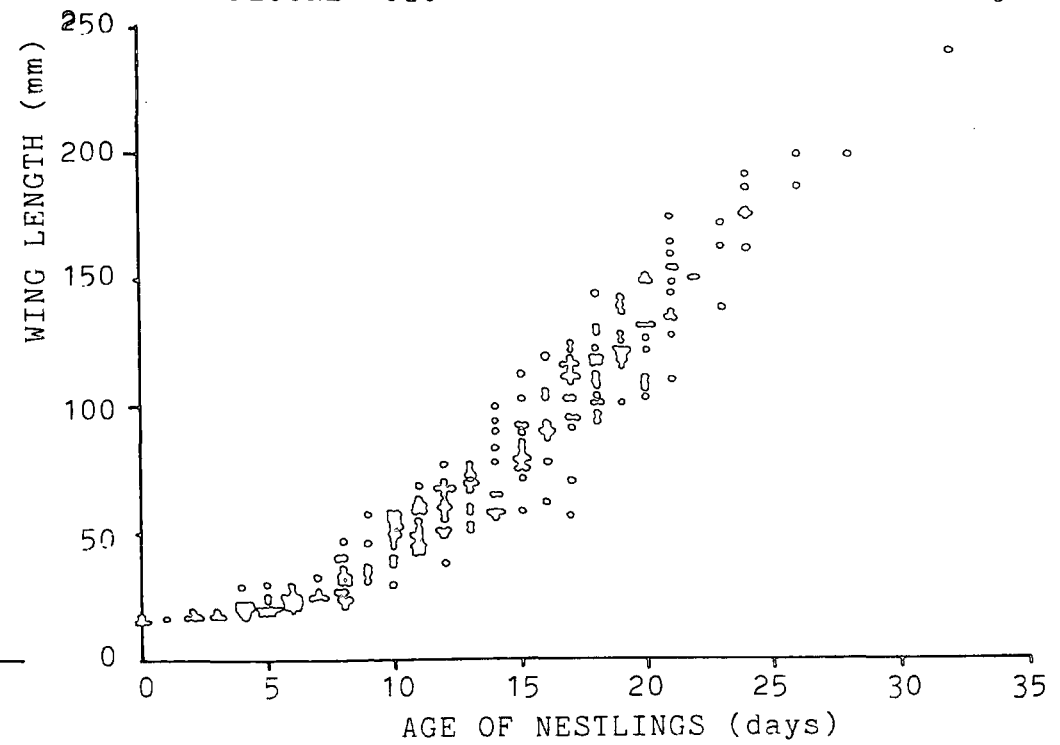


Table 4.4. Average daily growth increments (g day \pm 1 SE (N)) of nestling Purple Herons from broods of 3 and 4 chicks in the colonies of Mas Neuf and Landre in 1982 (see text for details of methods). There were no significant differences in mean growth rate (Students' t test) between chicks of the same rank in the two colonies, and the combined data are thus presented. (Nestlings which died are excluded from the analysis.).

Broodsize 4.

Rank	MAS NEUF	LANDRE	't'	BOTH COMBINED
A	37.3 + 1.5 (21)	35.3 + 1.1 (15)	ns	36.5 + 1.0 (36)
B	35.5 + 1.3 (21)	37.5 + 1.8 (15)	ns	35.8 + 1.0 (36)
C	32.2 + 1.4 (20)	32.9 + 2.3 (14)	ns	32.5 + 1.2 (34)
D	13.4 + 3.3 (9)	19.3 + 4.3 (11)	ns	16.6 + 2.7 (20)

Broodsize 3.

Rank	MAS NEUF	LANDRE	't'	BOTH COMBINED
A	34.6 + 1.2 (26)	36.2 + 2.0 (5)	ns	34.9 + 1.1 (31)
B	33.8 + 1.6 (25)	35.1 + 1.4 (5)	ns	34.0 + 1.3 (30)
C	23.4 + 1.7 (22)	29.0 + 3.6 (5)	ns	24.4 + 1.5 (27)

Growth rate was examined in relation to the order of hatching in a brood (Table 4.4). The mean rate of growth for 'A' chicks did not differ significantly from the mean for 'B' chicks, for broods of either 3 or 4 nestlings. However, 'C' chicks grew significantly slower than either 'A' or 'B' nestlings and in broods of four, rank 'D' chicks grew even slower. Comparing chicks of equal rank in broods of 3 and 4 nestlings, there were no significant differences in growth rate for 'A' and 'B' chicks, while 'C' chicks grew significantly more slowly in broods of three than in broods of four chicks.

I examined seasonal effects on chick growth rates by comparing the growth rate of individual chicks with the date of hatching of the first egg in their clutch. I used a non-parametric analysis (Spearman Rank Correlation) so that chicks which died (growth rate = 0) could be included. There was no significant relationship for 'A', 'B', 'C' or 'D' chicks from broods of four chicks, nor for 'A' or 'B' chicks in broods of three. 'C' chicks from broods of three however, showed a significant decrease in growth rate with season (Spearman = -0.4648 , $t = -2.8268$, $0.002 < P < 0.01$).

Nesting mortality.

Nesting mortality at the colonies of Couvin 1979, Couvin 1980, Mas Neuf 1982 and Landre 1982 was compared using the Mayfield 40% technique, described above.

The survival of entire nests during the incubation phase varied

(but not significantly) between colonies from 74 - 83%, while the survival during the nestling phase (98 - 100%) was consistently higher (Table 4.5). Of the 46 nests which lost their entire contents, only 2 (4%) did so after hatching. The causes of nest-losses were difficult to ascertain, because unprotected clutches were rapidly removed by Marsh Harriers. It was not possible therefore to distinguish between predation per se, and other factors which led to the abandonment/desertion of the nest.

The partial losses of eggs and nestlings from nests which survived, are shown in Table 4.6. Of the 60 eggs which were lost from such nests, only one was taken by a predator (1.7%), two fell out of their nests (3.3%), 47 failed to hatch (78.3%) and 10 disappeared from unknown causes (16.7%). Thus, failure to hatch (addled or infertile eggs) was the most important cause of partial losses, whereas predation by Marsh Harriers usually resulted in complete loss of the nest-contents. Partial losses of chicks from nests were strikingly greater in all colonies and years than were entire losses of nest contents during the nestling period. The majority of the chicks which died before 'fledging' were not found, but probably became trampled into the nest structure, or possibly were cannibalised by their siblings (see Walmsley 1974). Starvation and sibling aggression appeared to be the proximate causes of death. Most nests were visited at weekly intervals, and for the colonies of Mas Neuf and Landre in 1982, where all chicks were ringed, I have examined the nature of these partial losses (Figure 4.4). I assumed that nestlings which disappeared before 'fledging' had died at the 40% interval from

Table 4.5. Estimates of the survival probability of Purple Heron nests during the incubation and nestling periods, using the modified 'Mayfield 40% method' (Miller and Johnson 1978). The confidence limits on Mayfields' survival estimator are calculated by the method of Johnson (1979). See text for details of methods.

INCUBATION PERIOD.(26 days)

	Exposure nest days	Losses	Survival /nest day	Survival inc.period	95% conf.limits inc. period
Couvin 1979	2171	18	99.17%	80.54%	89.17 - 72.71%
Couvin 1980	1345	13	99.03%	77.70%	89.35 - 67.51%
Mas Neuf 1982	565	4	99.29%	83.13%	99.95 - 69.07%
Landre 1982	793	9	98.87%	74.32%	90.51 - 60.93%

NESTLING PERIOD (0-16 days)

	Exposure nest days	Losses	Survival /nest day	Survival nestl.period	95% conf.limits nestl. period
Couvin 1979	1436	0	100.00%	100.00%	-
Couvin 1980	917	1	99.89%	98.27%	100.00 - 94.89%
Mas Neuf 1982	800	1	99.88%	98.02%	100.00 - 94.17%
Landre 1982	501	0	100.00%	100.00%	-

Table 4.6. Survival estimates for eggs and nestlings from Purple Heron nests, using the modified 'Mayfield 40% method' (Miller and Johnson 1978). The confidence limits on Mayfields' survival estimator are calculated by the method of Johnson (1979). Nests which failed entirely were excluded from this analysis. See text for details of methods.

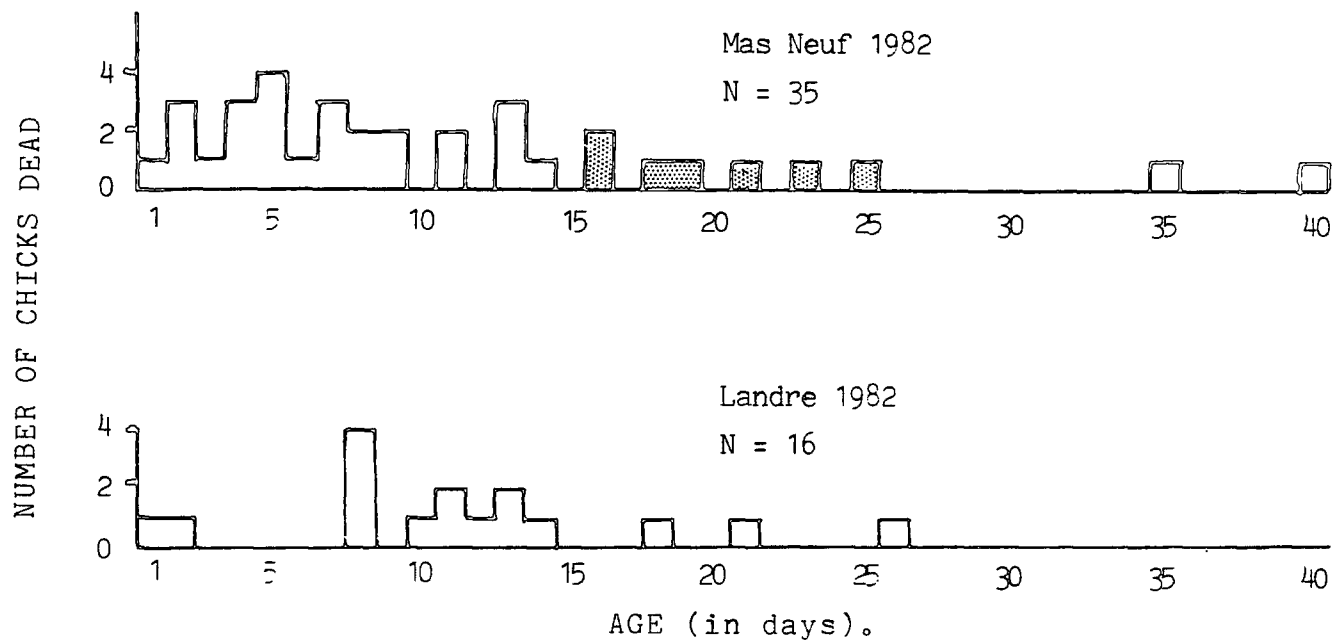
INCUBATION PERIOD (26 days)

	Exposure egg days	Losses	Survival /egg day	Survival inc.period	95% conf.limits inc. period
Couvin 1979	6917	26	99.62%	90.67%	94.22% - 87.25%
Couvin 1980	4545	8	99.82%	95.52%	98.67% - 92.48%
Mas Neuf 1982	1931	18	99.59%	89.77%	100.00% - 80.06%
Landre 1982	2634	8	99.70%	92.40%	97.70% - 87.37%

NESTLING PERIOD (0-16 days)

	Exposure nestling days	Losses	Survival/ nestling day	Survival nestl.period	95% conf.limits nestl. period
Couvin 1979	4169	15	99.64%	94.40%	97.25% - 91.62%
Couvin 1980	2759	30	98.91%	83.95%	89.48% - 78.75%
Mas Neuf 1982	2545	35	98.62%	80.13%	86.46% - 74.23%
Landre 1982	1670	16	99.04%	85.72%	92.57% - 79.36%

Figure 4.4. Age distributions of nestlings which died in the study nests at Landre and Mas Neuf in 1982. Shading indicates chicks found drowned under the nests. All others were either found dead on the nest or disappeared, before 'fledging'.



the date when they were last recorded to the date when they were first recorded as missing (the assumption of the Mayfield 40% method (Johnson 1979)). The chicks which died were always the youngest in the brood, except for the seven which were recorded as drowned, which included chicks of all ranks. (These were restricted to the colony of Mas Neuf, where the reeds were considerably taller than at Landre, and the nests were higher as a result. It appears that this may have caused difficulty to some chicks at the time when they first left the nest, since all such deaths occurred between the age of 16 and 25 days).

DISCUSSION.

What limits reproductive output in Purple Herons?

In birds, reproductive output is usually limited either by the investment that the female makes in her clutch, or by the investment that both parents make in their brood, through food-gathering (nidicolous species only).

Female condition on arrival at the breeding grounds is an important determinant of clutch-size in Arctic-breeding geese (Ankey and MacInnes 1978). For these highly migratory species, body condition on departure from the spring staging areas may be the critical factor limiting reproductive output (Drent and Daan

1980) since feeding on the breeding areas is not possible until the completion of laying and incubation. The situation in Purple Herons differs from that of the Arctic geese in two respects: firstly the eggs are relatively small in relation to female body weight (5% compared with 6-7%), thus requiring smaller reserves for the same clutch-size; secondly, females are able to feed both on arrival at the breeding areas (they have no snow-melt problem) and during laying as both sexes participate in incubation. Thus it is unlikely that their egg-laying reserves are limited in this way.

Drought in the wintering areas is correlated with the number of pairs of Purple Herons returning to breed in the following breeding season in Holland (Den Held 1981). Thus, in years of drought, females might fail to reach suitable condition for migration and/or breeding. Unfortunately, there are no data on the size of the non-breeding population (zero clutches), particularly since such individuals may remain on their winter quarters rather than migrate to the breeding areas. There is no information from West Africa concerning the occurrence of Purple Herons during the summer months.

Brood Reduction.

There are several lines of evidence to suggest that reproductive output is limited at the chick-rearing stage in Purple Herons. Firstly, many chicks die of starvation; secondly, two mechanisms are apparent in their breeding strategy which tie brood-size to the feeding conditions available at this time (see below).

It should be advantageous for a pair of Purple Herons to adjust their brood-size to the maximum number of chicks which they can rear to satisfactory nutritional condition in the prevailing feeding conditions, since trying to rear too many will jeopardise survival of both young and adults, whilst rearing too few will waste the potential of an increased breeding output (O'Connor 1984). There are two mechanisms by which Purple Herons could achieve such a maximisation process. They could either predict, from conditions at the time of arrival in Camargue, the conditions which are likely to occur during the nestling phase, and lay the appropriate number of eggs; or they could lay more eggs than they are likely to be able to rear and adjust their brood size early in the nestling period when feeding conditions are known. My study has revealed evidence of both mechanisms and I shall treat each separately, below.

1. Adjustment of clutch size.

Purple Heron eggs weigh approximately 50g (Figala 1959, Tomlinson 1975) or about 5% of the adult body weight, with a full clutch of four representing 20% of adult bodyweight. Egg-laying is spread over several days, which reduces the instantaneous demand on the female, but even so, egg formation is energetically costly (eg Ricklefs 1974). Females should therefore avoid investing in eggs which are not going to produce surviving chicks. The decision of how many eggs to lay must be made about 5 weeks before the peak in brood feeding requirements. Evidence that clutch-size is adjusted to the number of offspring that the herons will be able

to rear comes from two sources - regional and seasonal variations in clutch-size:

The average clutch-size (3.48) of the Purple Heron in the Camargue is the lowest recorded in Europe, by almost one egg. It compares with values of 5.1 and 4.5 in Central and Western France respectively (Ferry and Blondel 1960), 4.1 in Switzerland (Manuel 1957), 4.5 in Holland (Haverschmidt 1961) and 5.3 in Hungary. Evidence that this is a south to north cline of increasing clutch-size (Ferry and Blondel 1960) is rather weak, since values for Holland (the most northerly site) are no higher than for Central France or Hungary. Furthermore, Mountfort and Ferguson-Lees (1961) and Maluquer (1960) cite evidence that clutch-sizes in Spain, six degrees south of the Camargue, are larger than in the Camargue. Whatever the cause, female Purple Herons in the Camargue are laying smaller clutches than those in other parts of Europe, and I recorded no surviving broods of five chicks despite several clutches of this size being laid. My studies of chick growth rates and nesting success therefore indicate that clutch size in the Camargue is lower than in other areas because conditions for rearing nestlings are less good.

The second line of evidence for adjustments in clutch-size comes from the strong seasonal decline in average clutch-size which was observed in the Camargue colonies (Table 4.2). Examination of growth rate data (Table 4.4) shows that birds laying clutches of four eggs were predicting correctly that they would, on average, be able to rear more nestlings than those laying only three eggs



since the growth rate of 'C' chicks was significantly higher in broods of four than in broods of three chicks. This pattern is the converse of what would be expected if they were unable to predict their brood rearing ability.

2. Adjustment of broodsize at hatching.

Purple Herons eggs do not hatch simultaneously since incubation begins as soon as the first egg is laid. This enforces a competitive asymmetry in the brood, which is an important feature of brood reduction(see below).

For ten broods found one day or less after the hatching of the last egg and for which egg-sizes had been measured, I was able to assess the relative importance of egg-size variation and asynchronous hatching in providing competitive asymmetry within the brood. In six broods of three, variations in egg-size alone resulted in the largest chick being, on average, only 1.14 times the size of the smallest chick(expected hatching weights were calculated from known egg-volume by the equation given above), whilst after the asynchronous hatch this difference had risen to an average of 3.15 times. In four broods of four chicks, the same differences were 1.21 and 4.22 times, respectively. Thus, although egg-size variation within a clutch usually acts in the right direction, it contributes little to the final asymmetry within the brood.

There is strong evidence that brood reduction works through sibling feeding hierarchies (Hahn 1981), which result in a

disproportionate amount of the food delivered to the nest being consumed by the oldest nestlings. Evidence that the adults might be able to influence this mortality through aspects of prey selection are discussed in Chapter 5. Clearly, asynchronous hatching is an efficient mechanism for brood reduction since most chicks which are going to die through starvation do so before they are 15 days old (Figure 4.4). In addition, a significant depression of growth rate was observed only for the lowest ranking chicks in a brood (Table 4.4), implying that brood asymmetry protects the older nestlings from food shortage.

To summarise, both clutch size adjustments and asynchronous hatching are used to optimise brood size to the chick rearing capacity of the parents. The former mechanism provides a coarse tuning in relation to regionally and seasonally predictable changes in environmental conditions, while the latter provides a fine tuning, at the time of nestling demand.

Chapter Five.

Mechanisms of Prey selection in Herons, with special reference to the diet of Grey and Purple Herons during the breeding season in the Camargue.

INTRODUCTION.

A period of major energetic demand in the life cycle of most nidicolous birds occurs during the breeding season, when adults must forage to meet not only their own daily energy requirements, but also those of their offspring. Lack (1954) contended that the rate at which the adults could deliver food to the nest was the factor limiting reproductive output of many nidicolous birds. Lack argued that brood reduction mechanisms, such as asynchronous hatching, had evolved to maximise reproductive success even under a limited food supply. This is supported by my own evidence for Purple Herons, where reproductive output was limited during the chick rearing phase, and several breeding adaptations were recorded which maximise brood-size to the food gathering ability of the adults (see chapters 3 and 4). Thus, as time and energy are limited during this period, the adults should feed efficiently. Adult Herons have few predators, so that their food gathering efficiency can be measured in terms of time and energy only. They do not have to spend time in 'vigilance' activities which might require them to take smaller than optimal prey. They are thus particularly appropriate species for optimal diet studies.

There may be two constraints imposed on prey selection by adult Grey Herons when feeding nestlings: first, the nestlings may not be able to ingest the same sized prey as are consumed by the adults, which tend to feed on large prey items; second, the obligation to forage from a central place during the breeding season may alter their prey selection mechanisms, since theory (Orians and Pearson 1979) predicts that optimal prey-load sizes will change with foraging distance from the central place. I shall consider only the first constraint in detail, below. I was unable to test the second, which would require the use of nest balances to measure prey-loads of adults foraging at different distances from the colony. I do not however believe that this limitation would have greatly affected the composition of the diet, since Grey Herons are 'multiple prey loaders' and are therefore able to adjust their preyload by changing the number, rather than the size of individual items.

Since food gathering during the chick-rearing period may limit reproductive output, a knowledge of the diet and of the mechanisms of prey selection by the adults, is fundamental to an understanding of the species' ecology. Simple dietary descriptions cannot reveal the mechanisms underlying prey selection, since selection can only be judged against a spectrum of densities of available prey. Prey availability is controlled not only by the behaviour of the prey but also by the foraging method of the predator, and could not be measured adequately in the complex environment of the Camargue freshwater marshes. Instead, an experimental approach, in which the profitabilities

of a range of potential prey are measured, can be used. In this Chapter, I describe the use of this approach to examine prey selection by the Grey Heron, and in particular to explore the additional constraints that are imposed on prey selection during the breeding season. To do this, I compare the results predicted from the experimental approach with the diet of nestling Grey Herons in the Camargue. I chose this species for study because it was more easily observed in the wild, and had a more restricted diet than the Purple Heron. In addition, several individuals were available for study in captivity. The results, however, should be applicable to both species, since they have very similar morphology (Chapter 1).

PART 1. Mechanisms of Prey Selection.

METHODS

Profitability of prey for adults.

Prey profitability was calculated from the costs and benefits of consuming a prey item. Cost was measured as handling time (the interval between prey capture and the completion of swallowing), whilst benefit was measured by the dry weight of the item. An alternative measure would be the energetic value of the prey (used e.g., by Elner and Hughes 1978, Davies 1977a), but this tends to vary widely between fish species (Murray and Burt 1969, Horne and Birnie 1969) and within species at different seasons. Within a prey type, calorific value relates closely to the size of the prey at a particular time of year (e.g. Britton and Moser

1982), and thus selection within a prey type can usually be examined using size alone.

Thus,

$$\text{Profitability(g/sec)} = \frac{\text{Dry weight of prey (g)}}{\text{Handling time (seconds)}}$$

Prey handling times were measured for adult Grey Herons feeding on a wide size-range of several prey types which commonly occur in their typical foraging habitats. Most information was collected under field conditions, in situations where large aggregations of herons had formed to feed at prey concentrations in drying-out freshwater marshes. The most commonly taken prey were Eels and Carp.

Attention was focussed on individuals orienting as if ready to strike a prey. These were observed by 20 - 45X telescope until either a peck occurred, or they returned to the prey searching posture. Following a successful peck, I measured by stopwatch the handling time (seconds), recording the identity of the prey and its length, estimated against the bill length of the heron. I also noted any behaviour of the heron or its prey which might influence the handling time. For prey only rarely taken in the wild, I supplemented the observations using two captive adult Grey Herons. These were fed on live prey in an aviary (6m X 5m X 2,5m) for at least one week before any experimentation took place. These birds had handling times for Eels and Carp similar to wild birds. Observations were made by placing live fish, of known length, into the aviary pool (1,5m square filled to a depth of 10cm with clear water), and recording handling times as above.

The dry weights of prey were estimated from the equations and tables given in Appendix 2.

Prey handling limitations of chicks.

I measured the maximum sizes of Eels and Carp that could be consumed by Grey Heron nestlings, using six hand-reared chicks. These were taken simultaneously from the wild, under licence, when aged 3 - 7 days. They were arranged into two broods of three; heat from an infra-red lamp was provided until the chicks could thermoregulate, when they were placed in artificial nests in an outdoor aviary. The chicks were weighed and measured daily, and showed growth rates very similar to those of wild chicks from two broods in nests ca 2km away (Figure 5.1). All the hand-reared chicks fledged successfully and were later released. They were maintained on a superabundant diet of dead fish, of those species recorded in the diet of wild chicks (Eels, Carp and Mullet).

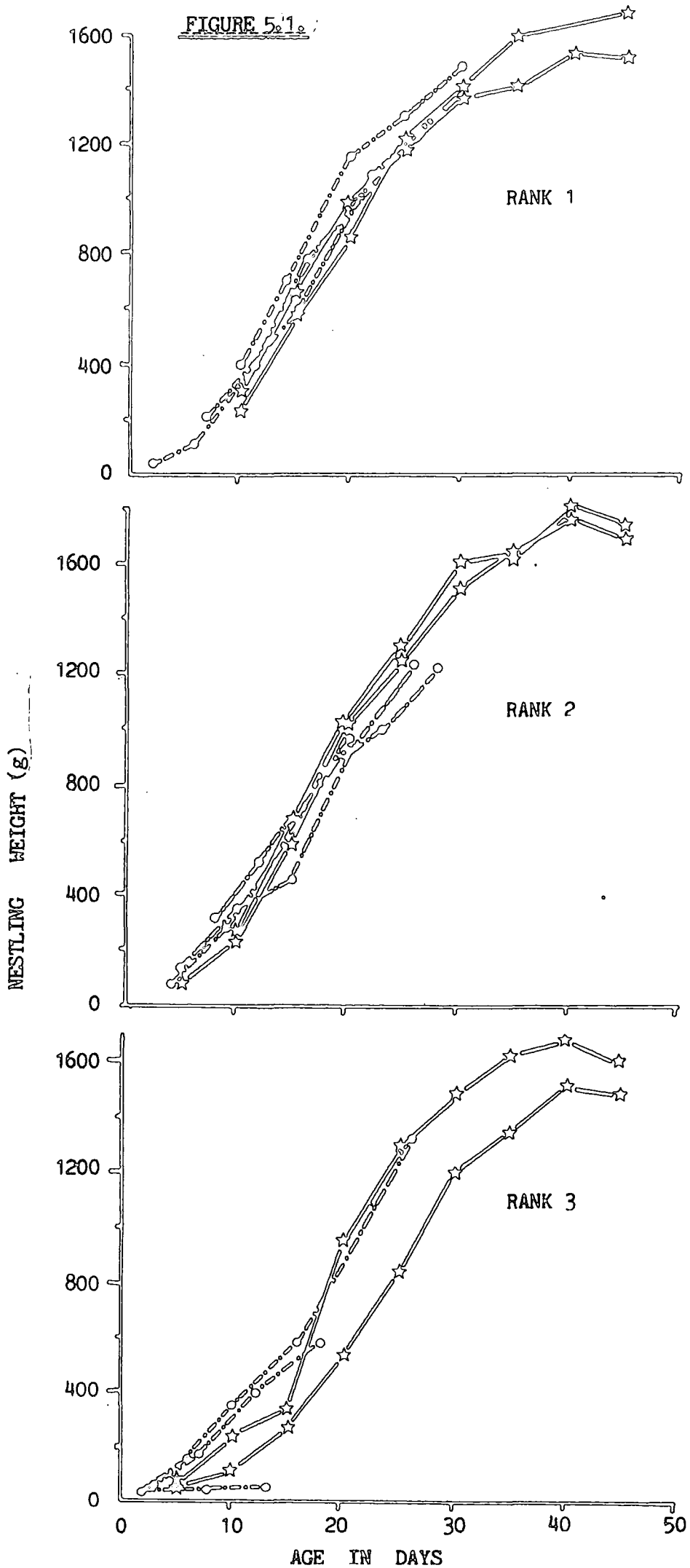
The measurements were made over a wide range of chick ages (5 - 53 days). Tests were carried out before the main feeds (two per day, morning and evening), when the chicks were hungry. Each was presented with a fish of known length, larger than it had previously been able to consume. If it was unable to swallow this within 30 seconds, it was presented with a smaller fish, repeating this procedure until the fish was swallowed. Eels and Carp were used on different days, depending on their availability.

FIGURE 5.1. Comparison of the Growth rates of six Grey Heron nestlings reared in captivity for experimentation, and the growth rates of two broods of wild chicks reared at the same time in the wild, at a colony 2 kilometres away from the aviary.

○-----○ Wild chicks.

☆=====☆ Captive Chicks.

FIGURE 5.1.



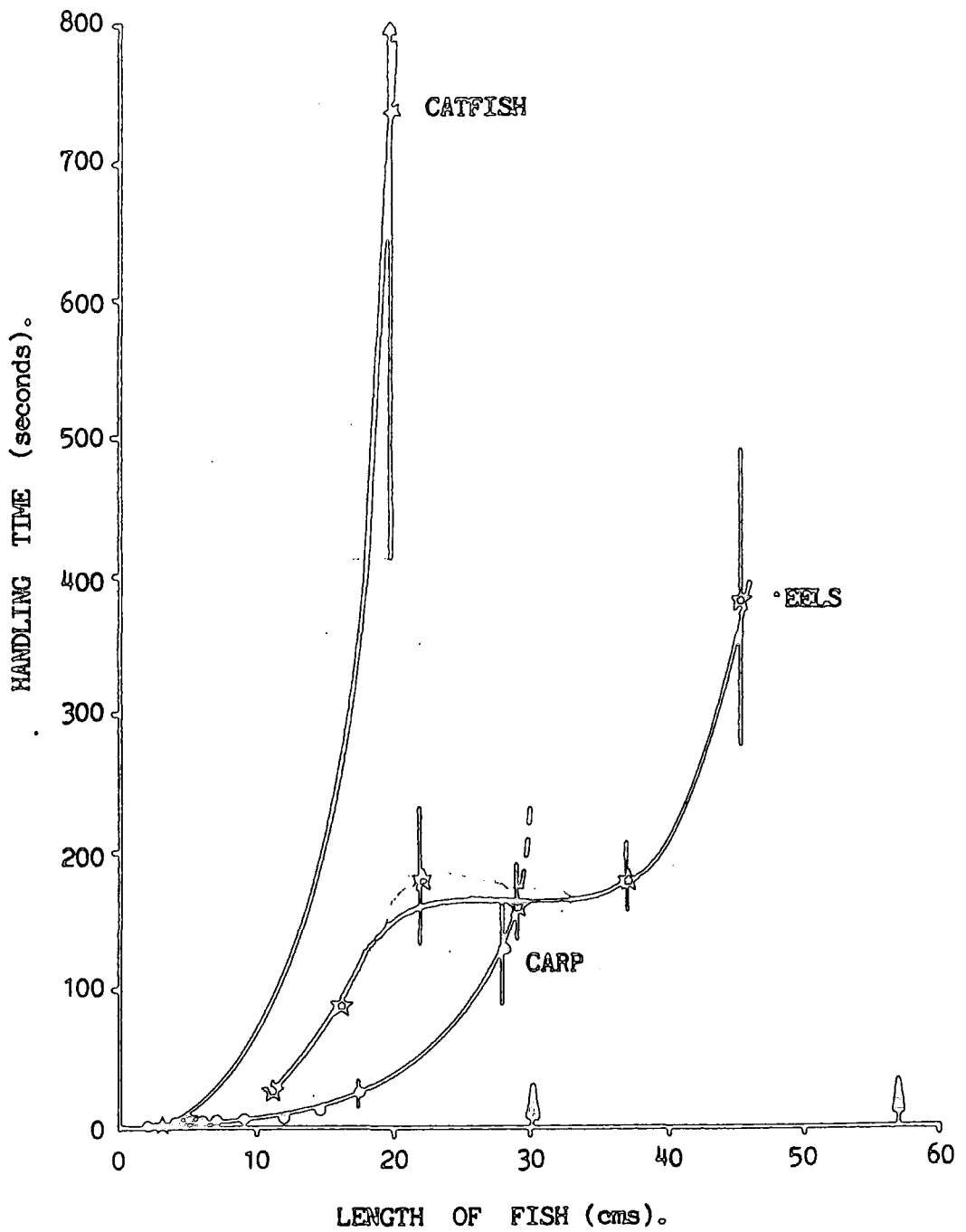
RESULTS AND DISCUSSION

1. Handling times.

The handling times for fish taken by Grey Herons varied between fish species, as well between size-classes of the same species (see also Kushlan 1979, Mock and Mock 1980, Recher and Recher 1968). In general, handling time increased with prey size (Figure 5.2). For Carp, which is typical in morphology for most of the fish species taken, handling times were lowest for the smallest size-classes, increasing exponentially up to those too large to be swallowed. The smallest fish were swallowed directly, whereas larger fish had first to be oriented correctly in the bill. All were swallowed alive, although the largest were first stabbed several times with the lower mandible.

Some fish species possess adaptations which protect them from predation. Catfish have long, sharp spines on their modified pectoral and dorsal fins. These are erected when the fish is captured by a heron, making it difficult to swallow. Although abundant in habitats used by foraging herons (Crivelli 1981a), Catfish were rarely recorded in their diet (see below). In captivity, handling times for 20cm long Catfish were more than 18 times longer than for Carp of a similar length. All were repeatedly stabbed and shaken by the spines (presumably to break them) before being swallowed. The only observation of a wild Grey Heron taking a Catfish, was of a juvenile which released the fish uneaten after .8 minutes of handling. The evolutionary consequences of taking such prey, or even very large individuals of 'safe' species, are severe, and Lowe (1954) cites several

Figure 5.2. Handling times (mean \pm 1 S.E.) for Carp, Eels and Catfish taken by adult Grey Herons. Lines are all fitted by eye. Arrows on the x axis denote the largest sizes recorded in the diet.



instances of dead herons which had apparently choked on such prey. Similarly the long handling time required to remove the sting of Bumble Bees, rendered them unsuitable prey for Spotted Flycatchers Muscipapa striata (Davies 1977). White (1938) showed that Kingfishers Megaceryle alcyon selectively avoided feeding Sticklebacks to their nestlings.

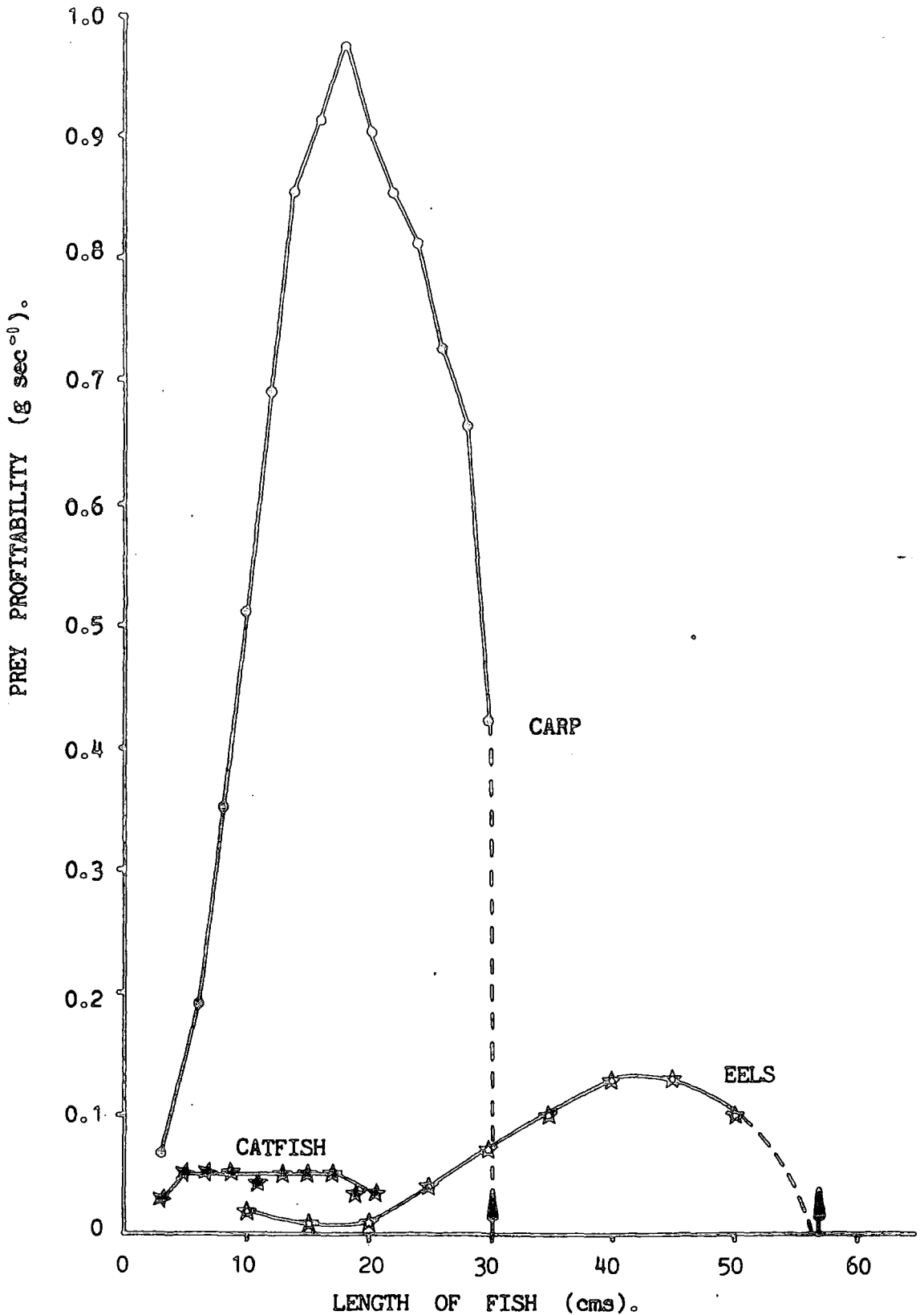
Handling times for Eels showed a pattern very different from those of the other species studied. Handling times for the smallest size-classes were again shortest, but they increased to a plateau value for Eels of 20 - 35cm, before finally increasing exponentially to the largest size-class taken. Eels struggle violently on capture by a heron, and although the smallest (<20cm) are normally eaten alive at the place of capture, the largest require more attention. These were usually carried to land (as much as 50m or more away), where the Eel was repeatedly stabbed until stunned, when it could be swallowed. The plateau in handling time thus represents the time taken to carry and stun the fish. A further cost to be considered when herons consume Eels (large specimens only), is the time required to preen the plumage free of slime. This may require as much as 15 minutes, and is always accomplished immediately.

2. Prey Profitability.

Values from Figure 5.2 and Appendix 2 were used to calculate the profitability curves for adult Grey Herons feeding on Carp, Eels and Catfish (Figure 5.3). In general, profitability is lowest for the smallest prey, increasing to a peak as the prey become more

Figure 5.3b Prey profitability curves for adult Grey Herons when feeding on Carp, Eels and Catfish.

Arrows on the x axis denote the largest size-class observed in the diet.

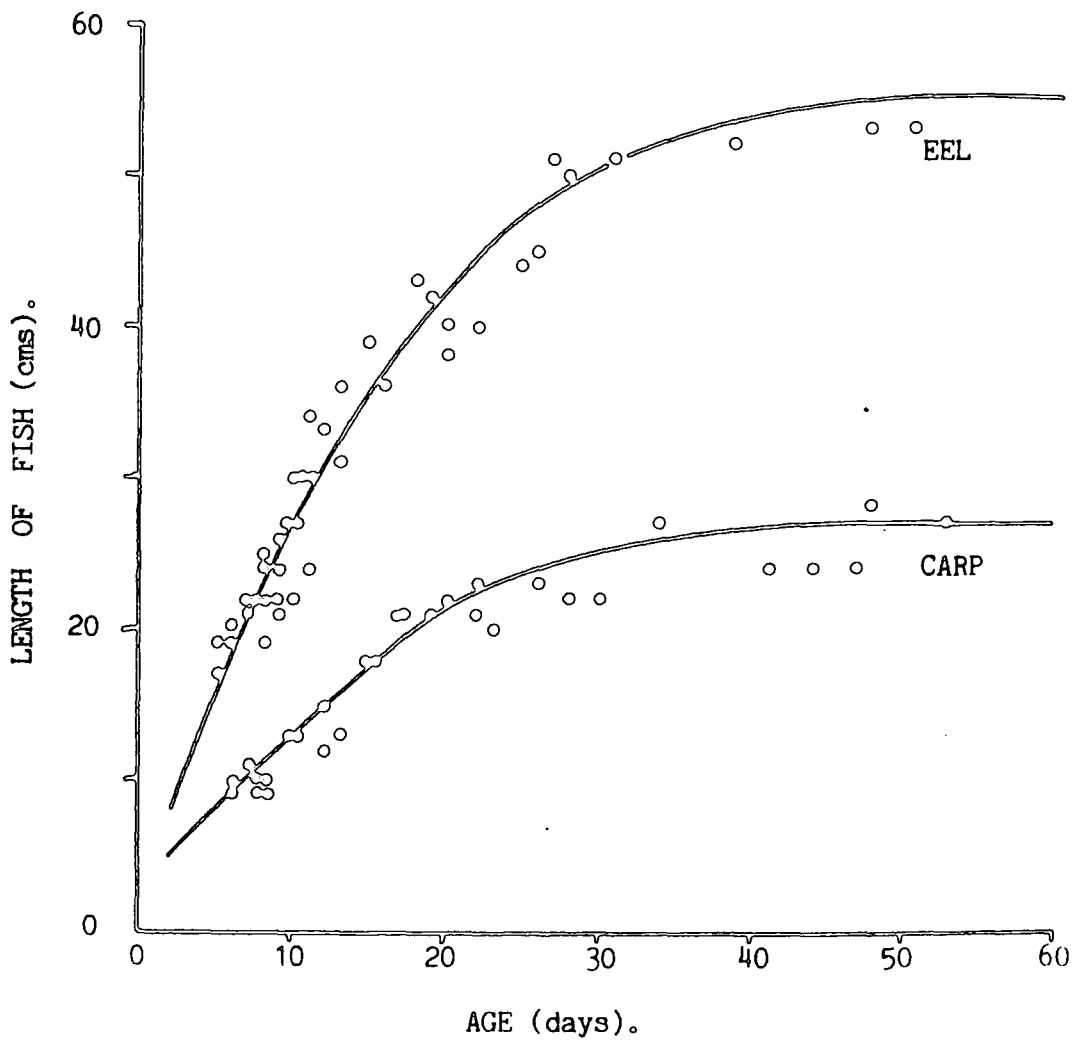


difficult to handle, and then decreasing to zero at the point where the prey becomes too large to swallow. This pattern is overlain by differences between prey types. Large Carp (15 - 20cm), and thus fish of similar form (eg Mullet, Tench, Roach and Trout) are the most profitable prey for adult Grey Herons. The maximum length they can handle is approximately 30cm. This limit may be determined by their ability to distend the gullet, as slightly longer individuals of the thinner species (eg. Mullet) could be ingested. Catfish, with their protective spines, have the lowest overall profitability, and are not normally recorded in the diet of wild birds. Eels were of intermediate profitability, with a peak for those of 35 - 50cm in length.

Prey-size constraints when feeding nestlings.

On hatching, Grey Heron nestlings weigh on average 30g (=1.8% of the average adult body weight) (Marion 1979). As with the young of other nidicolous birds, the locomotory abilities of young herons are poor for the first few days of life. For many skills such as prey capture and handling, young herons of several species do not achieve the ability of adults until some considerable period after fledging (Recher and Recher 1969a, Cook 1978, Quinney and Smith 1980). Although heron nestlings do not require the ability to capture or kill their prey, they do still require the ability to ingest those prey that are delivered to the nest by the adults. Young Grey Heron nestlings could not ingest prey as large as those that were most profitable for the adults to collect (Figure 5.4 c.f. Figure 5.2). The maximum size the chicks could consume increased with age, reaching almost that

FIGURE 5.4. Maximum sizes of Carp and Eels that could be swallowed by nestling Grey Herons, during experiments to determine the profitability of different sized prey for nestlings. See text for methods. Lines were both fitted by eye.



of the adults by the time they were 30 days old. Much longer Eels were taken at a particular age than were Carp; thus it appeared that gape width set an upper limit to the size of Carp that could be consumed. Similarly, Hulsman(1971) found that gape-width was the best indicator of prey-size in the diet of tern chicks.

Heron nestlings do not have to spend time collecting prey, and their handling time for an item is not therefore a good measure of its cost to a parent bird trying to maximise brood growth (although they will expend some energy doing so). For the adult, cost is incurred at the nest only if the chicks are unable to ingest the item. In another study, Grey Herons were observed breaking large prey into pieces for their chicks to eat, by predigestion (Marion 1979), although I did not record such 'pieces' of larger prey in my diet studies of nestlings (see below).

To summarise, the relatively large bill of adult Grey Herons, when compared with that of the other Camargue Ardeidae, is adapted for the capture of relatively large prey (see Chapter 1, Figure 1.4.). Small prey can also be taken, but are of relatively low profitability. The morphology, and behaviour on capture of a particular prey species, can exert a considerable influence on prey profitability. The selection of profitable prey must therefore be based on both prey type and prey size.

When feeding nestlings, the currencies used in prey selection may differ from those used by an adult feeding only itself. At this

time, the maximisation of brood growth may be a more likely goal than maximisation of the instantaneous rate of food intake. Young nestlings cannot ingest prey of the sizes which are most profitable for the adults to consume. If adult Grey Herons are to feed efficiently during the nestling period of the breeding season, several predictions can be made as to the nature of the diet given to their nestlings :

1. Within the size range that chicks can eat, prey types which have a low profitability as a result of long handling time (eg Catfish), should not be included in the diet, even when abundant, unless the availability of other prey is very low.
2. Young chicks should receive smaller prey than older chicks. This may result in differences in the species composition of the diet of each age group, because of differences in the abundance of the available size-classes of each species.
3. At all ages, chicks should be given prey near to the maximum size that they can consume, since these will be nearest to the sizes which are most profitable for the adults to collect. The size distribution of prey in the diet should therefore be skewed in favour of large prey.

Predictions (2) and (3) should be valid for any nidicolous species which feeds its nestlings on intact prey items, and whose preferred prey are relatively large when compared with the size of the bird (eg Kingfishers, Auks, Terns, some passerines) .

Part 2.

The Diet of Grey and Purple Heron Nestlings in Camargue.

INTRODUCTION.

Many techniques have been used in avian diet studies (Hartley 1948), but the choice of an appropriate method depends on the particular species, situation and aim of the study. Herons are carnivores, searching for and capturing live prey individually. They have an extremely efficient digestive system (Vinokurov 1960), and the only materials which are commonly ingested but not fully digested are the chitinous remains of insect exoskeletons, and the keratin of mammalian hair and bird feathers. These are regurgitated orally as pellets. Bone is digested completely. Adult herons may forage at considerable distances from the colony for their nestlings (see Chapter 3). They store prey in the oesophagus, to be regurgitated later in an undigested form to the nestlings. Heron nestlings will also regurgitate in the presence of a predator, as this has survival value if the predator chooses to eat the prey remains rather than the chicks (eg. Great Blue Herons and Turkey Vultures - Temple (1969)).

There are thus several possible ways in which the diet of herons can be studied, and four have been used in the past:

1. Analysis of stomach contents of birds killed deliberately (eg Vasvari 1948-1951, Moltoni 1936, 1948)

This method can no longer be justified on conservation grounds; it would deplete the study population, and has many inherent biases.

2. Analysis of pellets of undigested prey (eg Giles 1979).

Only those prey types which cannot be fully digested would be represented. Fish, the most important prey, would not appear in the recorded diet.

3. Direct observation of the prey taken by foraging adults(eg Cook 1978).

A feasibility study showed this method to be unsuitable for Grey and Purple Herons in the Camargue. Prey capture rates were sometimes as low as only one item per hour, and sufficient observations could not be obtained. Also, foraging adults were difficult to locate and follow, and could be observed only for short periods before being hidden by tall vegetation. Estimation of diet would thus be biased towards prey types which occur in open water. Also it was not possible to distinguish between breeding and non-breeding individuals since few adults were marked.

4. Analysis of food samples regurgitated by nestlings (eg Owen 1954, Amat and Herrera 1978).

The recorded diet will refer to that of nestlings only, which may not represent the diet of the adults. Thus, Furness and Hislop (1981) demonstrated that for Great Skuas Catharacta skua, there were differences in diet between breeding adults, non-breeding adults and nestlings at the same time of year. This method is also open to the potential

bias of differential digestion rates of each prey type (Owen 1975).

METHODS.

I chose to study heron diet from nestling regurgitations because relatively large samples could be collected, and because it was the least biased technique. The differential digestion rates of prey were not thought to be a serious problem for Grey Herons, since the diet was composed almost entirely of fish. Thus, all prey would be expected to have approximately similar digestion rates. For Purple Herons, which took a slightly wider range of prey types including some insects, bias was more likely to occur. This possibility was reduced by collecting prey samples in the morning, before extensive differential digestion had occurred, since this species does not forage at night (Chapter 3). Additionally, only fresh, undigested meals were collected.

Collection of samples in the field.

Variation in diet resulting from regional differences were reduced by collecting samples only from those colonies located within the Camargue delta, or those colonies whose adults exploited the delta as a major feeding area. Within these limits, study colonies were selected for their accessibility and numerical importance to the Camargue breeding population. Samples were collected intensively in 1979 and 1980, at frequent intervals throughout the breeding season.

Visits to each colony were made between 0800 and 1300 hours, to reduce the problem of differential digestion of prey, as discussed above (a few visits were made later in the day in 1979). Nests were located by walking transects through the reedbed. At each nest I noted the nest number, number of chicks and the estimated age of the oldest (see Appendix 3 for methods). For each regurgitated sample obtained, I noted the age and rank of the donor. Most food samples were sorted, and prey species identified and measured at the nest site itself, where they were left for re-ingestion by the chicks. Those samples containing many small prey, which could not be treated quickly, were placed in labelled jars, and stored in 50% alcohol for examination in the laboratory. All vertebrate prey were identified to species level. The scientific and English names of all vertebrate prey are given in Appendix 1. Sizes of fish were measured from the tip of the snout to the fork of the tail, while the overall length of other prey was measured, excluding appendages.

Dry weights were estimated for each prey item. For large prey, these were read from length/dry weight calibrations calculated from samples of prey captured in the field. For smaller prey, I used the average dry weight of a sample of prey collected in the field, of the same size range as that being taken by the herons. Further details of the methods used to estimate dry weights are given in Appendix 2, along with the values and equations used.

Three measures were used in the analyses to determine the relative importance of the different prey types in the diet:

1. Frequency of Occurrence(%), calculated as the number of regurgitated samples in which the prey type was found, divided by the total number of samples examined.(X 100).

2. % of total items, calculated as the number of items of this type recorded in all samples, divided by the total number of items (X 100).

3. % by dry weight, calculated as the overall dry weight of the prey type in the samples, divided by the total dry weight of all prey found in the samples. (X 100).

Collection of samples in the field, by the methods described above, is largely opportunistic, and it is not possible to collect adequate samples for detailed statistical analyses on each visit. Furthermore, composition of the samples collected may be influenced by a number of factors,(temporal changes in the availability of prey, foraging locations of the adults, weather conditions, age of nestlings which are to be fed, etc..) none of which can be controlled within the sample-sizes of regurgitates that can be collected. I have therefore grouped all the samples collected, to give a broad picture of the diet of each species, commenting wherever appropriate on salient changes in composition.

RESULTS

Grey Heron Nestling Diet.

The following analyses are based on 397 regurgitated food samples, containing 1536 prey items, collected from Grey Heron nestlings throughout the 1979 and 1980 breeding seasons (Table 5.1.1). Samples were taken from Les Bruns and Couvin, the two largest colonies, which together contained in the two years 99% and 96% respectively of the total Camargue breeding population. The colonies were separated by a distance of 8 km and in each season both colonies also held over 100 pairs of breeding Purple Herons.

The probability of obtaining a regurgitate was related to the age of the nestling, and was highest for those aged 20-30 days (Figure 5.5). Very young chicks, less than five days old, rarely regurgitated food either because they were unable to achieve the required muscular effort, and/or because they were normally defended from potential predators at this age by brooding adults. After 30 days, chicks became increasingly reluctant to regurgitate prey. At this age, a change may have occurred in the balance of the trade-off between the cost of losing food to a predator, and the increasing probability of successfully driving the predator away by overt aggression. In support of this, older nestlings frequently showed aggression before regurgitating. The number of samples collected from very old or very young chicks was therefore small.

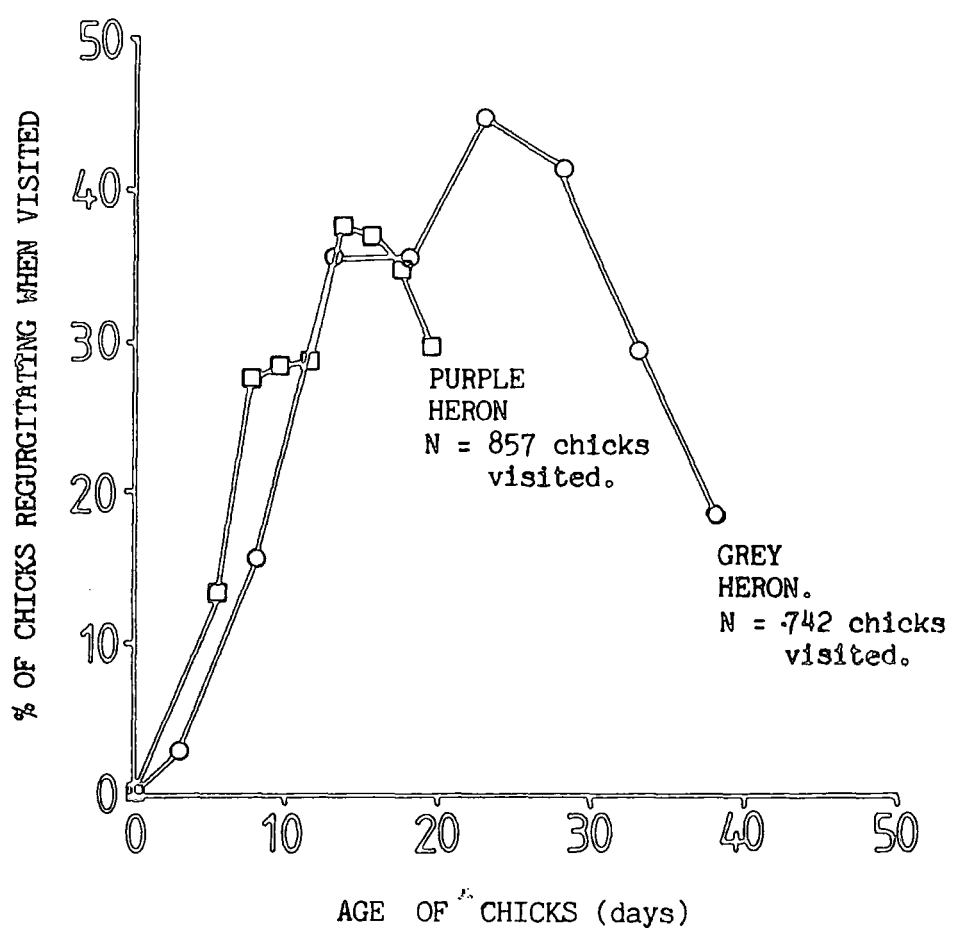
Table 5.1.1. Origin and number of regurgitated food samples collected for the analysis of diet of nestling Grey Herons.

Colony	No. samples	No. prey	%Camargue Breeding Population
Les Bruns 1979	113	385	84.4
Les Bruns 1980	88	357	71.2
Couvin 1979	60	122	14.6
Couvin 1980	136	672	24.9
TOTAL	397	1536	

Table 5.1.2. Origin and number of regurgitated food samples collected for the analysis of diet of nestling Purple Herons.

Colony	No. samples	No. prey	%Camargue Breeding Population
Les Bruns 1979	30	232	56.1
Les Bruns 1980	14	160	38.4
Couvin 1979	64	236	42.1
Couvin 1980	132	771	39.7
Landre 1979	12	42	Bred outside
Landre 1980	50	279	the Delta
TOTAL	302	1720	

FIGURE 5.5. Changes with age in the probability of obtaining a regurgitated food sample during a visit to the nest of Grey and Purple Heron nestlings.



Diet Composition.

The relative importance of the twenty-five types of prey, which were recorded in the diet of Grey Heron nestlings, is shown in Table 5.2. Although several species of invertebrates, Amphibia, mammals and Reptiles were represented, fish comprised more than 99% of the diet by dry weight.

Eels and Carp were the most important prey species, occurring in 53.9% and 36.8% of the samples respectively. Together, they made up more than 90% of the diet by dry weight. The only other prey species of major importance in the diet was Mullet, which occurred in 7.1% of the samples and made up 8.8% of the diet by dry weight. Three other fish species made up more than 1% of the diet by dry weight - Sun-Perch, Tench and Roach. There were single observations of a mammal, a snake and a frog in the diet. Although small prey species, such as Mosquito-Fish, Gobies, Pipe-fish, Atherina and Palaeomon, were recorded frequently (none in more than 8% of the samples), they did not contribute significantly in terms of biomass.

There were no major seasonal changes in the composition of the diet; Eels, Carp and Mullet remained the most important prey throughout. There were no significant differences between years or between early and late season periods in the frequency of occurrence of either Eels or Mullet in the diet (Table 5.3). Carp, however, occurred significantly less often in early samples in 1980 than in those from the same period in 1979 ($\chi^2 = 100.1$, $P \ll 0.001$), although there was no difference between years for the

Table 5.2. Composition of the diet of nestling Grey Herons in Camargue. Data were collected from regurgitated food samples from Couvin and Les Bruns in both 1979 and 1980. English names of the prey species are given in Appendix 1.

	% occurrence	% of of items	% by dry weight
<i>A.anguilla</i>	53.9	24.5	39.8
<i>Cyprinus carpio</i>	36.8	11.7	46.9
<i>Mugil spp.</i>	7.1	2.3	8.5
<i>Lepomis gibbosus</i>	5.8	2.7	1.3
<i>T.tinca</i>	2.0	0.6	1.1
<i>R.rutilus</i>	1.8	0.5	1.1
<i>L.lucioperca</i>	0.5	0.1	0.2
<i>Pomatoschistus microps</i>	3.3	11.0	+
<i>Sygnathus abaster</i>	4.3	3.3	+
<i>Gambusia affinis</i>	4.8	15.2	0.2
<i>Gasterosteus aculeatus</i>	1.8	2.0	+
<i>Atherina boyeri</i>	6.1	8.1	+
<i>Esox lucius</i>	0.3	0.1	+
<i>R. rattus</i>	0.3	0.1	0.2
<i>N. natrix</i>	0.3	0.1	+
<i>Rana ridibunda</i>	1.0	0.3	0.1
<i>Palaeomon sp.</i>	7.6	9.7	0.1
<i>G. gryllotalpa</i>	3.3	1.2	0.1
Gammaridae	0.5	2.4	+
Odonata larvae	2.0	1.3	+
Odonata imago	0.8	0.3	+
Coleoptera larvae	3.3	2.5	0.1
Coleoptera imagos	0.3	0.1	+
Hemiptera	0.3	0.1	+
Dermaptera	0.3	0.1	+
	N=397	N=1536	

Table 5.3. Comparison of the frequency of occurrence of Eels, Carp and Mullet in the diet of nestling Grey Herons in the early and late halves of the 1979 and 1980 breeding seasons. I chose 15th May as the division because adequate samples were available both before and after this date, and because no extensive drying out of the temporary fresh-water marshes had occurred before this date in either of the two years.

	EELS		CARP		MULLET	
	1979	1980	1979	1980	1979	1980
Before 15 May	57.9	58.1	39.5	18.9	7.9	9.5
After 15 May	53.6	43.4	45.4	57.9	5.2	4.0

later part of the season ($\chi^2 = 2.2$, $P > 0.05$). The spring of 1980 was exceptionally cold and windy (Hafner et al. 1982), and this may have reduced the activity and availability of Carp to foraging herons.

Sizes of Prey.

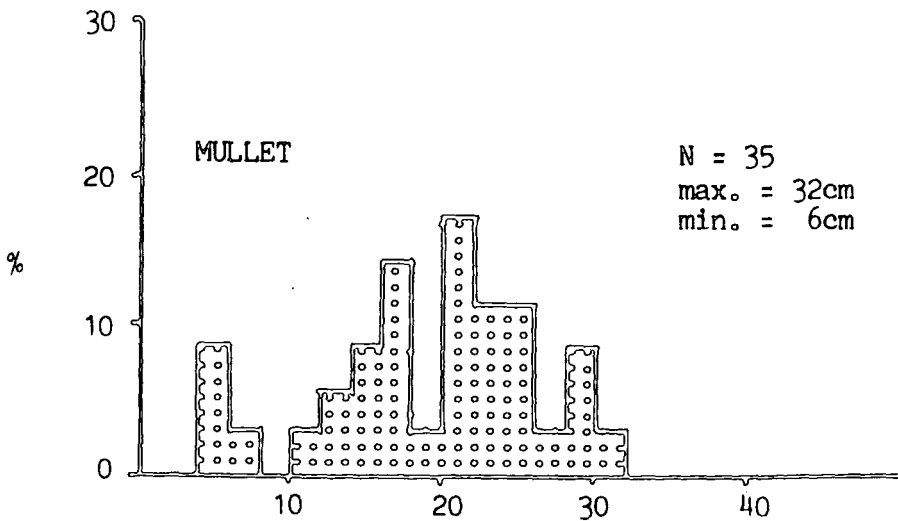
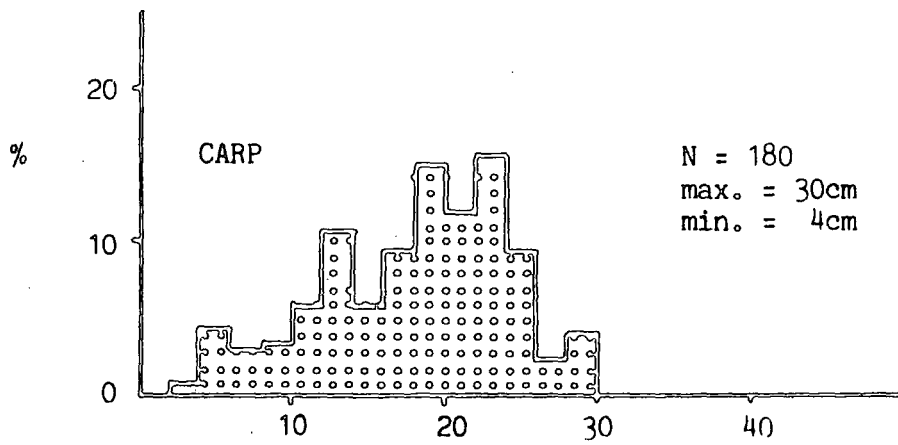
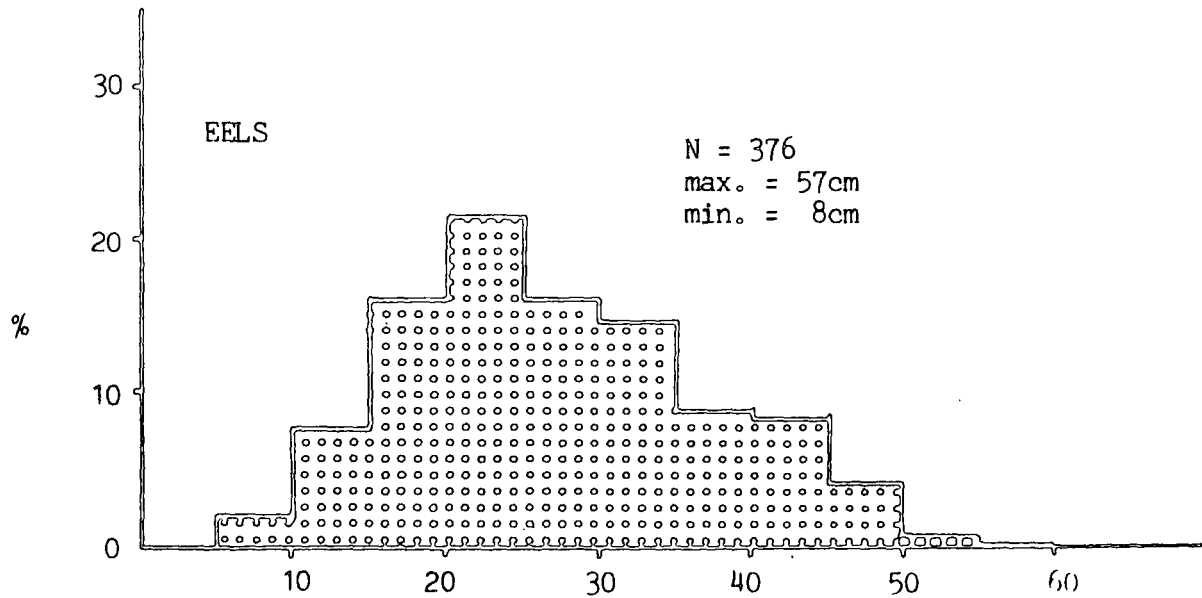
Although very small prey were recorded frequently, more than 92% of the diet by dry weight was made up by prey of over 10g dry weight. Prey varied in size from 1cm long fish and invertebrates, weighing less than 1g freshweight, to 30cm long Carp weighing 475g, and 57cm Eels. Length-frequency distributions of Eels, Carp and Mullet, the three most important prey species in the diet, are shown in Figure 5.6. The maximum lengths recorded for these prey were 57, 30 and 32cm respectively.

Diet of the Purple Heron.

The following analyses are based on 302 regurgitated food samples, containing 1720 prey items, collected from Purple Heron nestlings throughout the 1979 and 1980 breeding seasons (Table 5.1.2). Samples were collected at Les Bruns, Couvin and Landre. Birds from the latter colony used the delta as a major feeding area (Chapter 3), even though the colony was situated outside the delta.

The probability of obtaining regurgitates from Purple Heron nestlings followed a pattern very similar to that from nestling Grey Herons (Figure 5.5), although the peak occurred much earlier (12-15 days) than for the latter species. The chances of obtaining regurgitates after this dropped rapidly, since chicks

Figure 5.6. Length-frequency distributions of Carp, Eels and Mullet in the diet of nestling Grey herons in the Camargue.



LENGTH OF FISH (cm)

were both more reluctant to regurgitate, and became very difficult to find as they leave their nests to hide in the reeds from intruders. Very few regurgitates were therefore obtained for chicks over 20 days old.

Composition of the diet.

Purple Herons took a much wider range of prey than Grey Herons, and the relative importance of the 35 different prey types which were recorded in the diet is shown in Table 5.5. Fish comprised more than 85% of the diet by dry weight, with Eels, Carp and Mullet again being the most important prey. Roach, Sunperch, Tench, Bream, frogs and lizards were also important. Small prey, particularly Mosquito-fish, Coleoptera larvae and Odonata larvae occurred frequently, but contributed little in terms of biomass.

Sizes of prey.

The length frequency distributions of Eels, Carp and Mullet recorded in the diet of the Purple Heron are shown in Figure 5.7. The maximum lengths of each species observed were 51, 24 and 25cm respectively. The distributions for Carp and Mullet indicate that many fry were taken, as well as fish in their first and second years. The inclusion of these smaller size classes reflects the relatively late chick-rearing period of this species (cf. the Grey Heron), by which time most fish have spawned.

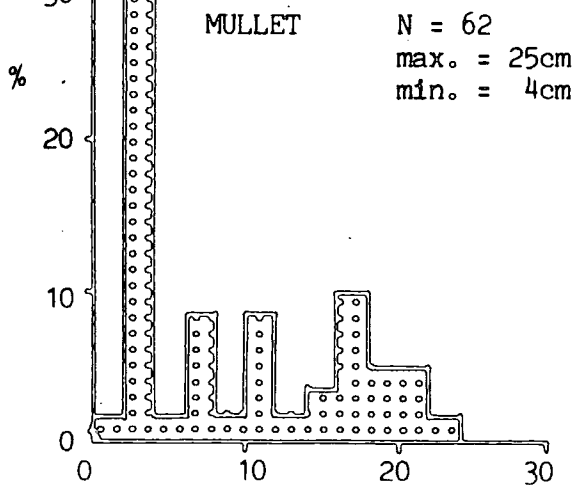
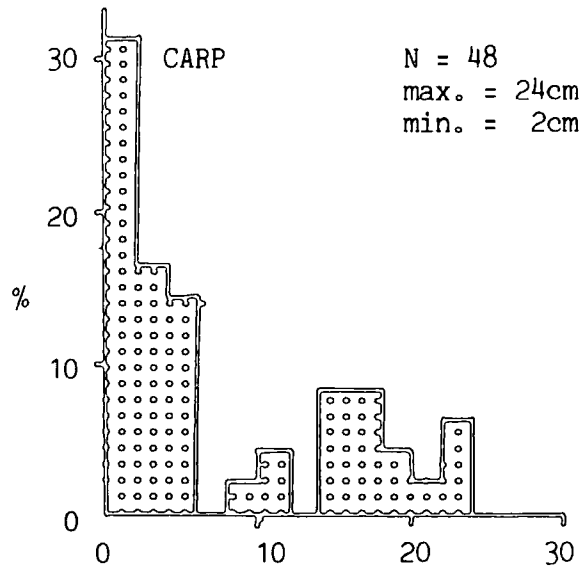
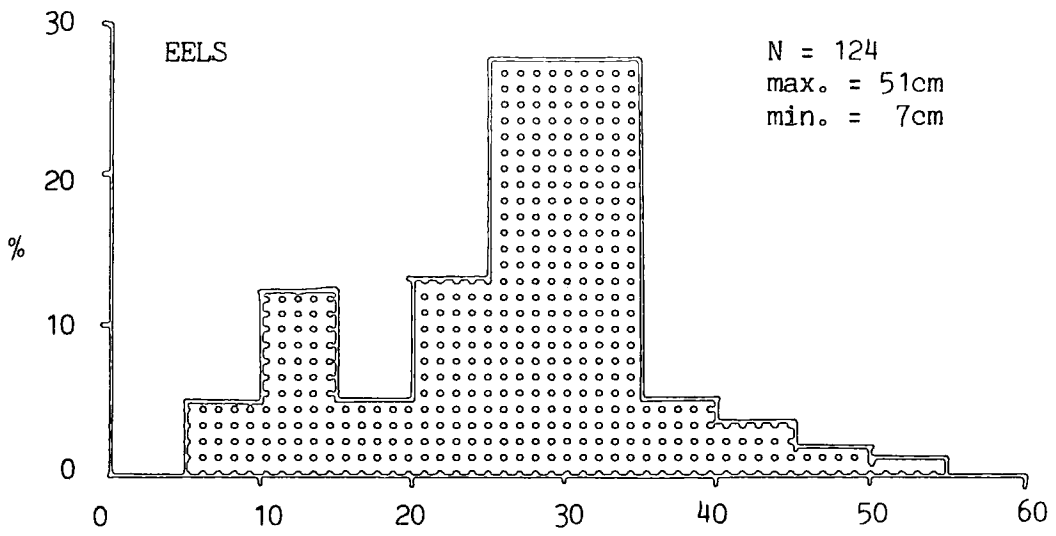
Table 5.4. Composition of the diet of nestling Purple Herons in the Camargue. Analysed from regurgitated food samples collected from the colonies of Couvin, Les Bruns and Landre in 1979 and 1980.

	% occurrence	% of items	% by dry wt.
<i>A. anguilla</i>	33.8	7.2	40.4
<i>Cyprinus carpio</i>	7.6	2.7	11.8
<i>Mugil sp.</i>	8.9	3.6	12.2
<i>Lepomis gibbosus</i>	16.9	4.4	6.1
<i>Atherina boyerii</i>	2.0	1.1	0.2
<i>Gambusia affinis</i>	28.8	38.5	1.6
<i>Barbus sp.</i>	0.3	0.1	0.1
<i>Perca fluviatilis</i>	0.7	0.1	0.2
<i>Pomatoschistus microps</i>	0.3	0.1	+
<i>Gasterosteus aculeatus</i>	2.0	1.2	+
<i>Abramis/Blicca</i>	1.0	0.3	3.2
<i>Rutilus/Scardinius</i>	6.3	1.5	6.4
<i>Esox lucius</i>	0.7	0.2	0.1
<i>T. tinca</i>	3.3	0.6	2.8
<i>Ictalurus melas</i>	0.3	0.1	0.3
Mammal	0.7	0.1	0.2
Bird	0.3	0.1	0.2
<i>Emys orbicularis</i>	1.0	0.2	0.2
<i>Natrix sp.</i>	4.6	0.8	1.6
<i>Lacerta sp.</i>	9.6	2.4	5.1
<i>Rana ridibunda</i>	14.6	7.2	4.2
Tadpoles	1.3	0.4	+
<i>Palaeomon sp.</i>	4.0	1.5	0.1
<i>Triops cancriformis</i>	0.3	0.4	+
Arachnida	2.7	0.5	+
Odonata imago	8.9	3.1	0.3
Odonata larvae	12.9	5.1	0.1
<i>G.gryllotalpa</i>	10.6	2.6	0.9
Coleoptera imago	0.7	0.1	+
Coleoptera larvae	19.5	12.8	1.9
Donassidae cocoons	1.0	0.9	0.1
Hemiptera	1.4	0.3	+
Dipteran imago	0.3	0.1	+
Diptera larvae	1.0	0.2	+
Lepidoptera larvae	0.3	0.1	+

N = 302

N = 1720

Figure 5.7. Length-frequency distributions of Carp, Eels and Mullet in the diet of nestling Purple Herons in the Camargue.



LENGTH OF FISH (cms).

DISCUSSION.

Prey Selection by Grey Herons.

Grey Herons are extremely specialised in diet during the breeding season in Camargue, being almost entirely piscivorous and preying mainly on large Eels, Carp and Mullet. This specialisation suggests that the Camargue is an area with high densities of available prey of their preferred sizes and types, since diet studies from elsewhere (Vasvari 1948, Moltoni 1936, Owen 1955, 1960) generally indicate a much broader diet. The exception is in an area with fishponds (Schlegel 1964), an artificial habitat with very high densities of preferred prey. The very rapid growth of the breeding population in Camargue (see Chapter 2) confirms that the region offers very good conditions for this species. It is known from the diet of the other species that a much wider spectrum of prey is present in the Camargue (Chapter 1) than is taken by Grey Herons, which because of their long legs can potentially forage in all the habitats available to the other species, and can handle all size-ranges of prey taken by them. Thus, it is likely that the wider spectrum of prey is also fully available to Grey Herons. If this hypothesis is correct, two predictions can be made, although only the first can now be tested:

1. Breeding adults should select profitable prey as determined by the prey selection measures reported earlier in this chapter.
2. Intraspecific competition may cause the diet spectrum of the Grey Heron to become broader if the population

develops further and becomes food-limited over the next few years.

Do Grey Herons select profitable types of prey?

Clearly, prey types of low profitability were avoided. Catfish, which were abundant in the feeding habitats (Crivelli 1981a), were not recorded in the diet, in accordance with their low profitability. Similarly, very small prey with low profitability for other reasons (eg Mosquito Fish, Sticklebacks and invertebrates) were only infrequently taken even though very abundant in the feeding habitats and taken by the smaller heron species (Chapter 1). Instead, large fish (excluding Catfish) predominated in the diet, as was predicted. The relative profitability measures of Carp and Eels would suggest that Carp should be taken more than Eels. This was not however the case; Eels were the more important prey, particularly at the start of the season. There are three possible explanations for this: firstly, the currencies used to measure profitability may not have been the same as those used by the herons, particularly as the diet was deduced from food brought to nestlings and not eaten by the adults. Indeed, Eels have higher calorific values than Carp (Murray and Burt 1969), which may explain this difference, if energy content rather than size is the currency on which selection is being made. Secondly, the two prey may not have been equally available to the herons; indeed, seasonal changes in their proportions in the diet reflect this. Studies of the availability of and encounter rates with different prey species

Figure 5.8. A comparison of the size distribution of Carp and Eels found in the diet of nestling Grey herons in the Camargue, with the size distributions expected from prey profitability experiments.

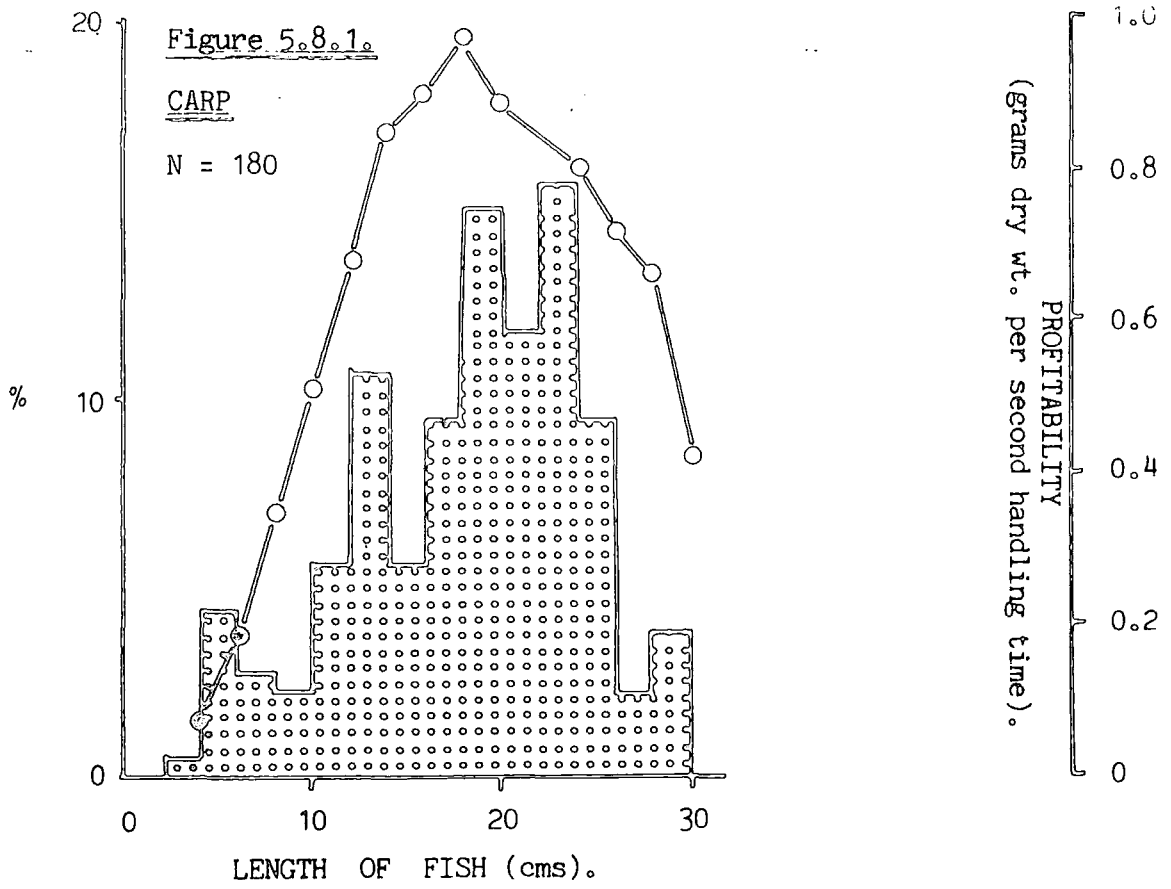
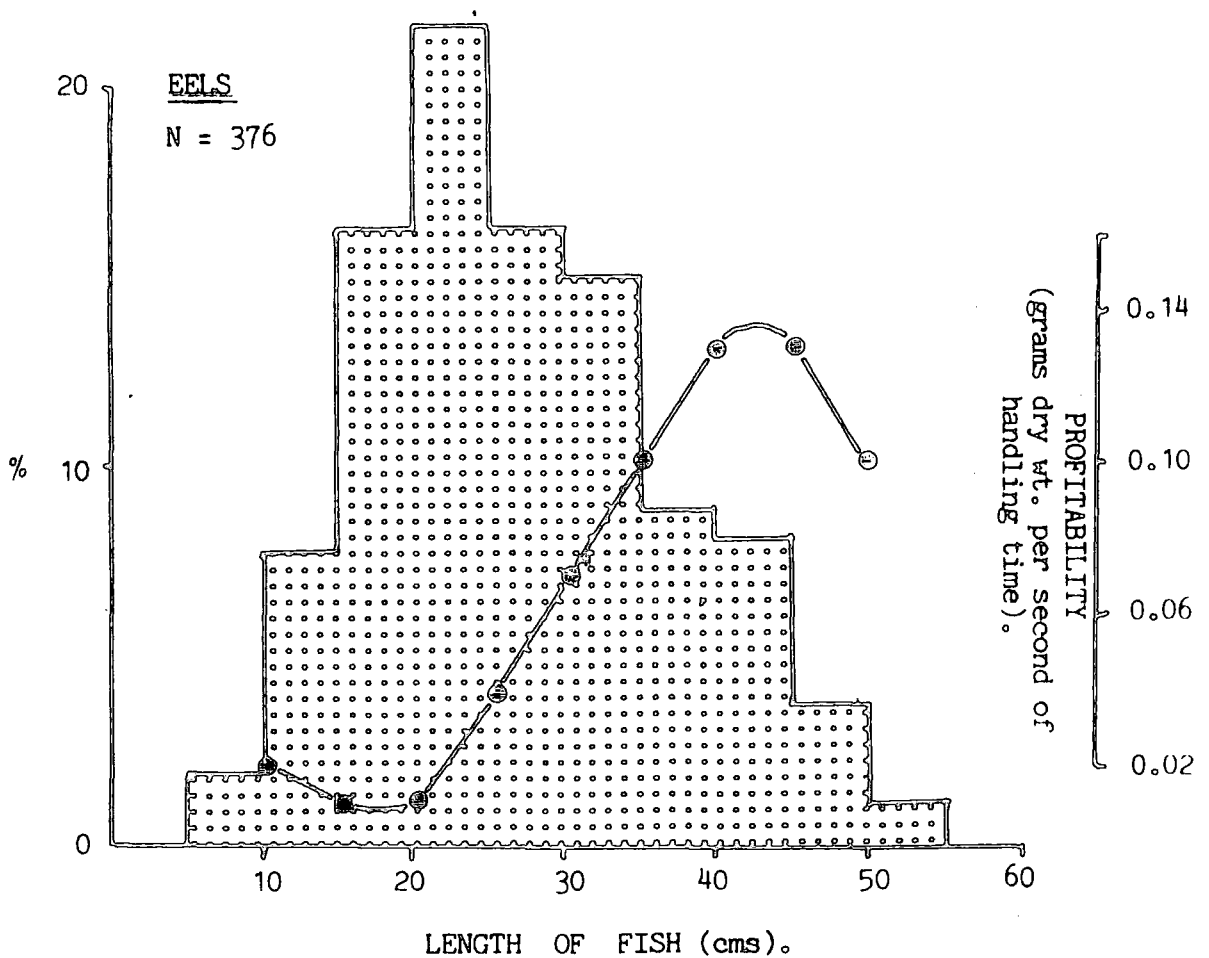


FIGURE 5.8.2.



are thus required, but will be very difficult to obtain. Thirdly, Carp contain thiaminase an enzyme that destroys vitamin B1 and is known to have caused nutritional deficiencies in various fish-eating animals (Kear 1973). Thus, the addition to the diet of Eels, which do not contain Thiaminase, may be important.

Do Grey Herons select profitable sizes of Prey?

It has been shown experimentally and reported elsewhere (Britton and Moser 1982) that adult Grey Herons were able to select between profitable and non-profitable size-classes of the Mosquito Fish. For other important prey species, I have examined the 'within-prey-type' size distributions in the diet, to see whether the herons are selecting profitable sizes, as predicted earlier in this chapter. For Carp (and presumably Mullet), the size distribution found in the diet fits the predictions very well, with a skewed distribution towards the largest classes that can be consumed (Figure 5.8.1). Comparison with the size-ranges of Carp present in the canals and marshes of the Camargue (Crivelli 1981a), indicates that the herons are making a very restricted selection of mainly second, and some first summer fish. Once a fish achieves its third summer (ie >26cm long), few can be taken by a Grey Heron. At two of his study sites, Crivelli (1981a) noted that Carp in their first and second summers showed wounds typical of heron attack. The Carp populations of canals and marshes in Camargue have very different size-distributions (Crivelli 1981a), with canals supporting populations of predominantly first and second year fish, whilst the marshes generally hold small numbers of these but much larger

numbers of Carp in their third year or older. Thus, it appears that a large proportion of the Carp taken by foraging Grey Herons must come from canals and ditches. These habitats also support densities of Carp which are up to 10 times greater than in the marshes(Crivelli 1981a).

For Eels, the size distribution observed in the diet fits less well to the frequency-distribution expected from the measures of profitability(Figure 5.8.2). The pattern of sizes taken fits the curve well, but the curve suggests that much larger Eels should be taken than were observed. A possible explanation is that the larger, most profitable Eels may not be abundant in the Camargue, as was suggested by Crivelli(1981a). Indeed, during the period May to June, he recorded very few Eels of over 40cm length in his study sites. In addition, large Eels may not be as profitable for nestlings(from which the diet has been measured). A number of Eels were recorded uneaten on the sides of nests, suggesting that they may have been too large(long) for the chicks to consume.

Thus, it appears that adult Grey Herons are making a very strong selection of prey during the breeding season, and that this selection is based both on prey size and prey type.

Clearly, the experimental approach described above has important possibilities for aiding the management of fish-farms to reduce heron predation. This will not be discussed in detail here, but measures of the profitability curves of different species of fish combined with a knowledge of their growth rates, will permit

predictions of the periods when they are most at risk from heron attack, and therefore in need of protection. Although the method has been described only for the Grey Heron, it could also be used for other species of piscivorous birds such as the Night Heron and Cormorant, which are both important predators at fish farms.

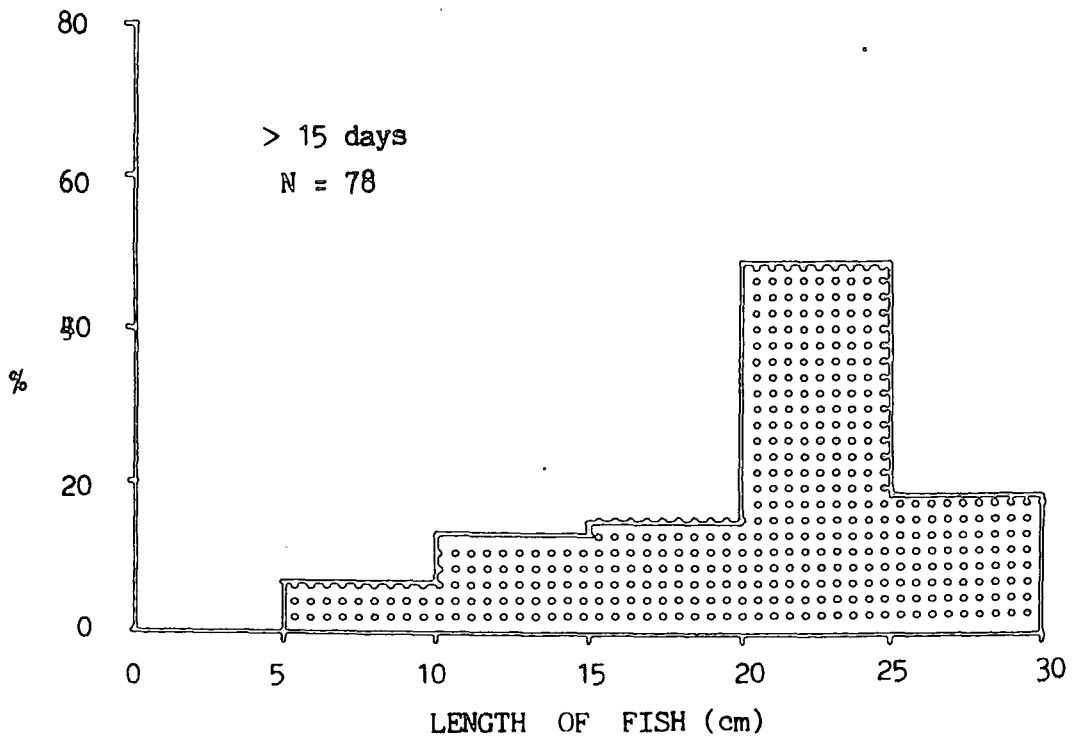
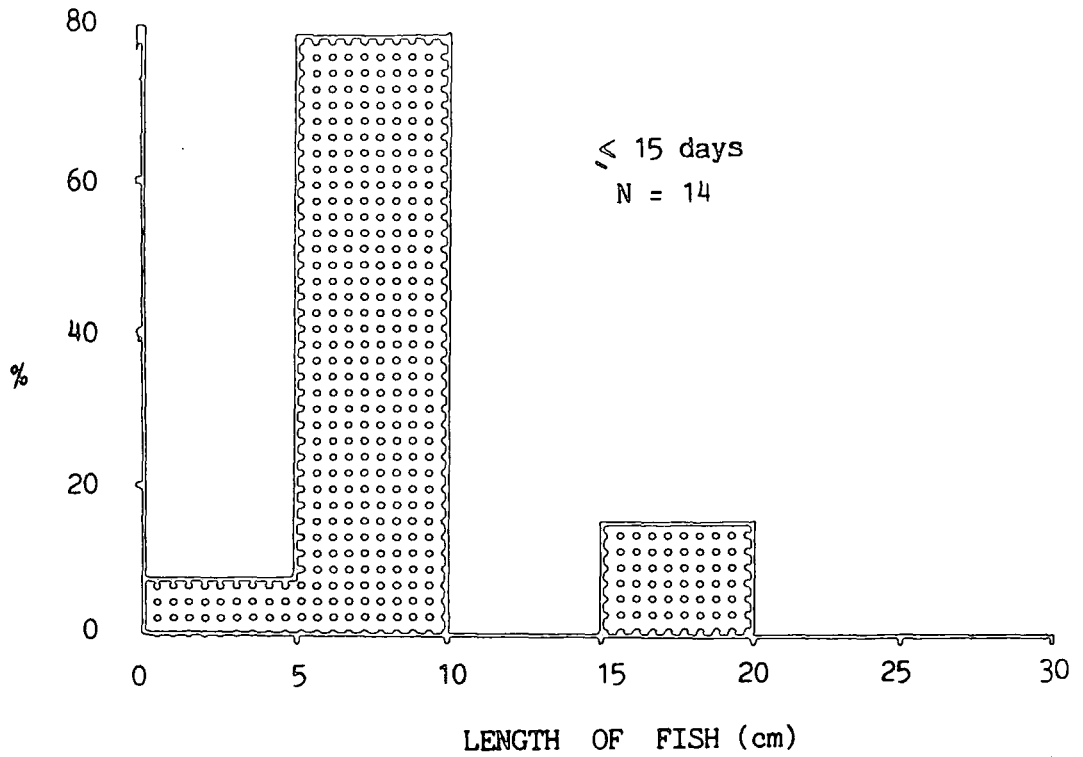
Do Grey Herons select prey during the breeding season which are profitable for their young chicks?

Prey-handling limitations prevent young Grey Heron chicks from consuming those prey-sizes which are optimal for an adult (Figure 5.4). It was therefore predicted that adult herons should select smaller prey during the early part of the chick rearing period. Such selection could occur either by capturing smaller size-classes of an individual prey type, or by selecting alternative prey types which are smaller. It is difficult to provide conclusive field evidence that adults are selecting different prey for young nestlings, since the chicks may themselves select from those prey brought back to the nest by the adults (eg Courtney and Blackpoel 1980). Also Marion (1979) reported that adults in his study area were observed to predigest large prey so that they could be broken up and fed to young chicks. I did not however find broken parts of larger fish in the diet of young chicks in Camargue.

Two lines of evidence suggest that the adult herons in Camargue are making a positive selection. Figure 5.9 shows the size distributions of Carp in the diet of Grey Heron nestlings of two age-groups. Clearly, younger chicks regurgitated smaller fish

Figure 5.9.

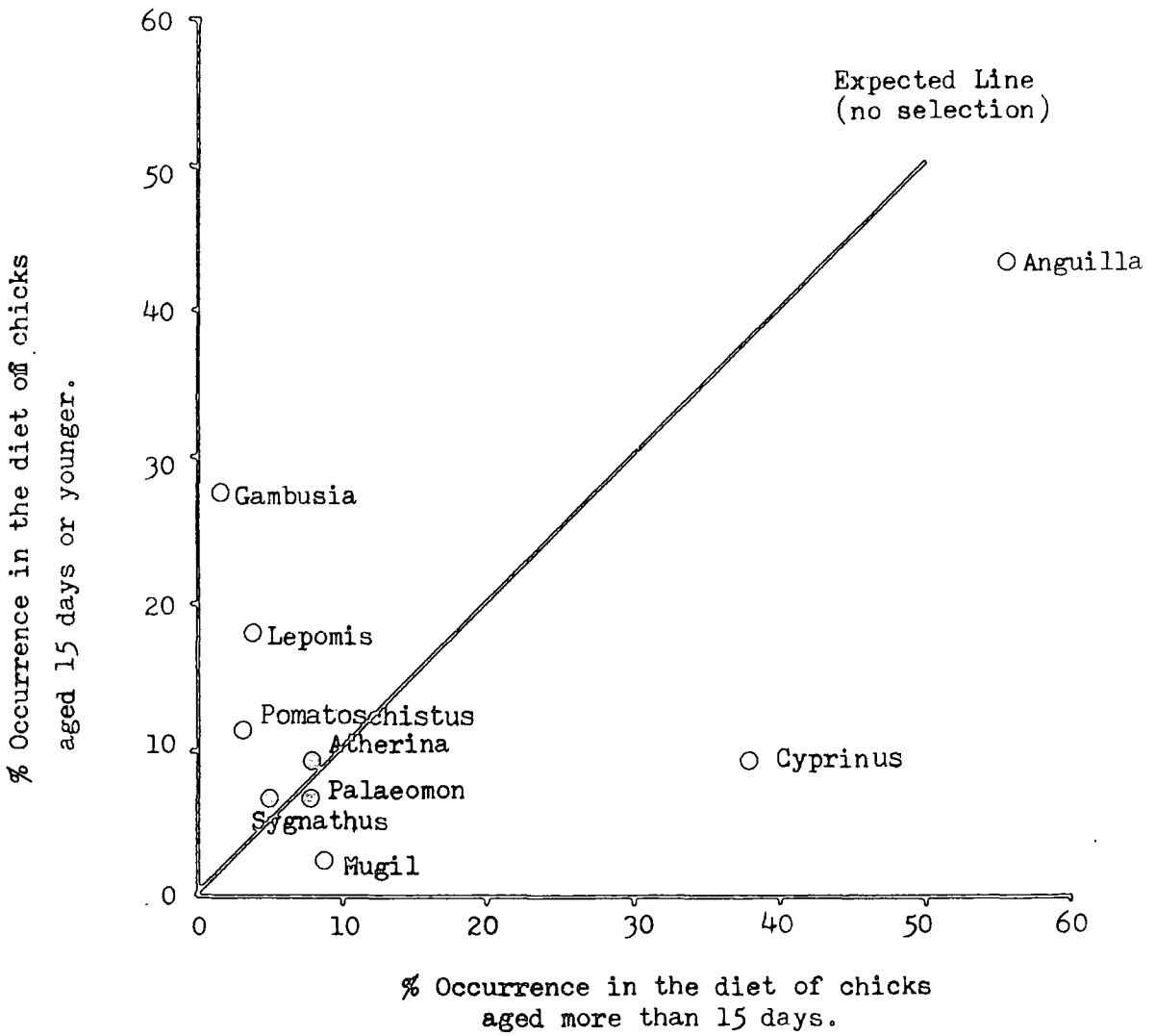
Length-frequency distribution of Carp taken from regurgitates of Grey Heron nestlings aged 15 days or less, compared with those from nestlings older than 15 days.



than older chicks. If the chicks were themselves making the selection, I would expect the regurgitates from older nestlings to contain many of the smaller size-classes as well as large ones. There is little evidence of this, suggesting that it is the adults which select smaller fish. White(1938) reached similar conclusions for nestling Kingfishers Megaceryle alcyon, a family which also feeds large prey to their nestlings.

The second line of evidence is provided by the species of prey found in the regurgitates of older and younger chicks. If adults are actively selecting smaller prey, smaller species should occur more frequently in the regurgitates of young chicks, since these were more abundant than the small individuals of large prey species. The data for 1980 (from both colonies combined) fit this hypothesis well(Figure 5.10). Small prey, such as Mosquito-Fish, Sunperch and Gobies (all small fish species) occurred more often than expected in samples from younger chicks, whilst Eels and Carp were found more frequently in those of older chicks. The difference for Carp is statistically significant ($\chi^2 = 12.1$, $P < 0.001$) but sample sizes for other species are too small. This implies that the adult herons are searching for the relatively more numerous small fish species, than the scarcer small Carp, when feeding young chicks. Similarly, Kirkham and Morris(1979) found that young nestlings of the Ringed-bill Gull Larus delawarensis were fed many insects which were not fed to older chicks. These were both easier to handle, and provided a good protein source.

Figure 5.10. The frequency of occurrence of different species of prey in the diet of nestling Grey Herons aged up to and older than 15 days. (Only those fish species occurring in more than 5% of the samples for either group are included for analysis.)



Thus there is evidence that adult Grey Herons are selecting smaller prey for younger than for older nestlings by selecting both within a species for smaller size-classes and amongst species for smaller species. This may require the adults to alter their hunting methods and perhaps search in different habitats, since smaller prey tend to occur in shallower water (pers. obs.). Evidence that the adults used shallow areas is given by the occurrence in the diet of younger chicks of frogs, earwigs and dragonflies (more terrestrial species) which were not found in the diet of older chicks.

Comparison of the diet of Grey and Purple Herons.

In morphology, Grey and Purple Herons are the two most similar Ardeidae which breed in the Camargue, overlapping extensively both in tarsus length and bill size (Figure 1.3). They are thus able to exploit similar habitats and consume similar sizes of prey. In Chapter 1, I showed that the two species overlapped by 69% in the types of prey consumed and 62% in the sizes of prey taken during the breeding season. Further information has been presented in this chapter, and it is therefore possible to compare the diets in more detail.

Eels are the most important prey fed to the chicks, comprising just over 40% of the diet by dry weight for both species. Mullet are also taken in very similar proportions, occurring in 7 - 8% of the samples. It is in the proportions of other large fish taken that marked differences are observed between the two species. For the Grey Heron, Carp account for almost all the

remaining 50% of the diet, with few other prey represented. In contrast, Purple Herons take a wide range of large fish species, not only Carp(11.8%), but also Roach/Rudd(6.4%), Sunperch(6.1%), Bream(3.2%), Tench(2.8%), as well as smaller proportions of Perch, Pike and Barbel. These differences reflect the foraging habitats used by the two species, Purple Herons tending to feed in much more densely vegetated, marginal sites than the Grey Heron, which usually feeds in open water. As a result of this difference, the diet of the Purple Heron also includes many terrestrial or shallow water species, such as frogs, small mammals, birds, lizards, snakes and numerous aquatic, terrestrial and aerial invertebrate species. Thus although the two species often forage in the same waterbodies, they are taking prey from rather different microhabitats.

The large bills of the two species enable them to consume a wider size-range of prey than the other Ardeidae examined, although the relatively low profitability of small prey makes these unimportant in the diet (Figure 1.4). On average, however, Purple Herons have rather smaller bills than Grey Herons(Figure 1.3), and this is reflected in the differences in the maximum sizes of prey that the two species consume(Figures 5.6 and 5.7). Although they can both consume Eels of similar maximum length (which weigh up to 300g freshweight), Purple Herons took Carp and Mullet only up to about 25cm, whilst Grey Herons took 30cm fish. These differences may be a result of gape width limitations. Such large Carp weigh approximately 500g freshweight, and might therefore restrict flying ability in Purple Herons, which weigh less than 1000g.

Comparison with other diet studies.

Most information on the diet of Grey Herons has been gathered from stomach contents of shot birds (see Cramp and Simmons 1977), a method rejected for this study. Owen (1955) studied chick diet from regurgitates at three colonies in England, and reported considerable variation in the prey from individual colonies as a result of regional variation in the availability of different prey. The diet at all colonies was less specialised than in the Camargue, with up to 10 different prey types (mainly fish and small mammals) being abundant in the diet. The size distribution of Eels taken was similar to that recorded in the Camargue, whilst the sizes of all other fish were smaller, and below the optimum as measured by the prey optimality measures reported above.

There have been only two major studies of the diet of Purple Herons based on nestling regurgitates, one in Spain (Amat and Herrera 1978) and one in Holland (Owen and Phillips 1956). In the former study, Carp comprised almost 70% of the diet, with nestlings of other waterbirds and Coleoptera being the main secondary prey. More than 95% of the Carp taken were between 4.5 and 16.5cm long. This specialisation and size-range strongly suggests that the herons were feeding in a situation with a very high availability of first-year Carp. (The larger second year Carp which were important in the Camargue diet were not represented). The less intensive study in Holland recorded a wide

variety of large freshwater fish (particularly Rudd, Pike, Perch, Bream and Eel), plus many mammals (Water-vole and Moles); very few small prey were found.

Thus for both species, regional variations in the availability of different types and sizes of prey determine which are included in the diet.

CHAPTER SIXConservation of the Purple Heron in the Camargue and western Europe.

The Camargue is a wetland of outstanding conservation value for colonial herons. In Table 6.1, I have summarised the numerical importance of the Camargue heronries expressed as a percentage of the populations of the whole of France and of the estimated maxima for the whole of western Europe. Using the internationally recommended '1% criteria' for waterfowl conservation (IWRB 1980), the Camargue must be considered as an area of both national and international importance for populations of all six colonial species. The only other regions of western Europe, of significance for so many species, are the Coto Doñana (Spain) and the Po valley and delta (Italy).

The conservation requirements of the tree-nesting herons have been described elsewhere (Hafner 1977), and appropriate management action undertaken (Hafner 1984). The Grey Heron is relatively numerous and expanding throughout western Europe, and not in need of special conservation measures. In contrast the Purple Heron, with a west European breeding population of only 8000 pairs, is relatively scarce with large numbers (> 500 pairs) occurring in only three areas of western Europe: Camargue, 1200 pairs (this study); Holland, 750 pairs (Den Held 1981); Marismas (Spain), 800-1000 pairs (Amat and Herrera 1977). Conservation of Purple Herons in the Camargue, which supports an estimated 15% of the west European breeding population, must

Table 6.1. The importance of the Camargue as a breeding area for populations of colonial Ardeidae, relative to the whole of France and the whole of western Europe. Data are for 1981, unless otherwise stated.

	Camargue population	French population	W. European population	% French pop ⁿ in Camargue	%W. European pop ⁿ in Camargue
Grey Heron	515	10000 ¹	max. 35000	5.2	1.5
Purple Heron	1241	2660 ²	max. 8000	46.7	15.5
Little Egret	1441	2300 ¹	max. 20000	62.7	7.2
Night Heron	531	4000 ¹	max. 25000	13.3	2.1
Squacco Heron	115	120 ³	max. 800	95.8	15.0
Cattle Egret	464	466 ⁴	max. 7000	99.6	6.6

Sources: Cramp and Simmons (1977) except for

¹ S.N.P.N. (1980).

² Hafner et al. (1984).

³ Marion and Marion (1982a).

⁴ Marion and Marion (1982b), Hafner et al. (1982).

therefore be of high priority, particularly in view of the downward population trends reported in this study.

A fundamental requirement for effective management of Purple Herons, indeed any declining species, is to identify the factor(s) which are limiting the population under study. There is, however, a major problem of scaling. At the colony level, I have demonstrated that the size of individual colonies may be limited either by the amount of suitable habitat available for breeding (Chapter 2), or by the food resources available in the surrounding feeding areas (Chapter 3). On a regional level, the breeding population within the delta is currently limited by the number of suitable breeding sites available (Chapter 2). On a still higher level, for the whole of western Europe, there are at least two more factors which may limit the population: first, the number and extent of wetland areas, such as the Camargue; second, mortality on the wintering areas (see Den Held 1981). Conservation/management actions should therefore differ depending on the scale of the area under investigation, and the size and distribution of the population desired. I shall now discuss aspects of the conservation of the Purple Heron both in the Camargue and throughout western Europe.

Conservation in the Camargue.

Although some 23% of the Camargue wetlands are protected under reserve status, not one of the reed-nesting heron breeding sites is included in this area. All are located on wildfowl hunting estates, where increasingly intensive management practices have

resulted in the destruction of many reedbeds. Within the delta, I have shown that the availability of suitable breeding sites is the factor which currently limits the breeding population and has been responsible for the observed decline. If the future existence of the Camargue breeding population is to be ensured, a first priority must be to protect the remaining breeding sites through a cooperative programme with the hunting estates, including maintenance of water levels in reedbeds during the summer months and careful reedbed management. There are however, good possibilities for creating suitable breeding sites on reserve areas, using techniques similar to those developed for the tree-nesting herons (Hafner 1983). In this case, a wood was designed and planted to create a suitable breeding site, the wood becoming occupied by breeding herons 11 years after the start of the project. Creation of suitable habitat for the reed-nesting species should certainly be a more rapid and simple process than is required to create a wood. The location of these reedbeds should be carefully chosen to ensure proximity of unexploited feeding areas away from other large colonies. Ideally, at least one site should be chosen in each of sectors C and D of Figure 2.4, these being areas where breeding has ceased altogether. Sites within the delta should be of highest priority, since breeding sites are apparently not limited in the Petite Camargue or on the Plan du Bourg.

Although the broad patterns of resource use have been described for all six species of colonial Ardeidae in the Camargue (Chapter 1), I have largely ignored the potential implications, for

interspecific competition, of the extensive overlap recorded between Grey and Purple Herons. This was because the observed decline in the Purple Heron breeding population could not be accounted for by interspecific competition with Grey Herons, and because the breeding population of the Grey Heron was still expanding rapidly during the study period and was presumably not therefore resource limited on the breeding grounds. My findings, however, strongly support a case for further research on possible interspecific competition between the two species, since this poses a potential threat to the future of the remaining Purple Herons breeding in Camargue.

Although sympatric over much of their breeding range, Grey Herons normally breed in trees, and the Camargue is the only place in western Europe where large numbers of the two species are found together in mixed-species colonies in reedbeds. Two resources were identified as limiting the numbers of pairs of Purple Herons breeding in the Camargue: breeding habitat and the availability of food resources near to the colony. The available surface area of suitable reedbed apparently limits the number of pairs of Purple Herons at many of the breeding sites within the delta (Figure 2.5). Both Grey and Purple Herons frequently nest together in mixed-species colonies (Table 1.1), in the same reedbeds. At the time of my study, almost all the Grey Herons bred at the colony of Les Bruns, the only site within the delta where breeding habitat was superabundant, apparently for both species. However, further expansion of the Grey Heron population within the delta poses a threat to Purple Herons, as this

breeding resource becomes limiting to the Greys. At least a proportion of the Grey Herons are winter residents in Camargue and begin nesting in early February, while the majority of pairs have taken up nesting sites by the time the Purple Herons return from their winter quarters in early April. Thus, Greys have access to the most favourable nesting sites without competition from the Purples. This might result directly in Purple Herons being unable to obtain nesting sites, or alternatively in the Purples occupying less suitable breeding sites where, for instance, the risk of predation may be higher. In a similar situation concerning territorial warblers in England, Garcia (1983) showed experimentally that Blackcaps Sylvia atricapilla set up breeding territories earlier and competitively excluded the later breeding Garden Warblers Sylvia borin from these same areas. In addition to their temporal advantage, adult Grey Herons are some 500g larger than adult Purple Herons. Kushlan (1978) and many other workers have shown that the outcome of interspecific aggressive encounters in herons is related to body size. It is therefore unlikely that Purple Herons could displace already established Greys from their breeding sites; indeed, the converse could occur.

Intraspecific competition for feeding sites adjacent to the colony was an important mechanism for the density dependent regulation of colony size at breeding sites where the number of Purple Herons was not limited by the available breeding habitat (chapter 3). Birds feeding at increasing distances from the colony incurred the costs of extra travel time. I have no

evidence for interspecific territorial aggression between Greys and Purples since my studies were carried out at an almost monospecific colony. The two species, however, overlap considerably in the sizes and types of prey taken, and in their foraging habitats. In addition, Marion (1984) has demonstrated that Grey Herons maintain feeding territories during the breeding season, in a manner very similar to that described for the Camargue Purples. Thus, the temporal advantage of breeding earlier could again allow the Greys to occupy the 'best' feeding sites, before the Purples return from Africa; this competitive advantage might again be maintained through body-size differences of the two species. Such displacement might either force the Purple Herons to forage in less optimal habitats, or to forage further from the colony. Both effects would be predicted to result in a reduced breeding output, and in a smaller total number of Purple Herons breeding in the colony. The total number of pairs of herons in the colony (both species) would, however, be predicted to increase, since mixed-species colonies of herons should be larger than monospecific colonies, where resource levels remained constant (Burger 1981).

To summarise, morphological and ecological overlap between Purple and Grey Herons poses a potential threat to the remaining Purple Heron breeding population in the Camargue, through interspecific competition for breeding sites and food resources. The opportunity for investigation of these effects has been created by this study, since the limiting resources have been identified, and baseline patterns of resource exploitation by Purple Herons

have been described for a colony, Landre, before invasion by Greys. It is recommended that the development of the breeding population of Grey Herons should be followed closely at this site, in conjunction with regular assessments of the usage of different feeding zones by the two species, and a program to monitor reproductive output. At sites where breeding habitat is limited, experimental removals of Greys could be undertaken to investigate whether they are displacing potential Purple Heron breeders.

Conservation in western Europe.

The specialised wetland habitat requirements of Purple Herons for both feeding and nesting, coupled with the very small number of suitable areas remaining, have given this species an extremely discontinuous breeding distribution in western Europe (see map in Cramp and Simmons 1977). This type of distribution poses several conservation problems, firstly because the loss of any one of the main areas could very significantly reduce the west European population, and secondly because the individual populations may not be self-sustaining.

Conservation assessments of the importance of ornithological sites are usually made on numbers alone. However, for breeding areas, productivity may also be an important measure. I showed in Chapter 4 that the average clutch-size of Purple Herons in the Camargue was the smallest recorded in western Europe, being some 1.5 to 2 eggs lower than for those breeding in some other parts

of their range (Holland, Hungary). I argued that adjustments in clutch-size provide a coarse-tuning mechanism by which the adults can adjust their brood-size to the maximum number of chicks that they can rear to fledging. If mortality rates of juveniles between fledging and departure are the same for the different breeding areas, this implies that the productivity per pair of the breeding population of Purple Herons in the Camargue is, on average, 1.5 to 2 chicks lower than for pairs in these other regions. Van der Kooij (1976) showed that birds from these different breeding areas follow similar migration routes and winter in the same areas; it can therefore be assumed that they experience similar mortality rates outside the breeding season. If these arguments are correct, the Camargue population, although important numerically, may contribute disproportionately fewer juveniles to the breeding population than the other areas. Indeed, it may be that production from the Camargue colonies is so low as to be inadequate for maintaining the breeding population, and that immigration of birds reared in other areas is required to maintain numbers. There is no available evidence to confirm or refute this hypothesis, which requires further investigation.

Purple Herons spend 8 months of each year outside the Camargue either on, or on migration to and from their wintering areas in tropical west Africa. Although Den Held (1981) has demonstrated a convincing relationship between winter drought in this area and the number of pairs returning to breed in the Dutch colonies, there is no evidence that this effect is sufficient to limit or

regulate the population in a density dependent fashion. Thus, without the detailed results of a series of coordinated counts from different breeding areas there is not, at the present time, sufficient evidence to determine whether the west European breeding population of Purple Herons is limited either on the breeding or the wintering areas. In view of the local declines which have occurred on several breeding areas, the potential threats to wetland habitats in general, and the small size of the population concerned, it is recommended that the following actions be taken: firstly, an international program of synchronised counts on the breeding areas be implemented, with the aims of monitoring regional and overall variations in the size of the west European breeding population; secondly, further research be initiated to examine, directly (cf Den Held 1981, Cave 1983), the ecology of wintering Purple Herons in west Africa, and their conservation requirements; and thirdly, conservation measures should be implemented to protect the remaining breeding areas of Purple Herons in western Europe, as discussed above for the Camargue.

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SUMMARY

This study examines the factors which limit the numbers of colonial reed-nesting herons in the Camargue, S. France. Aspects of the ecology of these species on their breeding areas are described to identify the periods during the breeding cycle at which time reproductive output may be limited. The two approaches are combined to formulate conservation and research recommendations to safeguard breeding populations of the Purple Heron in western Europe.

Six species of colonial heron breed in the Camargue. These are the Grey and Purple Heron, which breed together in reedbeds, and the Little Egret, Night Heron, Cattle Egret and Squacco Heron which breed together in trees. There have been major changes in the relative abundance of these species over the last 20 years, which can be explained largely by the successful establishment of the Grey Heron and the Cattle Egret, and a simultaneous decline of the Purple Heron. Examination of the patterns of resource overlap of all six species indicate that the Cattle Egret may have occupied an empty niche; in contrast, the Grey Heron overlaps broadly in morphology, breeding sites, feeding sites and food with the Purple Heron. Interspecific competition could therefore have been responsible for the observed decline of the Purple Heron. However, detailed examination of changes in the numbers of the two species at individual colonies discount this hypothesis, since the main declines of Purples have been in areas with few Greys, whilst numbers have remained constant in the

colony where the greatest increase in Greys has occurred. Instead, the decline is explained by increasingly intensive management of the hunting marshes where these herons breed. This has resulted in a reduction in the number of breeding sites available, and in the size of those reedbeds that remain.

An investigation of the factors limiting colony size of Purple Herons was made at a colony where suitable breeding habitat is superabundant. A review of the literature suggested that food resources might be important, although there was no evidence of the mechanism. Purple Herons did not feed their chicks by night, although one member of each pair was normally absent from the colony by night. They fed at distances from a few metres from the colony, up to 15km away. Four distinct feeding zones could be recognised at different distances from the colony. There were differences in the patterns of usage of these areas during the breeding season. At the start of the season most birds fed in the marshes nearest to the colony, while as the season progressed and the colony became larger, a higher proportion of birds fed at greater distances. It is argued that the near marshes are the preferred feeding areas, and that they are filled early in the season to a level which is not exceeded later in the season, even though more birds are present in the colony.

Individual adults were extremely faithful to particular foraging zones throughout the breeding season. Intensive observations of six individuals feeding in the marshes near to the colony revealed that they were defending exclusive feeding territories

on them. The two members of a pair did not share or even visit each others territory, strongly implying that these territories were established for access to food resources rather than mates. A comparison of food delivery rates to the nest of birds feeding at different distances from the colony showed that birds feeding at greater distances incurred extra costs from the increased travel time. There was indirect evidence that these costs were reduced by bringing back larger prey loads. I argue that territoriality on the feeding areas, with intraspecific competition for those areas nearest to the colony, offers a density dependent mechanism for the regulation of colony size in relation to available food resources.

The breeding biology of the Purple Heron was examined. 96% of all clutches were initiated in April and May. Clutch size varied from 3 to 5 with an average of 3.5 eggs, which is the lowest recorded in Western Europe. There was a significant decline in clutch-size with season. Although contributory, egg-size differences were not large enough to account for observed size differences in siblings, which were a result of asynchronous hatching. The smallest (youngest) chick in each brood often died of starvation. It is argued that brood size is maximised to the number of chicks that the adults can rear, by two processes: firstly by adjustments in clutch-size which provide a coarse-tuning to predictable patterns in food availability etc.; secondly, through brood reduction which works through sibling feeding hierarchies to provide a fine tuning at the time of peak nestling food demand.

The diets of Grey and Purple Heron nestlings are examined in relation to patterns of prey selection, which were predicted from experimental studies. Both species are highly piscivorous. The Grey Heron feeds almost entirely on Carp, Eels and Mullet, whilst the Purple takes many Eels, a wide variety of other fish and some invertebrates. Prey species which are of low profitability either because of their size or because they possess special adaptations against predation, did not feature significantly in the diet of either species. The diet of young nestlings changed significantly with their age, as predicted from prey selection experiments; this was a result of their inability, when very young, to manipulate or swallow the prey which were most profitable for the adults to consume.

The findings are discussed in relation to the conservation of reed-nesting herons in western Europe. It is suggested that interspecific competition may yet pose a threat to the remaining Purples as the Greys become resource limited, because Greys can occupy breeding and feeding sites earlier than Purples, and defend them successfully on account of their larger size. My studies have shown that the reproductive output of Purple Herons in the Camargue may be the lowest in western Europe, and that immigration from other areas may be necessary to maintain the population.

Appendix 1. Scientific and English names of all vertebrate prey recorded during dietary studies of the Camargue herons.

	SCIENTIFIC NAME	ENGLISH NAME
MAMMALS		
	<i>Rattus rattus</i>	Brown Rat
BIRDS		
	<i>Lusciniola melanopogon</i>	Moustached Warbler
REPTILES		
	<i>Emys orbicularis</i>	Pond Tortoise
	<i>Natrix natrix</i>	Water Snake
	<i>Natrix maura</i>	Grass Snake
	<i>Lacerta viridis</i>	Green Lizard
	<i>Lacerta muralis</i>	Wall Lizard
AMPHIBIA		
	<i>Rana ridibunda</i>	Marsh Frog
FISH		
	<i>A. anguilla</i>	Common Eel
	<i>Cyprinus carpio</i>	Common Carp
	<i>Mugil sp.</i>	Mullet
	<i>Lepomis gibbosus</i>	Sunperch
	<i>Atherina boyeri</i>	Atherine
	<i>Gambusia affinis</i>	Mosquito Fish
	<i>Barbus sp.</i>	Barbel
	<i>Perca fluviatilis</i>	Perch
	<i>Pomatoschistus microps</i>	Goby
	<i>Gasterosteus aculeatus</i>	Three-spined Stickleback
	<i>Abramis brama</i>	Bream
	<i>Blicca bjoerkna</i>	
	<i>Alburnus alburnus</i>	
	<i>Rutilus rutilus</i>	Roach
	<i>Scardinius erythrophthalmus</i>	Rudd
	<i>Esox lucius</i>	Pike
	<i>Tinca tinca</i>	Tench
	<i>Ictalurus melas</i>	Catfish
	<i>Sygnathus abaster</i>	Pipe-fish
	<i>Stizostedion lucioperca</i>	Zander

APPENDIX 2Estimations of the Dry Weights of Prey found in the Diet of Heron Nestlings.

It was not valid to measure directly the dry weight of each prey in a food sample, because the majority had already undergone slight pre-digestion. Instead, the following measures were used to estimate the original dry weights of the items, before ingestion:

1. Large Fish, Amphibia and Reptiles.

Each prey item was measured, and its dry weight estimated from a length/dry weight calibration curve. These were constructed from samples of each prey species of the size-range being consumed by the herons. Fish were measured from the snout to the fork of the tail, whilst the overall length of amphibia and reptiles was measured, excluding appendages. Samples used in the construction of calibration curves were first measured, and then dried to constant weight at 65°C (No vacuum oven was available in the Camargue, but a small sample of prey returned to the UK and dried in vacuo at 50°C, showed less than a 1% difference from the original figures). From the values obtained, I calculated the linear regressions for each prey species, where :

$$\log \text{ dry weight} = \log a + b \log \text{ length}$$

The estimated dry weights of prey were then calculated from the equations shown in Table A.2.1.

2. Small Fish, Tadpoles and all Invertebrates.

Such prey comprised only a very small part of the diet of Purple and Grey Herons, and dry weight values were estimated from the average dry weight of samples of each species collected in the field for the size

ranges being taken by herons. Those prey types showing a large variation in size (small fish, Coleoptera, Diptera and Odonata larva, Odonata imago) were divided into appropriate size-classes. The values used are shown in Table A 2. 2

The dry weights of a few very uncommon prey, such as birds, mammals and Pond Tortoises, were measured directly from the individuals found in the regurgitates.

Table A2.1. Equations used in the calculation of the dry weights of prey in the diet of Camargue herons, where $y = \log$ dry weight(g) and $x = \log$ length(mm).

<u>SPECIES</u>	<u>EQUATION</u>	N	r
Anguilla anguilla	$y = -7.29 + 3.37x$	58	0.93
Cyprinus carpio	$y = -5.59 + 3.07x$	22	0.96
Mugil spp.	$y = -6.34 + 3.33x$	22	0.99
Lepomis gibbosus	$y = -6.50 + 3.61x$	20	1.00
Ictalurus melas	$y = -5.61 + 3.02x$	22	0.99
Tinca tinca	$y = -5.55 + 3.03x$	26	0.93
Rutilus rutilus	$y = -6.60 + 3.57x$	20	0.99
Blicca bjorkna	$y = -6.52 + 3.49x$	20	0.98
Esox lucius	$y = -5.94 + 3.05x$	10	1.00
Lacerta viridis	$y = -6.22 + 3.55x$	7	0.99
Rana ridibunda	$y = -5.08 + 3.23x$	31	0.98
Natrix maura/natrix	$y = -7.80 + 3.23x$	22	0.99

Table No.2. Values used in the estimation of the dry weight of small prey items recorded in the diet of heron nestlings in the Camargue.

<u>PREY TYPE</u>	<u>SIZE-CLASS</u>	<u>DRY WEIGHT(g)</u>	<u>N</u>
Small Fish (Gambusia,	15-24mm	0.02	55
Gasterosteus and Pomatoschistus)	25-34mm	0.07	40
	35-44mm	0.16	14
	45-54mm	0.37	23
	55-64mm	0.71	10
Sygnathus abaster		0.09	6
Atherina boyerii		0.33	7
Tadpoles		0.04	23
Triops cancriformis		0.06	21
Palaeomon		0.07	52
Gammarus spp.		0.01	37
Arachnida		0.02	10
G. gryllotalpa		0.70	7
Other Orthoptera		0.11	21
Coleoptera larvae	<30mm	0.04	20
	30-60mm	0.24	20
	>60mm	0.31	21
Coleoptera imagos		0.03	8
Odonata larvae		0.04	41
Odonata imago (Zygoptera)		0.01	14
Odonata imago (Anisoptera)		0.18	20
Diptera larvae		0.05	4
Tabanidae imagos		0.03	20
Hemiptera (Naucoridae)		0.01	21

APPENDIX 3Validation of technique for estimating the ages of nestling Grey and Purple Herons.

The age of a nestling in a brood was calculated by extrapolation from the hatching date of the oldest chick, allowing an average hatching interval of two days between each egg (see refs. in Cramp and Simmons 1977). In nests for which the hatching date of the oldest chick was not observed directly, I estimated its age from details of plumage development etc.. In order to verify my ability to estimate the age of nestlings of the two species, I compared the estimated ages of a series of nestlings with their real ages (which were known accurately from their observed hatching date). There was no evidence that I consistently over- or under-estimated their real ages for either species (Figs A3.1 and A3.2) since the observed pattern did not differ significantly from the expected.

