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THE FORAGING ECOLOGY AND FEEDING BEHAVIOUR OF THE GREY HERON (Ardea cinerea) IN THE CAMARGUE, S. FRANCE.

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ABSTRACT

THE FORAGING ECOLOGY AND FEEDING BEHAVIOUR OF THE GREY HERON (Ardea cinerea) IN THE CAMARGUE, S. FRANCE.

Author: Stuart Noel Gregory

Foraging patterns of breeding Grey Herons were studied in the Camargue. Most individual birds used several different and widely dispersed feeding sites during the season. Some birds abandoned certain foraging sites but no seasonal trends were detected. There was evidence of both flock and territorial feeding at different sites.

Birds were observed feeding in a number of different food patches (discrete feeding sites). There was evidence that the biomass intake rate influenced how long a bird would remain in a patch. When this was high, birds remained in patches, conversely when the rate was low birds left to feed elsewhere.

Departures from a breeding colony to the feeding grounds were clumped. Birds leaving the colony together were likely to go to the same feeding site more often than birds leaving successively, but not together. It is argued that the colony may have been used as an information centre.

The diet of chicks in different colonies was compared. The proportions of the important prey types from different colonies and from different broods were different. There was evidence that adults sometimes pre-digest large prey so that their small chicks can consume prey that would normally be too large for them to eat.

An experiment on prey selection provided evidence that chicks could select between two prey types which differed only in their relative profitability. The chicks consumed the most profitable prey type first. When the relative profitability of the prey types was reversed, the chicks reversed their selection. This may be an adaption to maximise prey intake rate in the face of sibling competition.

The results are discussed in relation to the success of the birds at different stages of their life cycle. The implications for the conservation of the species are considered.

CONTENTS

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If I have omitted any one from the acknowledgements please accept my apologies.

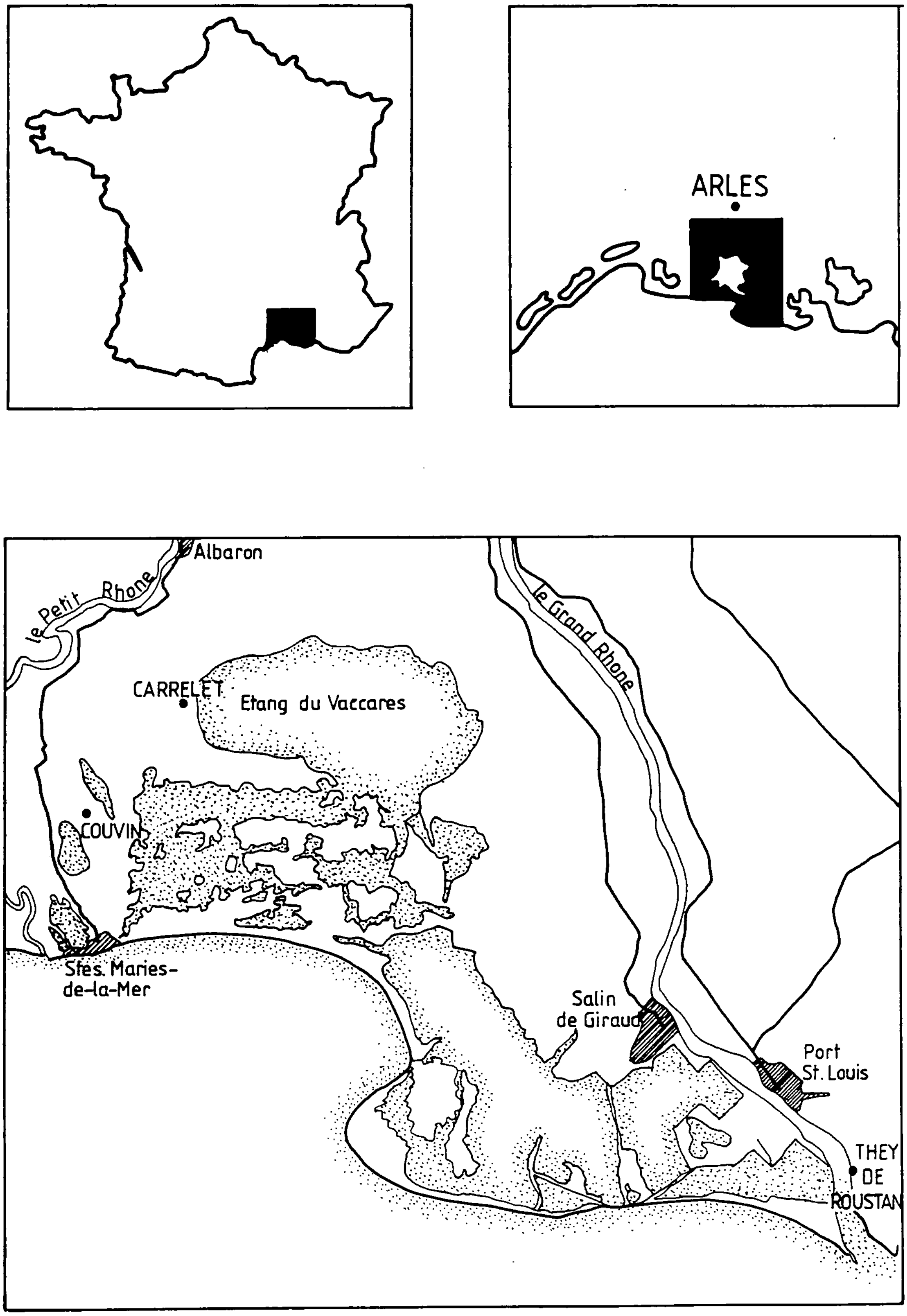
INTRODUCTION

This thesis is concerned with the feeding ecology and foraging behaviour of the Grey Heron (*Ardea cinerea*) in the wetlands of the Camargue, an unpredictable foraging environment. In particular it examines some of the problems met by the birds while foraging and looks at some of the adaptations that they have developed to cope with such an environment.

The Study Area (Fig 1)

The Camargue (40°30'N 4°30'E) is located in the south of France and is formed by the delta of the river Rhone where it flows into the Mediterranean sea. The delta covers approximately 780 km^2 and is triangular in shape. It is bordered on the east by the river Rhone and on the west by the Petit Rhone. To the west of the Petit Rhone lies the Petit Camargue. This covers an area of about 380 km^2 and contains similar habitats to the Camargue. For the purposes of this thesis I have included both together under the general title "the Camargue". The Camargue consists of a mosaic of natural, semi-natural and man made habitats over half of which are wetlands. The Camargue wetlands include man made saline lagoons, temporary and permanent brackish

FIGURE 1. The Camargue showing the location of the Grey Heron colonies used in the study.



marshes and lagoons, temporary and permanent fresh water marshes and lagoons, canal and drainage ditch systems and a number of commercial fish farms. Much of the remaining land is cultivated with cereals (especially rice), sunflowers and vines.

All the wetland habitats are used to a lesser or greater degree by Grey Herons. The five principal wetland habitats are described below:

Saline Lagoons

These form a complex of shallow artificial lakes covering 120 km^2. of the delta. They were constructed for the commercial extraction of salt by the evaporation of sea water. Fish occur in the least saline waterbodies, whilst aquatic invertebrates exist in all but the most saline. Grey Herons occasionally use this habitat for foraging although not on a regular basis.

Brackish marshes and lagoons

These cover much of the land adjacent to the sea which is not used for salt extraction. These brackish areas are mainly very shallow and during summer some can dry out completely. Within the drying marshes there are rapid changes in water depth and salinity as well as large changes in the density of fish and other aquatic animals. As they become concentrated in the shrinking water bodies they form ideal prey for Grey Herons.

Fresh water habitats

These form a mosaic of permanent and temporary fresh water bodies interconnected by irrigation canals and drainage ditches. Many are dominated by emergent vegetation such as *Scirpus maritima*, *Phragmites australis* and *Typha* sp. Many of these fresh water systems are managed for wildfowl (particularly duck) hunting. Such marshes contain important populations of fish such as Carp, Eels, Sun Perch and mosquito fish (latin names are given in Appendix 1) as well as large populations of aquatic insects. Like the brackish marshes, many fresh water marshes dry out in summer and provide ideal foraging habitat for Grey Herons.

The large Phragmites reedbeds within these marshes also provide the principal nesting habitat for the Grey Heron in the Camargue although some Grey Heron colonies are also found in trees, chiefly Tamarisk (*Tamarix gallica*).

Rice Fields

Although these habitats cover a relatively large area (8000 ha. in 1984) the fast growing rice produces a dense sward which is soon unsuitable for foraging Grey Herons. Some fields contain populations of fish and aquatic insects and are occasionally used for foraging by Herons.

Fish Farms

These are man made lagoons usually created from enlarged and deepened fresh water marshes. They are similar in many ways to fresh water marshes and some are managed for wildfowl hunting. Fish farms provide ideal foraging habitat for Grey Herons since they are stocked with high densities of commercial (mirror) Carp. The fish farms also contain other fish species such as Mosquito fish, Sun Perch and Eels.

Although most of these aquatic habitats often provide suitable foraging conditions for Grey Herons the availability of prey within such water bodies can vary in an unpredictable manner. For example, in late spring and summer, water levels in both brackish and fresh water temporary marshes fall because of high evaporation rates, and prey populations can become rapidly concentrated in the shrinking water bodies. This increases the availability of prey to herons and egrets (Hafner 1978, Hafner _et_ _al_. 1982, Hafner & Britton 1983, Erwin _et_ _al_. 1985). Other changes in prey availability can occur when prey populations enter newly flooded temporary marshes and rice fields, either when they flood naturally or when they are flooded for management purposes. Some fish species also migrate from permanent water bodies to temporary marshes to breed. The fish populations of the Camargue have been studied in detail by Crivelli (1981a, 1981b). Such changes in prey populations within the waterbodies of the Camargue make foraging conditions unpredictable for Herons and Egrets.

The Study

The majority of the data for this thesis was collected at Carrelet fish farm near Albaron although additional data was also collected from the colonies at Couvin and They de Roustan. The locations of these colonies are shown on Fig 1. Further details about the colonies are given, where appropriate, within the relevant chapter.

The colony at Carrelet was chosen primarily because it was located in trees and most of the nests were clearly visible from an observation hide. It was possible to observe individual Grey Herons arriving at and leaving their nests, thus the colony was ideal for observing the patterns of foraging site use by individual birds. The Carrelet colony was also chosen because it was located within a fish farm and incidental data could be collected on the predation, by the birds, on commercial fish.

The data are presented in five chapters, each dealing with a different aspect of the foraging ecology of the Grey Heron during the breeding season. The sixth chapter discusses the results in broader terms. An outline of the content of each chapter is given below:

Chapter 1 - investigates the patterns of foraging site use of individual breeding birds over the course of the breeding season. Data are presented to show how the patterns of foraging vary between individual birds, during the day and during the season.

Chapter 2 - attempts to explain some of the foraging patterns shown in chapter 1 by investigating how birds allocate their foraging time in food patches of different quality.

Chapter 3 - is concerned with the question of how Grey Herons locate new food patches in an unpredictable environment and in particular examines the hypothesis that Grey Herons use the breeding colony as an information centre.

Chapter 4 - examines the food fed by parents to their chicks. It compares how the diet varies between colonies and between individual birds. It also examines how the diet varies with the time of day and with chick age.

Chapter 5 - looks at the foraging behaviour of Grey Heron chicks whilst they are still in the nest and tests the hypothesis that chicks select prey items in an optimal way from the food brought to them by their parents.

Chapter 6 - is a general discussion which deals with some of the results from previous chapters in broader terms. It looks at how different aspects of the feeding ecology of the birds could affect their survival at different stages of the life cycle. I conclude the chapter by discussing the relevance of such factors for the conservation of the species.

CHAPTER 1

FORAGING PATTERNS OF THE GREY HERON DURING THE BREEDING SEASON.

1.1 INTRODUCTION

Recent work indicates that Grey Herons Ardea cinerea show a high degree of area restricted foraging during the breeding season, and that adults often defend feeding territories during the chick rearing period (Marion 1984, 1989, Van Vessem et al. 1984 and Van Vessem and Draulans 1987). Territorial feeding has also been recorded outside the breeding season (Cook 1978, Richner 1986) although Richner also observed some birds feeding in flocks. Territorial feeding was recorded for Purple Herons Ardea purpurea breeding in the Camargue, S. France where the birds often forage in similar habitat to the Grey Heron (Moser 1984).

Despite the evidence that some Grey Herons use feeding territories during the breeding season there remains doubt that the behaviour is ubiquitous in all feeding areas. Van Vessem and Draulans (1987) found that some birds did not take up territories until late in the breeding season when they moved to feeding areas further from the colony. They also observed that other, apparently territorial, breeding birds occasionally moved between several foraging sites and that the youngest breeding birds did not use territories at all. Marion (1984) also occasionally observed territorial breeding birds feeding in flocks or using feeding sites outside their normal territory.

Richner (1986) suggested that, in winter, territoriality in the Grey Heron is dependent on patterns of food distribution and availability and showed that some adults switched from territorial to flock feeding behaviour as they moved between feeding sites. Thus it is possible that the Grey Heron is similar to the Great Blue Heron *Ardea herodias*, a species which exhibits a high degree of variation in foraging sociality and territorial behaviour during the breeding season (Krebs 1978).

Marion (1984) suggested that the distribution of breeding Grey Herons on the feeding grounds may follow a despotic behaviour pattern such that the better quality birds occupy permanent territories in the best feeding areas and exclude competitively inferior birds from these areas. Despotic foraging distribution patterns were also predicted for the Purple Heron by Moser (1984). However, the distribution pattern suggested by these authors may represent only one of several alternative patterns.

Territorial behaviour can be influenced by factors such as the distribution and availability of resources (Zahavi 1971 and Rubenstein 1981) and the economics of territory defendability (Davies and Houston 1981 and 1983). It is therefore possible that both territorial and non territorial breeding birds may be found in the same feeding area at different times or in different feeding areas at the same time. If birds are non territorial there may be overlap in the use of foraging sites amongst individuals and their distribution may resemble an Ideal Free Distribution (Fretwell and Lucas 1970) where each individual is free to choose the feeding area where its food intake rate is greatest.

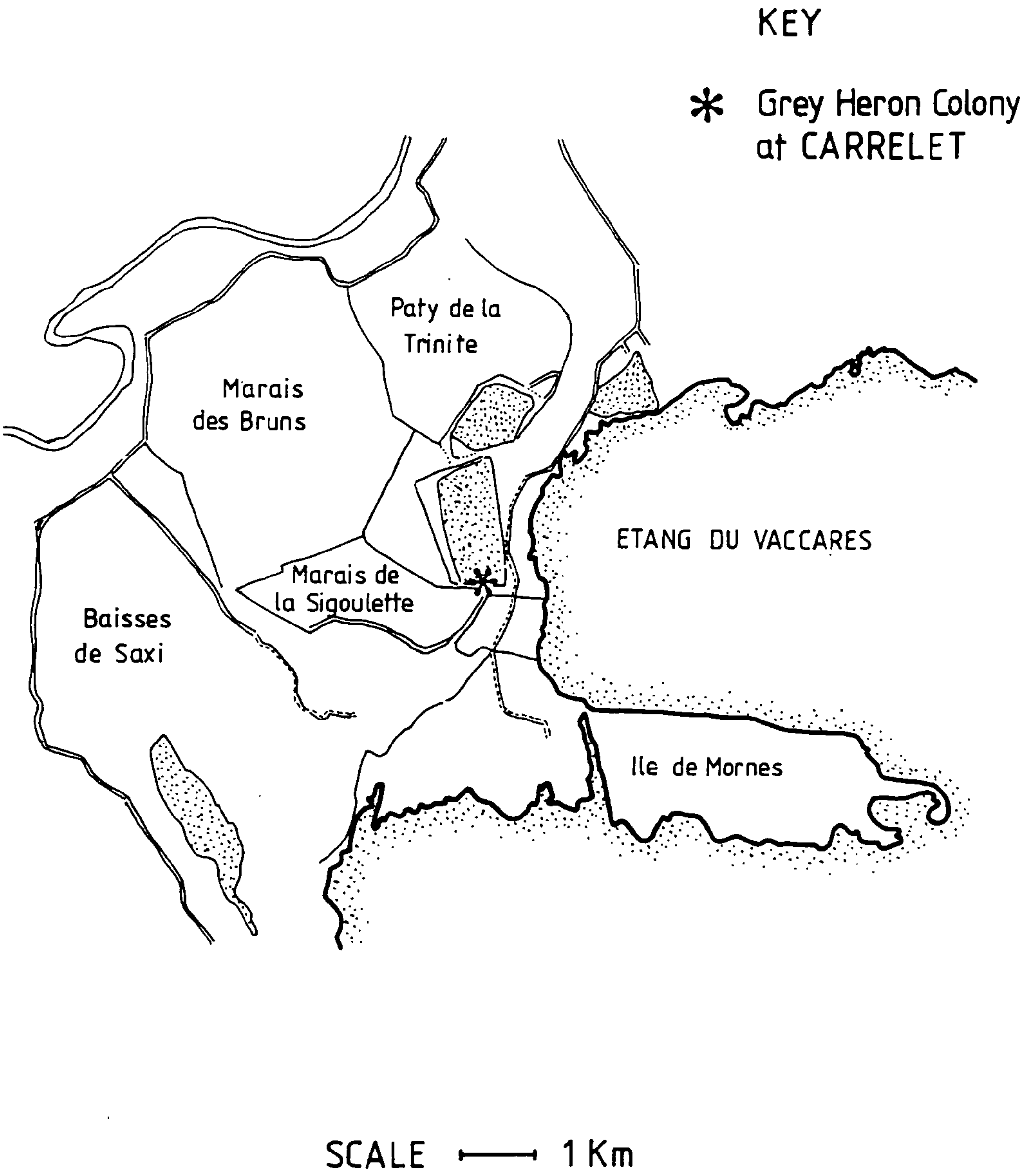
The aim of this study was to describe the patterns of foraging site use of as many individual birds from the same breeding colony as possible. This was to establish general patterns of foraging site use and foraging sociality for Grey Herons in the Camargue. The study also examined the relative distribution of colony members over the available foraging habitat. The factors that may have influenced individual and overall patterns of foraging site use are discussed.

1.2 METHODS.

The study was carried out in 1985 at Carrelet fish farm near Albaron in the Camargue S. France (see Fig 1.1). The colony was comprised of 63 pairs of Grey Herons nesting in partially submerged Tamarisk trees *Tamarix gallica* in the southern end of a 150 hectare fish basin. The colony was linear and about 100 m. long with nests located between 1 and 5 m. above the water level. Observations were made from a 5m. scaffold tower hide situated approximately 75m south of the colony centre. Data were collected from dawn till dusk six days a week between 29/3/85 and 02/07/85.

Patterns of foraging site use were determined by recording the flight destinations and the date and time of departure of birds as they left the colony for the feeding grounds. Birds were observed through binoculars until they landed at a feeding site or until they were lost from view. Each destination was plotted on a map and recorded as an (x,y) coordinate with the two axes running North-South and East-West through the colony. When birds were not observed landing, the direction of the foraging flight was recorded in place of the foraging site coordinate. The whole colony was observed simultaneously by myself and one or two assistants working under my direction in order to collect

FIGURE 1.1 The location of the Grey Heron colony at Carrelet Fish Farm in the Camargue.



foraging site data from as many birds as possible.
When birds were observed leaving a nest they were assigned an identity at one of two levels:

Pair Identity, where the bird could not be individually recognized but was seen leaving an identified nest and was therefore known to be an unidentified member of a recognised pair (tree and nest markers were used in conjunction with a map of the colony to identify nests).

Individual identity, where the bird was observed leaving its nest and could also be distinguished from its partner by plumage or other characteristics. To facilitate the recognition of individual colony members 18 breeding adults were caught on their nests and equipped with numbered leg flags and radio transmitters.

Data were grouped to determine the foraging patterns of each individually recognizable bird during the course of its breeding cycle. Data were also grouped within each recognized pair to give the combined "pair foraging pattern". Combining data within pairs allowed departures which could be assigned an identity only at the pair level, to be used in some analyses. In total, sufficient data were collected to determine 28 pair-foraging patterns (i.e. about half the pairs nesting at Carrelet) and, from within these, the foraging patterns of 15 individual birds.

An attempt was made to supplement data collected from direct colony observations, by radio-tracking birds in the field. However access could not be obtained to many of the feeding areas used by these birds and radio-tracking was abandoned.

Field observations were made to determine the degree of foraging sociality and territorial behaviour shown in different feeding areas. Most birds fed in marshes which were used for duck hunting during the winter and access to these areas was either forbidden or severely restricted by the land owners. Observations were therefore made in only 5 of the 12 feeding areas which were located near to the colony. Descriptive data were collected on territorial aggression and foraging site use and wherever possible focal observations were made on individually marked birds. These observations were used to determine how birds behaved whilst feeding and to help interpret the overall distribution patterns observed for colony members.

1.2.1 Analysis of patterns of foraging site use.

The location of the foraging sites used by all the birds from recognised pairs were plotted on a map to determine the total number of visits made to each of the different "feeding areas" surrounding the colony during the breeding season. Feeding areas were defined as large water bodies and interconnecting marsh systems where birds fed. The boundaries between the feeding areas were established from field observations, maps and aerial photographs.

The degree of area restricted foraging shown by individually recognised birds was tested, using the kolmogorov-Smirnov two-sample test, to compare the number of visits made by each individual bird to each feeding area with the number of visits made by other birds from the colony. Where this test gave a non significant result the more sensitive Chi^2 test of contingency was used on data grouped from different feeding areas. Data were grouped to ensure that the visitation frequency to each of the grouped areas was greater than 5. The Kolmogorov-Smirnov test allows the use of sample sizes less than 5 in each category being compared. This test was therefore used in preference to the Chi^2 test since it allowed the comparison of distributions to be made over all the feeding areas even when the visitation frequency was 0.

Patterns of "foraging site" use within the home range of individual birds were examined by dividing the feeding area map into squares of 0.5 x 0.5 km. Flight destinations within the same square were considered to be on the same foraging site. Foraging sites were therefore 0.5 x 0.5 km. subdivisions within each feeding area.

This scale of subdivision of feeding areas was chosen because it was considered to be the limit of visual accuracy obtained by plotting flight destinations from the tower. Birds often used a mosaic of feeding sites separated by large areas of unsuitable or unused habitat. Thus there were large areas the home range of each bird that was not used for feeding. Patterns of foraging site use were analysed in several different ways:

1) The Kolmogorov-Smirnov one-sample test was used to compare the relative frequency of visits made by each bird to each of the foraging site squares within its home range. This was to test for "core areas" of significantly higher usage after the methods of Samuel et al. (1985).

2) The temporal sequence of foraging site visits for each bird was examined using the "Runs test" Siegel 1956. This was to test whether birds made repeated visits to the same foraging site before moving on to another site.

The Runs Test can only test for non random sequences in the listed order of two variables. For this reason foraging site visits were combined into two groups: a) visits to the most frequently used foraging site, and b) visits to all other sites. The sequence of visits to sites a) and b) was then determined and the number of switches between sites calculated for analysis.

3) The mean distance between consecutively used foraging sites and total number of foraging site changes were calculated for each bird.

4) The mean Bivariate foraging site vector (centre of foraging activity) of each individual bird was calculated from the coordinates of the foraging site locations (see Batchelet 1981 for details). This descriptive statistic gives the mean direction and distance of foraging sites from the colony. Birds using the same foraging sites with equal frequency will have the same centre of foraging activity. Comparison of bivariate foraging site vectors between birds therefore indicates whether birds were using the same range of foraging sites.

5) Individual patterns of foraging site use were grouped for two different stages of the breeding cycle to see if there were significant changes in foraging site use as the breeding cycle progressed.

The stages of the breeding cycle chosen for analysis were as follows:

Early. Incubating eggs and rearing young chicks between 0 and 20 days old.

Late. Rearing chicks older than 20 days

There were insufficient data to make finer divisions between different stages of the breeding cycle. No data were collected on parental foraging patterns after chicks had fledged (chicks approximately 65 days old) since after this period parents rarely visited the colony. The stages of the breeding cycle at each nest were determined using data on egg laying dates, chick hatching dates and other data on chick age collected during visits to the colony and from observations made from the tower hide.

Three analyses were made to compare foraging patterns between the different stages of the breeding cycle:

5.a) The centre of foraging activity for each bird was calculated for the early and late stages of breeding. These were compared using the Mardia, Watson, Wheeler statistic (B), in Mardia's two sample test (see Batchelet 1981 for details of both tests). This tests whether individual birds used different activity centres during the separate periods. These tests involve circular statistics and compare both the mean vector angle and mean vector length of the foraging site coordinates.

5.b) The dispersion of the foraging sites making up the home range of each bird during the two periods was measured by calculating the area of the maximum area polygon (maxon) enclosing all the feeding sites used during each period.
The sign test was used to test whether there were consistent changes, amongst birds, in the dispersion of the foraging sites used between the two stages of breeding. It should be stressed that the Maxon area is not a measure of the area of the home range, as defined earlier, since each polygon enclosed many areas that were not used by the birds.

5.c) The number of different foraging sites used by each bird during each of the two periods was calculated. The sign test was used to test whether there were consistent changes, amongst birds, in the number of foraging sites used between the two periods.

1.2.2 Analysis of the distribution of colony members over the foraging grounds.

Pair-foraging patterns were compared to determine the relative distribution of colony members over the available habitat. Since pair foraging patterns combined the home ranges of both pair members it was not possible to identify which pair member was using each site. However a comparison between the data from each of the 28 identifiable pairs (which represented the foraging patterns of 56 individual colony members) allowed a more detailed analysis than would have been possible if only the 15 individual foraging patterns had been compared.

The pair-foraging patterns were plotted on the foraging map to locate the foraging sites used by each pair. These data were analysed to see how, a) distance of the foraging site from the colony affected the number of pairs using the site, and b) the relative frequency of site use was related to the number of pairs using the site. Details of analyses are given below:

a) The number of pairs with members using each site was plotted against the distance of the foraging site from the colony (distances were calculated in km. from the centre of the foraging site square to the centre of the colony). The correlation between these two variables was then calculated. Only foraging sites visited by birds from the colony were used in the analysis.

b) The relative frequency (proportion) of visits made by the pair to each foraging site within their combined home range was calculated. The number of pairs which used each site was then plotted against the mean proportion of visits made by the pairs visiting the site (data were arcsine transformed to allow the calculation of mean proportions). This shows how the relative frequency of site use by pair members was related to the relative distribution of pairs.

Summary of Definitions Used

Feeding Areas - large water bodies and interconnecting marsh systems the boundaries of which were established from field observations, maps and aerial photographs.

Foraging Sites - 0.5 x 0.5 km. subdivisions within each feeding area.

Core Areas - Foraging sites used significantly more often than expected from random.

1.3 RESULTS.

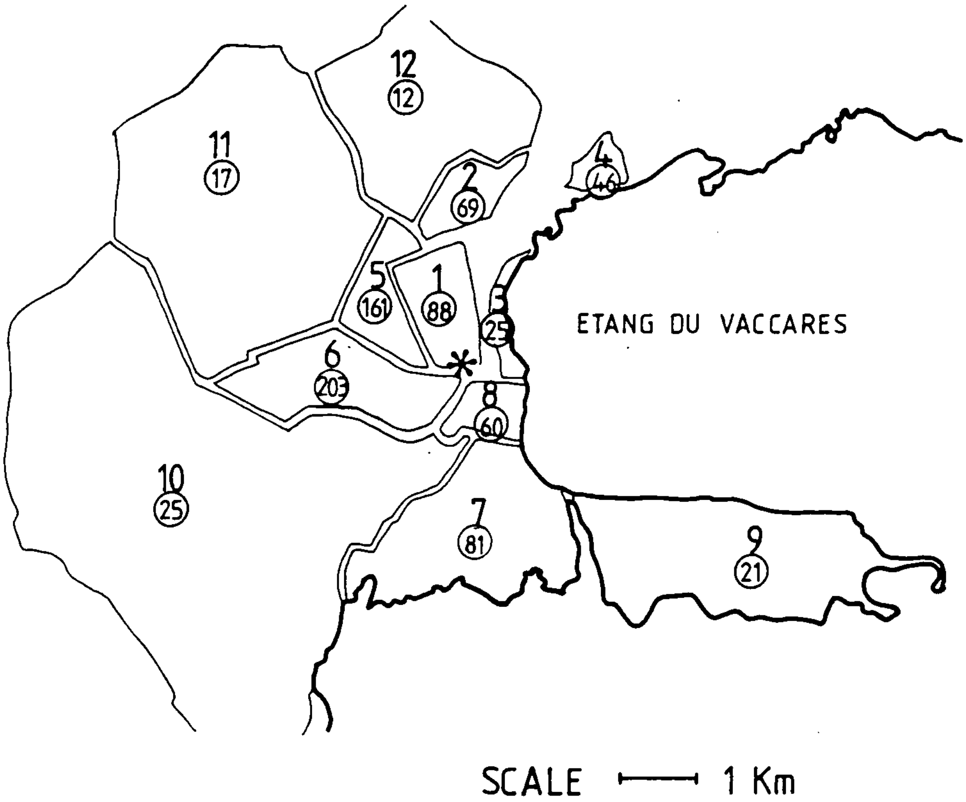
1.3.1 Individual Foraging Patterns.

In total 12 main feeding areas were identified from the pair foraging patterns. The feeding areas are shown in Fig. 1.2 which also shows the frequency of visits to each separate feeding area (calculated from the pair- foraging pattern data). When compared with the pairs, all 15 individually recognisable Herons concentrated their foraging activities in a significantly smaller number of feeding areas than expected (see table 1.1). This shows that the individual birds were not using all the feeding areas available to them, although all birds except (i) used more than one area.

The frequency of visits to the foraging sites within the home range of each individual bird and the maximum site fidelity (maximum percentage of observed visits to one site) are shown in table 1.2. The home ranges of all but one bird were comprised of several different foraging sites (mean = 9.47 ± 1.08 S.E. n = 15). Bird (i) which visited only one feeding area (see table 1.1) visited only one foraging site (0.5 x 0.5 km. square) within this area during the entire observation period.

FIGURE 1.2 The location of the feeding areas used by the breeding Grey Herons from the Carrelet colony.

Note: The figures in circles indicate the total number of observed visits to each feeing area.



KEY

*	Colony
1	Big Basin
2	Little Basin
3	Vaccarès West
4	Méjannes
5	Carralet
6	Sigoulette
7	Frignants
8	Mass Michel + Vaccares + Rice Fields
9	Mornes North
10	Bardouine + Saxi
11	Les Bruns
12	Paty de la Trinite

TABLE 1.1 Number of visits made by individually recognisable Herons to the 12 feeding areas used by the colony as a whole.

	Feeding area												
	1	2	3	4	5	6	7	8	9	10	11	12	
Bird													
a	0	1	0	0	0	0	4	25	0	0	0	0	***
b	0	0	0	1	0	2	14	4	1	0	0	0	***
c	0	0	0	0	2	15	1	0	0	9	0	0	***
d	0	0	0	0	0	1	5	9	3	0	0	0	***
e	0	0	0	0	3	8	0	8	0	0	0	0	*
f	0	7	12	1	3	0	2	0	0	1	0	0	***
g	5	3	0	0	1	0	0	0	0	0	0	1	**
h	0	0	0	0	26	4	0	0	0	0	4	0	**
i	0	0	0	30	0	0	0	0	0	0	0	0	***
j	10	2	1	0	0	2	0	0	0	0	0	0	***
k	0	0	0	0	0	10	8	1	0	0	0	0	***
l	1	4	0	0	8	6	0	0	0	0	0	0	+
m	0	0	0	0	5	9	0	0	0	1	1	0	++
n	1	0	0	1	0	5	6	0	3	0	0	0	*
o	15	1	0	0	1	3	0	0	0	0	0	0	***
Total pair obs	88	69	25	46	161	203	81	60	21	25	17	12	n=808

*** $p<0.001$, ** $p<0.01$, * $p<0.05$ Kolmogorov Smirnov 2 sample test. + $p<0.05$ Chi^2 test (areas 1-4, 5, 6-12 grouped for analysis). ++ $p<0.01$ Chi^2 (areas 1-5 & 7-12, 6 grouped for analysis).

Note: Feeding areas were grouped to a give sample size greater than 5 in comparisons where the Chi^2 test has been used.

TABLE 1.2 **The number of foraging sites (0.5 x 0.5 km. squares) visited by individually recognisable herons.**

	number of foraging sites	number of obs.	Max site fidelity %	Number of visits to each foraging site.	
BIRD				Core sites	other sites
a	9	29	45	** 13,8	2,1(6)
b	13	22	18	--	4,3,2(4),1(7)
c	15	27	15	--	4,3(3),2(3),1(8)
d	9	18	44	** 8,3,	1(7)
e	6	19	37	--	7,4,3(2),1(2)
f	13	36	36	** 13,6,4,	2(3),1(7)
g	6	10	40	--	4,2,1(4)
h	17	34	18	** 6,5,4(2),3	1(12)
i	1	30	100	--	30
j	9	15	40	--	6,2,1(7)
k	9	19	47	** 9,	2(2),1(6)
l	9	19	37	* 7,3,	2(2),1(5)
m	5	16	50	** 8,5,	1(3)
n	13	16	13	--	2(3),1(10)
o	8	20	40	* 8,3(2)	2,1(4)

** $p<0.01$, * <0.05, -- not significant; Kolmogorov Smirnov one sample test for non random frequency of visits to foraging sites within the home range.

Note: The number of observed visits to each site are given in the body of the table, sites are separated with a comma. Figures in parentheses indicate the number of foraging sites (N) in the home range with the same number of visits (if N >1).

There was no significant correlation between the number of foraging sites visited by a bird and the number of times the bird was observed (rs = 0.3875 n = 15 p>0.05 Spearman Rank correlation). This indicates that differences in the observed number of foraging sites used by the birds were not due to differences in observation frequency.

Eight of the fourteen birds which visited more than one foraging site did not visit each site with equal frequency, but concentrated their activity in core sites of significantly higher usage. Seven of these birds also used more than one core site. This shows that although most birds visited several foraging sites, some sites were visited more frequently than others.

The centre of foraging activity, given by the bivariate mean vector of foraging sites, differed for each of the individually recognisable birds (table 1.3). Herons (a) and (b), (c) and (f), (g) and (l), and (j) and (k) were partners from the same pairs. Since no two members of the same pair had the same centres of foraging activity these data also indicate that pair members differed in their use of foraging sites and probably acted independently while foraging (they rarely coincided in the timing of visits to the nest to feed chicks). Differences in mean vector may occur even when birds share some of their foraging sites so these data do

TABLE 1.3 Length and angle of bivariate Mean foraging site vector (centre of activity) of the 15 individualy recognisable Grey Herons.

	mean vector angle	Length of mean vector (L) S.D. of X and Y coordinates (km.).		
bird		L	S.D. X	S.D. Y
a	135	0.5	0.374	0.930
b	151	1.73	0.838	1.366
c	244	1.15	0.844	0.524
d	151	0.90	0.631	0.805
e	221	0.20	0.245	0.156
f	21	1.25	0.441	1.216
g	8	1.65	0.517	0.887
h	306	1.15	0.565	0.563
i	36	3.10	0.199	0.076
j	357	1.40	0.319	0.738
k	160	1.00	0.791	1.036
l	342	0.60	0.322	0.971
m	247	0.75	0.019	0.328
n	147	0.85	1.249	1.350
o	354	1.20	0.134	0.751

Note: All angles given in degrees clockwise from N (0 degrees) relative to the centre of the colony.

not prove that each bird used completely different sites, rather they indicate that each bird used a different set of sites.

Although most individual birds used several different feeding sites, visits to particular sites did not usually occur in sequential runs. Only two birds (d & f) of the eleven from which sufficient data were available, made non-random switches between their most frequently used foraging site and the other sites that they visited (table 1.4). If birds had been making a sequence of visits to the same site before moving to a new site then the sequence of site visits would have been non random. The random sequence of foraging site visits shown by most birds indicates that they often revisited foraging sites after temporarily deserting them i.e. that most movements between sites were the result of temporary and not permanent changes in the factors affecting site use. It should be noted that not all foraging site visits were observed. Some sequential "runs" of visits to individual foraging sites may have been missed.

Table 1.5 shows the total number of foraging site changes observed for each of the individually recognisable birds. Foraging site changes included both switches to previously used sites and visits to new sites. The table also gives the mean distance between consecutively visited sites. The

TABLE 1.4 **Switches in foraging site use by individual Grey Herons between the most frequently used foraging site and other sites.**

	number of visits to:		
bird	most frequently used site (A)	other foraging sites (B)	number of switches. between A & B
a	13	16	17
d	8	9	1 ***
e	7	12	9
f	13	23	9 **
h	6	28	10
j	6	10	6
k	9	10	6
l	7	12	5
m	8	8	8
o	8	12	6

*** = $p<0.001$, ** = $p<0.01$, runs test.

Note: Only birds which used more than one site and which made a minimum of 5 visits to the most frequently used site have been included in the analysis.

TABLE 1.5 The number of foraging site changes and the mean distance between consecutively visited sites for each of the individually recognisable herons.

BIRD	total number of sites	Number of site changes	Mean (±SE) distance between sites	Number of Obs.	Obs Period
a	9	18	0.95 ± 0.20	29	19
b	13	18	2.19 ± 0.36	22	43
c	15	18	1.42 ± 0.18	27	65
d	9	10	1.05 ± 0.20	18	41
e	6	13	0.27 ± 0.04	19	29
f	13	17	1.61 ± 0.27	36	66
g	6	6	2.13 ± 0.40	10	21
h	17	20	1.03 ± 0.14	34	52
i	1	0	0.00 ± 0.00	30	66
j	9	10	1.00 ± 0.16	15	44
k	9	10	1.50 ± 0.22	19	56
l	9	7	1.27 ± 0.37	19	19
m	5	9	1.42 ± 0.42	16	27
n	13	8	1.03 ± 0.22	16	72
o	8	10	2.80 ± 0.49	20	78

Note: Distances are given in Km. The observation period is the number of days over which the observations on each bird were collected. However, individual birds were not seen on every day during this period.

results show that most birds made many foraging site changes during the course of the breeding season and that the mean distance between sites was often large. The timescale of foraging site changes was variable and is difficult to quantify since individual birds were observed a different number of times and over different periods. The mean number of foraging site changes per observation for the individually recognisable birds was 0.54 ± 0.047 (S.E.) (n= 15) the number of observations and the observation period for each bird are given in Table 1.5.

Territorial birds would have been able to defend a previously visited site only if they moved to a foraging site very close by. However, since the mean distance between consecutively used sites was often large, it is unlikely that most birds would have been able to continue defending the previously visited site after making a foraging site change. This suggests that, for most birds, defence of foraging sites, where it occurred, was temporary. Bird (i) made no foraging site changes and would therefore have been able to defend a permanent territory.

There were no consistent changes in the foraging patterns of individual birds between the different stages of the breeding cycle. Table 1.6 details the position of the centre of foraging activity of each bird during the early and late

TABLE 1.6 Length, angle and S.D's of mean bivariate foraging site vector (centre of activity) of individual birds at different stages of the breeding cycle.

	Early			Late			
	Angle	Length	S.D.(x,y)	Angle	Length	S.D.(x,y)	B
a	---	---	---	135	0.5	(0.37,0.93)	--
b	---	---	---	151	1.73	(0.84,1.37)	--
c	250	1.50	(1.95,1.11)	232	0.95	(1.27,0.97)	14.7
d	---	---	---	151	0.90	(0.63,0.81)	
e	---	---	---	221	0.20	(0.25,0.16)	--
f	75	0.40	(1.46,2.74)	17	1.75	(0.16,0.94)	67.1***
g	---	---	---	8	1.65	(0.52,0.89)	--
h	298	1.50	(1.62,1.02)	307	1.10	(1.04,1.19)	17.8
i	40	3.25	(0.17,0.17)	40	3.25	(0.17,0.17)	--
j	357	1.25	(0.72,1.71)	2	1.70	(0.63,1.15)	3.9
k	230	0.40	(0.36,1.14)	153	1.26	(1.62,2.17)	6.7
l	286	0.30	(0.25,1.36)	4	1.20	(0.68,1.94)	36.1***
m	---	---	---	247	0.75	(0.02,0.33)	--
n	178	0.90	(2.22,2.04)	100	1.10	(2.58,3.61)	3.9
o	358	1.25	(0.21,1.39)	355	1.20	(0.28,1.60)	4.4

Note: All angles given in degrees, clockwise from the Y axis, and length in km.*** $p<0.001$ Mardia's two sample test using the Mardia-Watson-Wheeler test statistic (B). It was not possible to derive B for bird (i) since it only used one site. Sample sizes are given in table 1.7.

stages of the breeding cycle. Only two birds (f) and (l) of the nine for which sufficient data were available, showed significant changes in the centre of foraging activity between the two periods. Both birds changed their mean angle of foraging flights and used sites more distant from the colony during the later period. The mate of bird (f) made no such change in foraging pattern. Furthermore there were no consistent changes in the dispersion of foraging sites within the home range ($p > 0.1$ sign test) or the total number of foraging sites visited ($p > 0.1$ sign test) between the early and late stages of breeding (see table 1.7). These results indicate that although some individuals changed their patterns of foraging during the breeding cycle, the changes formed no fixed pattern that could be described as a general trend.

Comparing between birds, there were considerable differences in foraging site dispersion (see table 1.7). Some birds used foraging sites which were very close together (small Maxon area) while others foraged at sites several kilometers apart (large Maxon area). There was no significant correlation between Maxon area and the number of observations ($r_s = 0.3362$ $n=24$ $p> 0.1$ Spearman Rank correlation) so this result is not due to differences in observation frequency between birds.

TABLE 1.7 Foraging site dispersion during the Early & Late stages of the breeding cycle.

bird	Maxon Early Period	number of foraging sites	Maxon Late Period	number of foraging sites.
a	--	--	4.29 (26)	10
b	--	--	7.06 (22)	16
c	1.92 (12)	09	1.80 (14)	08
d	--	--	2.42 (18)	09
e	--	--	0.28 (17)	05
f	7.05 (14)	08	0.62 (21)	06
g	--	--	0.36 (07)	03
h	1.28 (08)	07	2.15 (26)	13
i	0.07 (06)	01	0.07 (24)	01
j	0.56 (06)	06	0.80 (09)	06
k	0.24 (06)	03	1.44 (13)	07
l	0.31 (11)	05	0.75 (08)	06
m	--	--	2.34 (13)	04
n	3.58 (10)	08	6.95 (06)	06
o	0.22 (10)	04	0.61 (10)	06

Note: The number of observations is given in parentheses after each area. Only areas based on >5 observations have been included in the table. Areas are given in Km·2.

1.3.2 Relative distribution of colony members over the available habitat.

The frequency of use of foraging sites by the 28 pairs from which sufficient data were collected is shown in table 1.8. Core sites of significantly higher usage were found in the combined home ranges of 16 of the 28 pairs. Since pair foraging patterns do not distinguish between pair members it was not possible to determine which of these were sites of concentrated activity within the home ranges of the individual pair members, or sites which had a high frequency of visits because they were used by both pair members. However, the ratio of core to non core sites in the pair foraging patterns (66/370 - see Table 1.8) was not significantly different to that in the individual foraging patterns (20/122 - see Table 1.2), (chi^2 = 0.029 d.f.= 1 p >0.1). This suggests that most of the core sites found in the pair foraging patterns were core sites in the home ranges of the individual pair members. If pair core sites had been the result of both members sharing the same site, the proportion of core sites would have been higher in pair foraging patterns than in the individual foraging patterns.

Table 1.9 shows the number of foraging sites, within the combined home range of each pair, which were also used by

TABLE 1.8 The use of individual foraging sites within the combined home range of pair members.

	Number of sites	Number of obs.	Number of visits to each foraging site.	
Pair			core sites	other sites
1	20	35	** 8,4,3(2),2,	1(15)
2	13	36	** 10,8,4,3,	2,1(8)
3	19	34	** 9,5,2(3)	1(14)
4	15	33	** 6,5,4,3(2)	2(2),1(8)
5	22	43	** 6,5,4(2),3(2),2(2)	1(14)
6	5	31	** 19,6,	3,1(2)
7	20	35	** 10,5,2(2)	1(16)
8	17	37	** 13,4,3,	2(3),1(11)
9	31	87	** 12,11,8,7,6,5,3,	2(11),1(13)
10	28	60	** 11,6(2),4,3(4)	2(2),1(17)
11	12	17	--	2(5),1(7)
12	20	31	--	3(4),2(3),1(13)
13	11	23	** 9,3,	2(2),1(7)
14	15	18	--	2(3),1(12)
15	24	29	--	3(2),2,1(21)
16	13	21	--	3(2),2(4),1(7)
17	11	17	--	5,2(2),1(8)
18	12	32	** 17,5,	1(10)
19	16	26	** 8,3,2,	1(13)
20	17	25	--	7,2(2),1(14)
21	15	19	--	2(4),1(11)
22	12	27	** 7(2)	2(3),1(7)
23	15	18	--	4,1(14)
24	18	21	--	4,1(17)
25	8	24	** 8,4(2)	3,2,1(3)
26	11	15	--	3,2(2),1(8)
27	8	31	** 10,6(2),4,	2,1(3)
28	12	18	--	4,3,2,1(9)

Note: The number of visits to each foraging site is given in the body of the table, sites are separated with a comma. Figures in parentheses indicate the number of foraging sites (N) in the combined home range, with the same number of visits (where N >1). ** $p<0.01$, -- not significant; Kolmogorov Smirnov one sample test for non random distribution of foraging site visits within the combined home range of pair members.

TABLE 1.9 Degree of overlap between foraging sites used by different pairs.

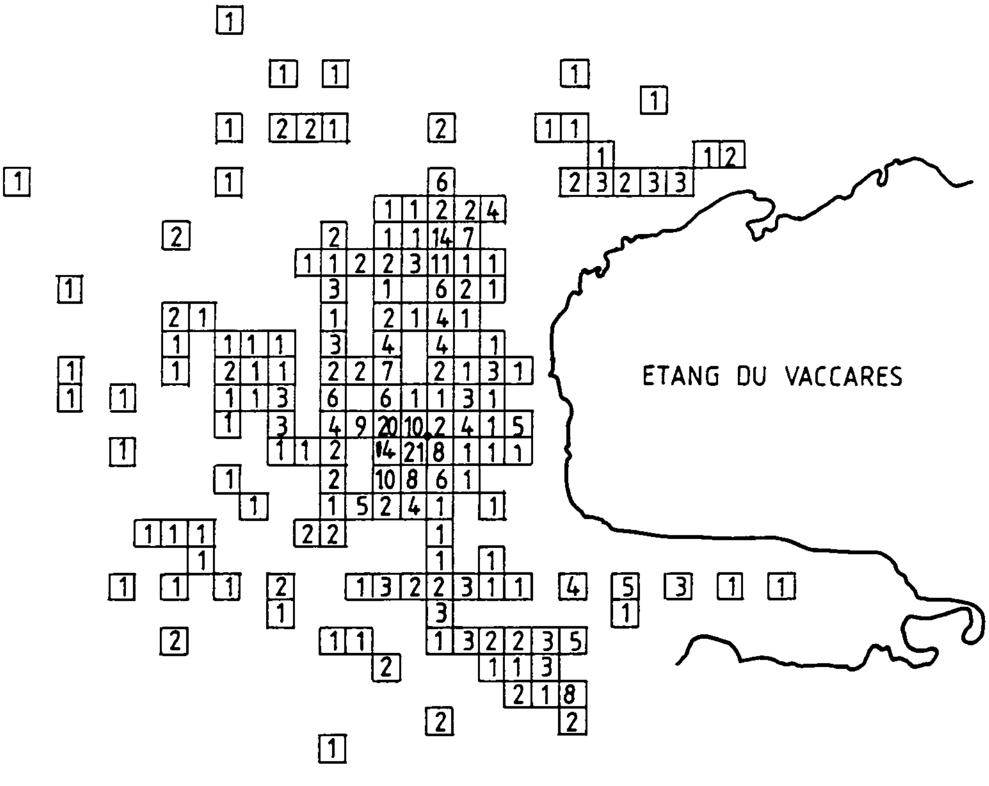
	core sites		other foraging sites	
Pair	shared	not shared	shared	not shared
1	5	0	10	5
2	4	0	6	3
3	5	0	12	2
4	5	0	8	2
5	6	1	11	3
6	2	0	2	1
7	3	1	12	4
8	3	0	13	1
9	5	2	21	3
10	6	2	13	6
11	-	-	8	2
12	-	-	14	6
13	2	0	6	3
14	-	-	13	2
15	-	-	17	7
16	-	-	10	3
17	-	-	11	0
18	2	0	7	3
19	3	0	10	3
20	-	-	13	4
21	-	-	14	1
22	2	0	8	2
23	-	-	11	4
24	-	-	16	2
25	3	0	5	0
26	-	-	11	0
27	4	0	4	0
28	-	-	9	3
total	60	6	295	75

birds from other pairs. There was considerable overlap in foraging site use between pairs in both core sites and non core sites.

Figure 1.3 shows the position of the 163 foraging sites identified from the combined pair foraging patterns and the number of pairs which used each site. Foraging sites adjacent to the colony were visited by birds from most pairs, however activity was also concentrated at foraging sites within feeding areas 2,4 and 7, further from the colony. There was a significant negative correlation between the distance of the foraging site from the colony and the number of pairs using the site ($r= -0.33995$ $p<0.001$ $n= 163$). Although this correlation was highly significant, distance accounted for only approximately 12% of the variation in the number of pairs observed using the site ($r^2 = 0.1156$). This shows that factors other than foraging site distance were also affecting the number of birds using each site.

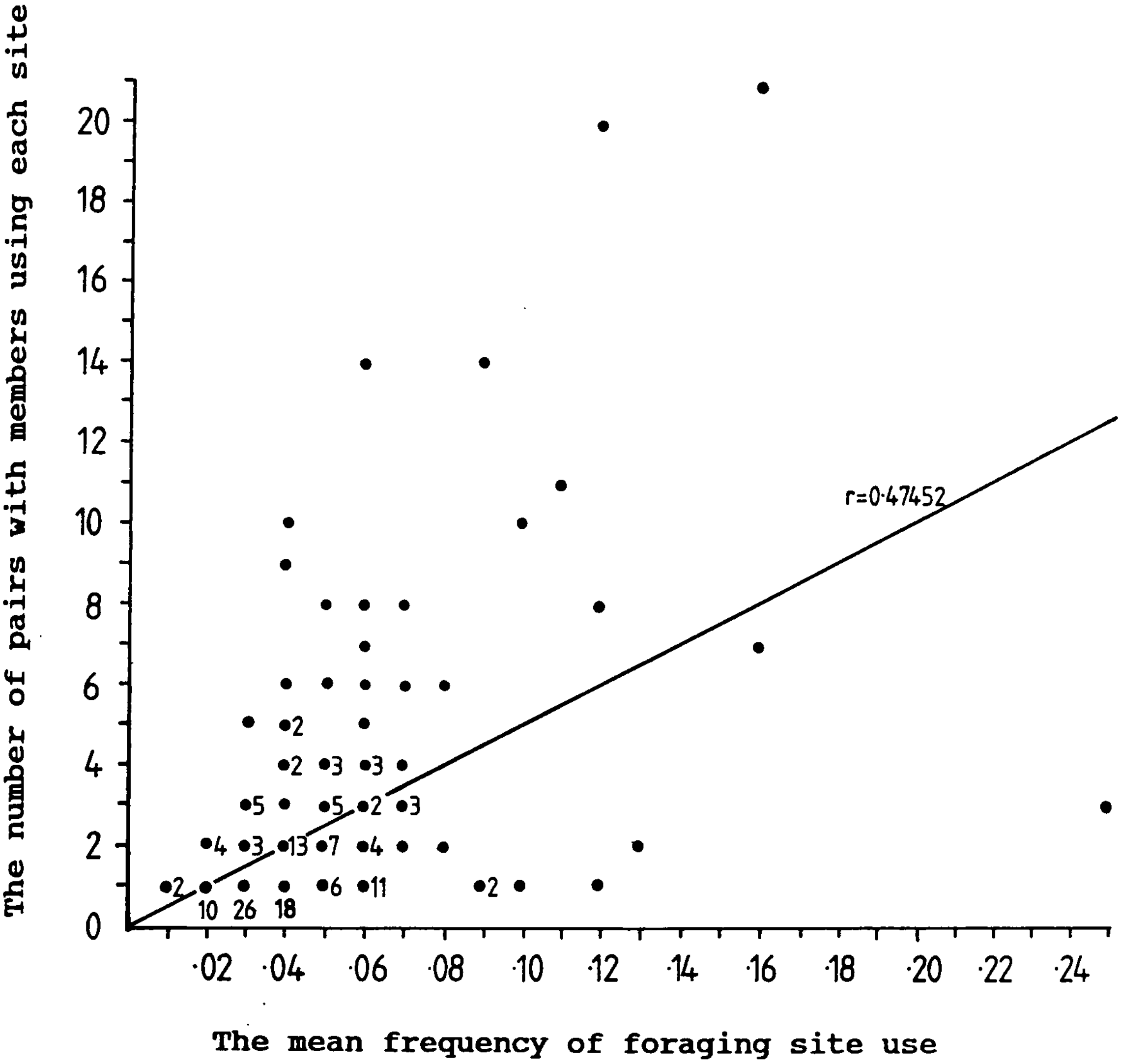
Fig 1.4 shows the relationship between the number of pairs which used each site and the mean proportion of visits made by all the different pairs using the site. There was a significant positive correlation between the two variables ($r= 0.475$ $p<0.001$ $n=163$) showing that the sites where pair members concentrated their activity were also the sites where foraging site overlap between pairs was highest.

FIGURE 1.3 The position of the foraging sites (0.5 x 0.5 km. squares) used by the grey Herons from the Carrelet colony.



Note: The numbers within each foraging site square indicate the number of Grey Heron pairs with members observed using that foraging site.

FIGURE 1.4 The number of Grey Heron pairs using each foraging site square plotted against the mean frequency of use of that foraging site.



Note: The mean frequency of foraging site use was calculated from the combined pair foraging pattern data. The mean for each site was calculated from the frequency of site use of only those pairs observed visiting that foraging site.

Figures adjacent to data points indicate the number of overlapping coordinates.

1.3.3 Foraging sociality and territorial behaviour in different feeding areas.

The results presented in the previous section indicate a high degree of overlap in foraging site use between birds, in the areas where individual birds concentrated their foraging activity. These results, however, do not preclude the possibility that individual birds feeding at these sites, were holding temporary feeding territories and excluding conspecifics from within the territory boundaries.

There are two reasons for this; firstly the foraging site scale chosen for the analyses was based on 0.5 x 0.5 km. squares; this is large in comparison with the scale of real foraging sites which may sometimes be as small as several square metres. Apparent foraging site overlap between birds may therefore have occurred where there was a high density of small territories within the foraging site square. Secondly the results consider foraging site overlap during the entire breeding season. Measured over the duration of a single feeding trip, each site may have been visited by only one bird at a time.

Field observations were made in feeding areas 1,2,3,4 and 5 to investigate the foraging sociality and feeding behaviour of birds in these areas. A summary of these observations is presented below:

Feeding areas 1 & 2. Both feeding areas were permanent flooded marshes used as fish rearing basins on the fish farm (there were probably no gross changes in prey availability in these areas throughout the breeding season since stocking densities were high and no fish harvests were carried out during the observation period). Most birds in these areas were aggressive and rarely tolerated other birds within a radius of approximately 20-30m. They appeared to defended individual feeding territories

Two individually marked birds were observed (bird f & another marked bird from which insufficient data were collected to determine its individual pattern of foraging site use) and neither were seen feeding in the same place on all occasions. Individual birds were occasionally seen moving their position within the feeding area during the course of a single foraging trip. In a small stocking basin (75m x 30m) containing a high density of fish) in the northern part of feeding area 1, flocks of up to 10 birds were seen feeding simultaneously around the basin perimeter.

Here birds were exceedingly aggressive towards each other and sometimes managed to temporarily defend a small part of the basin. However, supplanting was frequent and the turnover of birds within the flock was high.

Feeding areas 3 & 4. Within these areas birds were also aggressive whilst feeding and individuals appeared to hold feeding territories similar to those seen in areas 1 & 2. Two marked birds were observed. Bird (f) was observed feeding alone in area 3 although it frequently fished in different parts of the feeding area on different foraging trips. The bird was also seen moving to different fishing positions during the same foraging trip. Bird (f) defended only the fishing position where it was feeding at the time.

Feeding area 3 was a temporary marsh system which dried up during the course of the observation period. As a result of this all the prey in the area died and bird (f) abandoned the area and concentrated its foraging activity in feeding area 1. This seasonal drying out of the feeding area was therefore primarily responsible for the significant change in the centre of foraging activity of bird (f) between the early and late periods of the breeding cycle. However even while concentrating its activity in feeding area 3, bird (f) occasionally visited other feeding areas.

Bird (i) was always observed foraging in the same small part of feeding area 4 (an area of about 1.0 ha.). Feeding area 4 was a permanent marsh which did not dry out during the breeding season. Bird (i) defended its permanent territory at all times and on one occasion decapitated two stuffed herons which had been placed in its territory in an attempt to attract other birds there. On one day another bird was seen occupying part of the territory normally defended by bird (i). Bird (i) continued to feed in the rest of its territory. Neither bird intruded on the other and both appeared to share defence of the site, often flying over each other to supplant intruders. After this bird (i) was always seen alone. Although bird (i) was always seen at the same place, other birds feeding here often moved between feeding sites while fishing.

Feeding area 5. This feeding area was a large semi-permanent hunting marsh which never dried out fully although the water level gradually fell throughout the season. Gradual changes in prey availability probably occurred during the season, the density of prey increasing as prey became concentrated in lower water volumes. Some birds appeared to defend individual territories whilst others fed in flocks in different parts of the marsh. The birds often made frequent short flights between different feeding sites during the course of a single feeding trip. No dense flocks of birds were observed and individuals appeared to act independently of each other when moving to new fishing positions within or outside the marsh.

One marked bird was observed in this feeding area (bird h) and on different days and at different times during the same foraging trip, it was seen in different parts of the marsh. At one particular site where the bird fished in a canal on the perimeter of the marsh, it vigorously defended its fishing position. However, the bird was also frequently seen feeding with other birds in loose flocks in other parts of the marsh. The individual distance between flock members varied considerably from about 2 m. to about 15 m. The highest densities of birds were observed in part of the marsh adjacent to the colony.

These observations suggest that foraging site overlap between birds may have been the result of both a high density of exclusive temporary territories, and the presence of flock feeders, at different feeding sites. Foraging site overlap may also have occurred when a bird moved fishing positions and another bird took over the original position. The observations also confirm that the movements of birds between and within foraging sites were frequent in many of the feeding areas. Birds often changed fishing positions during a foraging trip, whilst water levels were not visibly changing. Birds often revisited sites they had abandoned during the same or a previous foraging trip. This supports the previous conclusions that some foraging site changes were the result of temporary changes in the factors affecting foraging site use. Different birds were often seen at the same fishing position, on different occasions.

The seasonal drying out of feeding areas probably resulted in some long term foraging site changes but would not have caused short term movements of birds between different feeding areas or between different sites within the same area.

1.4 DISCUSSION.

1.4.1 Individual Patterns of Foraging Site Use.

The home ranges of each of the 15 individual adult breeding birds observed at Carrelet, encompassed only a small part of the foraging habitat used by the colony as a whole (see Table 1.1). There were, however, considerable differences in the degree of area restricted foraging shown by different birds (see Table 1.2). One bird (i) held a small permanent territory throughout the entire breeding season. The other birds used a number of different foraging sites (0.25 km^2 squares) and made frequent foraging site changes during the course of their reproductive cycle. However, despite making foraging site changes, birds often re-visited previously deserted sites and as a result the centre of foraging site activity for all individual birds, except birds (f)and (l), did not change significantly during the course of their reproductive season (see Table 1.6). The centre of foraging activity of bird (f) changed during the season because its favoured feeding area, a temporary marsh, dried out and became unsuitable for foraging during the early part of its breeding cycle. It was not possible to determine why bird (l) moved its centre of foraging during the season.

The distribution of visits to the foraging sites within the home range of some individual birds was not even. Eight of the individually recognisable birds concentrated their foraging activity within core sites of significantly higher usage whilst the other seven tended to visit all the foraging sites within their home range with equal frequency (see Table 1.2). The maximum proportion of visits to the most frequently used foraging site within the home ranges of all birds except (i) was less than 50%.

The distance between the different foraging sites within each bird's home range was often large (see Table 1.5) and it is highly unlikely that any of the birds, except (i) which only used one foraging site, could have simultaneously defended or even seen all the feeding sites within their home range. The field observations showed that although many feeding sites were temporarily defended, at other sites birds fed in loose flocks.

These results suggest that although the breeding Grey Herons from Carrelet showed area restricted foraging, there was considerably more movement between foraging sites than described in other studies.

Other aspects of the behaviour of the birds at Carrelet was similar to that observed by Marion (1984) who found that some breeding Grey Herons in Brittany (France), occupied permanent feeding territories whilst others switched between temporary territories and "communal feeding areas". Marion, however, did not observe birds moving frequently between temporary territories and concluded that most birds held permanent or semi-permanent territories at the same feeding site for most of the breeding season.

The results from the present study contrast strongly with those of Van Vessem and Draulans (1987) who observed that adult breeding Grey Herons at two colonies in Belgium used several different foraging sites during the early part of the breeding cycle and then moved to feeding sites further from the colony and occupied small permanent feeding territories during the late chick rearing period. The mean dispersion of foraging sites used by adult birds during the late part of the breeding cycle was significantly higher in the present study (mean = 2.129 km.2 ± 0.585 S.D n=15 data from table 1.7) than that observed by Van Vessem and Draulans (mean = 0.375 km.2 ± 0.133 S.D n=8 data from Van Vessem and Draulans 1987) t = 2.922 d.f.=15 (unequal variance) $p<0.05$.

Van Vessem and Draulans found age-related differences in foraging patterns with sub-adult breeders following individual patterns of foraging site use similar to those observed in the present study. However, since all the birds studied at Carrelet were full adults, age related differences cannot account for the differences in foraging patterns observed in the two studies. It is more likely that the differences in foraging pattern observed between the adult birds in the current study and between other studies result from differences in the distribution and availability of prey in different feeding areas.

During the summer the Camargue represents a changing and unstable foraging environment with temporary marshes drying out completely in most years. Permanent changes in prey availability resulting from the seasonal drying out of temporary marshes were probably the cause of the feeding area change shown by bird (f) from the current study and have also been shown to influence the foraging patterns of the Little Egret <u>Egretta garzetta</u> in the Camargue (Hafner and Britton 1983). The feeding areas used by the Grey Herons observed by Van Vessem and Draulans (1987) were relatively stable and did not dry out during the breeding season. This may explain the more stable foraging patterns observed by these authors. Not all the marshes in the Camargue dry out in summer and this may explain why some birds, such as bird

(i) showed more stable patterns of foraging site use than others.

The results from the current study also show that many birds revisited foraging sites (see Table 1.4). This suggests that in addition to the permanent drying out of marshes other, temporary factors, must have influenced foraging site changes. Temporary changes in prey availability resulting from localised depression or depletion of prey around the feeding site, were shown by Hafner et al. (in Prep) to be the cause of some foraging site changes in the Little Egret in the Camargue. Such changes in prey availability may have also been responsible for some of the foraging site changes shown by birds in the current study. However, the results presented in Chapter 2 of this thesis suggest that prey depression or depletion during foraging bouts may not have been an important factor causing foraging site changes.

Richner (1986) studying the foraging patterns of Grey Heron on the Ythan estuary in Scotland, found that, in winter, some birds moved between foraging sites to maximise their prey intake rate. Other birds did not move between sites even though they would have achieved a higher prey intake rate by doing so. This equivocal evidence suggests that under some conditions Herons may follow an optimal patch use strategy and make foraging site changes to maximise their prey intake rate.

If herons use optimal patch use strategies to maximise their prey intake whilst foraging then factors such as the relative availability of prey in alternative patches, the time and energy costs involved in finding new patches and the time and energy constraints on individual birds would all be expected to influence patch changing decisions (see Chapter 2 for a discussion of these points).

In an unstable foraging environment such as the Camargue we would expect birds to move between patches as local foraging conditions, and thus the relative value of patches, changed. In a stable foraging environment we would expect much more stable foraging patterns with birds remaining for the full breeding season in the patches which afforded them the greatest foraging success. This may be more like the foraging situation observed by Van Vessem and Draulans.

Differences in all these factors may account for the different patterns of foraging site use shown by individual Grey Herons from the colony at Carrelet and between birds from different studies. The foraging site movements of Grey Herons in relation to prey intake rate are discussed more fully in the following chapter.

Despite the differences in the foraging patterns shown by adult breeding Grey Herons in different colonies, the results from all studies to date indicate that individual birds show a considerable degree of area restricted foraging. This confirms the original conclusions of Owen (1955) who suggested, on the basis of dietary differences between birds, that each individual breeding Grey Heron uses a "favourite feeding area".

It is not clear why individual Grey Herons should show area restricted foraging during the breeding season. Kushlan (1979) suggested that the repeated use of the same foraging sites by the White Ibis Eudocimus albus may improve the birds "knowledge" of feeding site characteristics and therefore improve foraging success. Area restricted foraging may be similarly adaptive in the Grey Heron. It may also help reduce the time and energy costs associated with sampling new foraging sites when time and energy budgets are limited (eg. during the breeding season). In an environment where prey availability is unpredictable, it may take a considerable amount of time (and energy) to sample prey availability in a new patch (prey inter-catch intervals for Grey Herons can exceed 4 hours - pers obs.). If an adult is required to catch prey regularly (for example when it is feeding chicks) it may choose to concentrate its foraging activity in previously experienced patches rather than spend time and energy sampling new patches.

1.4.2 Foraging Sociality within the feeding areas.

A further aspect of individual patterns of foraging site use was the apparent switching between territorial and non-territorial feeding behaviour, observed when birds moved within and between feeding sites. This supports the view that territorial behaviour is facultative in this species. Differences in the degree of social foraging of Grey Herons feeding in different areas were also observed by Cook (1978), Richner (1986), Marion (1984) and Van Vessem and Draulans (1987), and in the Great Blue Heron (Ardea herodias) by Krebs 1974. Both Krebs and Richner proposed that differences in the availability and distribution of prey were responsible for differences in foraging sociality at different foraging sites.

Van Vessem and Draulans suggested that competitive pressure between birds might also influence territorial behaviour, since adults occupied permanent territories only at sites some distance from the colony where competition between colony members was low. There is evidence that all the factors suggested above, affect the economics of territorial feeding behaviour (Zahavi 1971, Myers et al. 1979, Rubenstein 1981 and Davies and Houston 1981). In general one would expect birds to feed in flocks when the long term costs of maintaining a territory are not offset by the long term benefits (usually through increased food intake).

Flock feeding may also be favoured in conditions where it actually leads to improvement in foraging success, as for example when prey can be herded by a flock or group of predators or where individuals use other flock members to locate a patchy and unpredictable food supply. It has also been suggested that under certain circumstances Herons benefit from foraging in flocks, through decreased vigilance costs and hence increased time for foraging. The evidence for this is discussed by Kushlan (1981). Krebs (1974) however, studied the benefits of social foraging in the Great Blue Heron (which is similar in morphology, behaviour and foraging sociality, to the Grey Heron), and found little conclusive evidence for social foraging benefits in this species. It is possible, however, that Grey Herons may sometimes feed in flocks to obtain social feeding benefits.

Prey type may also affect foraging sociality. Goss Custard (1976) found that Redshank Tringa totanus alter their social foraging strategies when feeding on different prey types. He suggested that the birds alter their individual spacing in a response to the degree of interference, through prey depression (sensu Charnov 1976), suffered when feeding together on different prey types. Interference between birds may also occur through kleptoparasitism which is similarly dependant on prey type Kushlan (1979).

If Grey Herons hold territories to reduce kleptoparasitic or other forms of interference whilst feeding then prey type may be another factor affecting their foraging sociality.

1.4.3 Relative distribution of colony members over the available habitat.

The apparent mixed social feeding strategies (flock and temporarily territorial) shown by many of the birds from Carrelet, resulted in considerable foraging site overlap between birds (see Figs. 1.3 & 1.4). Foraging site overlap occurred both where birds were feeding in flocks and where birds held temporary territories that were taken over by other birds whilst the previous territory holder was feeding in another part of its home range or returning to the colony.

As a result, the distribution of colony members over the available feeding grounds did not follow the pattern proposed by Marion (1984) for the Grey Heron. Marion predicted that each colony member should occupy and defend an exclusive feeding territory during the whole breeding season, and that the better birds should occupy territories in the best feeding areas. A similar distribution pattern, for Purple Herons foraging during the breeding season, was proposed by Moser (1984). This suggests that limitations on the size of Grey Heron colonies in the Camargue is not set by competition for feeding territories.

The relative distribution pattern of colony members predicted by Moser and Marion is one of two alternative patterns, based on different social foraging strategies, proposed by Fretwell and Lucas (1970). Fretwell and Lucas suggested that where birds are territorial the number of birds that can feed at any site is dependent on the space available for territories. When all the space in the best feeding areas is occupied by territories other birds will be forced to feed in less suitable foraging sites (ideal despotic distribution). In despotic distribution patterns, birds with territories in the best feeding areas will have a higher prey intake rate than birds in other areas. The second distribution pattern (ideal free distribution), based on non-territorial foraging, states that each bird is free to choose the foraging site which maximises its prey intake rate whilst feeding. Competition between birds may eventually reduce the prey intake rate of flock members. The ideal free distribution model predicts that birds should occupy the best feeding areas until competition between birds is such that the prey intake rate of each bird falls below that of single birds feeding in other areas. Birds should then begin to occupy the next most profitable feeding area etc. In this situation the birds should eventually be distributed such that they all achieve the same prey intake rate in all feeding areas.

In the present study the field observations suggest that flock and territorial feeding strategies may have occurred in different feeding areas and even within the same feeding area at different times. This suggests that there was no consistent overall distribution pattern during the breeding season that resembled either the Ideal Despotic or Ideal Free patterns. It is possible that, during the season there was a temporal and spatial mixture of the two strategies with Ideal Free Distribution occurring in foraging sites where birds fed in flocks and Ideal Despotic patterns occurring where birds held temporary territories. Data obtained on foraging success of individual birds were not sufficient to show differences in feeding success in flock and territorial situations.

Foraging sociality was not the only factor affecting the overall distribution of colony members over the foraging grounds. There was considerable overlap, between pairs, in the use of foraging sites near to the colony (See Fig. 1.3). Further from the colony there was significantly less overlap in foraging site use. Why the distance of a foraging site from the colony should affect the number of birds feeding there is not clear, although Moser (1984) suggested that birds should occupy feeding sites as near to the colony as possible to reduce the time and energy costs associated with traveling to the feeding place. This was also suggested for the Grey Heron by Marion (1984). Such behaviour would be particularly adaptive when time and energy budgets were limited. Evidence for this is shown by Van Vessem and Draulans 1987 who found that breeding Grey Herons often foraged close to the colony at the start of breeding when nest building and nest and mate guarding constraints limited the time and energy available for feeding. It should be noted, however, that there was no such seasonal trend in the use of foraging sites close to the colony, in the present study.

Despite the significant negative correlation between overlap in use of foraging sites and distance of the site from the colony, some sites adjacent to the colony were used only by birds from one pair whilst sites several kilometers away were used by birds from many pairs (see Fig. 1.3). This suggests that factors other than foraging site distance may have also affected the number of colony members using a site. The relationship between the mean frequency of site use and the number of pairs using a site (see Fig 1.4), indicates that sites which were visited by most pairs were the sites where the individual pair members concentrated their foraging activity. This tendency for individuals to make frequent visits to sites which were used by large numbers of other birds was also observed in the White ibis by Kushlan (1979). Tinbergen (1981) observed that starlings (Sturnus vulgaris) frequently re-visited foraging sites where prey intake rate and prey density was highest and Krebs (1978) showed that Great Blue Herons foraged in the greatest numbers in areas where prey intake was highest. Krebs found that flock size had little effect on foraging success and concluded that birds were congregating in areas of high prey availability. Therefore the most likely explanation for the relationship between frequency of site use and foraging site overlap is that birds often revisited sites where prey availability was high and these sites also attracted large numbers of other colony members during the course of the breeding season.

Other factors that have been shown to affect the number of Grey Herons using a feeding area and hence their distribution over the available foraging grounds include: the structure of the landscape especially the presence of cover and the incline of the land at the water margin (Geiger 1984a, 1984b), and disturbance (Van Vessem and Draulans 1987). Given that the foraging habitat used by the birds at Carrelet was very heterogeneous and that some feeding sites were near to roads and buildings it is very likely that such factors were also affecting the distribution of the Carrelet birds over the available habitat. Unfortunately access could not be obtained to many of these feeding areas; therefore sufficient data could not be collected to test the significance of these factors.

In conclusion, the results from this chapter show that, although all the individual birds studied showed some degree of area restricted foraging, the Grey Herons at Carrelet were less faithful to individual foraging sites and showed a greater range of foraging sociality than the breeding Grey Herons that have been studied in other areas. This was probably the result of temporary and permanent changes in prey availability in the feeding sites used by individual birds. Because of the variable foraging patterns and apparent variations in foraging sociality shown by individual birds, the distribution of the colony members over the foraging habitat showed no fixed pattern over the season. Factors which may have influenced the distribution pattern include intraspecific aggression, prey availability, distance of the foraging area from the colony and the structure and landscape of the foraging habitat.

1.5 SUMMARY

1) Each individual bird used only a limited number of the foraging areas used by the colony as a whole.

2) Most birds used more than one feeding site during the season and some individuals used particular sites (core sites) more often than others. Some birds also used more than one core site.

3) The centre of foraging activity for each bird was in a different place showing that individual birds tended to use a different range of foraging sites.

4) Most birds did not visit individual foraging sites in sequential runs.

5) There were no consistent changes in the foraging patterns of individuals between the early and late stages of the breeding cycle.

6) Measured over the duration of the breeding season and on the 0.5 x 0.5 km. square foraging site scale, there was considerable overlap between foraging sites used by different birds.

7) Field observations suggested that birds held temporary feeding territories and fed in loose flocks in different feeding areas.

CHAPTER 2

PATCH CHOICE IN RELATION TO BIOMASS INTAKE RATE: FIELD OBSERVATIONS ON THE GREY HERON.

2.1 INTRODUCTION.

The results from the previous chapter show that the majority of Grey Herons from the colony at Carrelet used several different foraging sites during the breeding season. In that chapter I discussed some of the evidence that related the foraging patterns of the birds to the spatial and temporal availability of food. This chapter examines field evidence to show how the rate of prey capture (prey biomass intake rate) changes during a foraging bout and how this may influence the patch leaving decisions, and thus the foraging patterns, of individual Grey Herons in the Camargue.

As outlined in the previous chapter the quality of the feeding areas used by Herons in the Camargue can change rapidly during the late spring and summer. Feeding areas vary from permanent water bodies which hold relatively stable prey populations, to ricefields and temporary marshes where the densities of available prey can change enormously over a period of a few days as water levels drop (Hafner 1977 and Hafner _et_ _al_. 1982). On a shorter time scale the movements of fish and to a lesser extent other aquatic prey (which are usually less mobile than fish), within both permanent and temporary water bodies, may also result in rapid changes in the density and availability of prey at individual feeding sites.

Only one of the 15 individually recognisable Grey Herons from Carrelet was known to have made foraging site changes that resulted from the drying up of its favoured foraging area. Most birds frequently revisited foraging sites that they had previously deserted and it is possible that many foraging site changes were the result of temporary variations in the number or availability of prey at feeding sites.

When feeding chicks Grey Herons not only have to catch sufficient prey for their own requirements but they also have to catch food for their brood. Since Grey Heron chicks remain in the nest until they can fly (at about 60 days of age), parents must make frequent flights to the colony in order to feed them. It has been shown that, when feeding chicks, birds increase the time that they spend foraging often at the expense of other activities such as roosting (Van Vessem and Draulans 1987). They must also suffer increased energetic costs resulting from increased foraging time and frequent flights to the colony (Bryant 1979). As a result of the extra time and energy budget constraints on parents one might expect them to forage most efficiently, and follow optimal patch use strategies, to maximise their intake rate of prey, during the nestling period. Some of the important optimal patch use strategies that the birds would be expected to follow are outlined below.

The Marginal Value Theorem (Charnov 1976) is the principle theory of patch use and makes precise predictions about how predators should choose between patches and how long they should remain within a patch. The Theorem is based on the concept of prey depression (sensu Charnov _et_ _al_. 1976) and predicts that predators should leave a patch when the rate of biomass gain (food intake rate) in the patch falls below the average for the environment. In general the Theorem predicts that birds should forage for longer periods in patches with higher initial rates of biomass gain. The Theorem also predicts that increased travel time to a patch will increase the optimal patch residence time and that birds should not use patches where their cumulative rate of biomass gain is lower than average. Where the rate of biomass gain within patches is not influenced by prey depression the optimal patch choice depends upon both biomass gain rate within each patch and travel times between patches. Where the rate of biomass gain in a patch is constant (linear gain curves) and travel times to different patches are equal or are very short in comparison to foraging times, the optimal patch choice solution approximates to rejection of poor patches and continued foraging in the best patches. When the travel time to good patches is much longer than to poor patches then the time spent travelling to a patch with a high potential gain rate may be more profitably spent foraging in a patch of lower quality.

The Theorem outlined above predicts how predators should exploit patches of food efficiently but it does not predict when the predator should stop feeding. Normally we would expect a predator to stop feeding when it has sufficient food to meet its own requirements or when it is temporarily satiated. However, when a predator is collecting food for delivery to a central place (eg. a Grey Heron collecting food for its brood) we must take into account the optimal prey load that it should carry. The central place foraging theory of Orians and Pearson (1979) considers how travel time between the central place and the foraging site affects the optimal prey load, and consequently the total time the predator must spend foraging before returning to the central place. In general the hypothesis predicts that animals should bring back larger prey loads, and thus forage for longer periods, when they are feeding further from the central place. The Marginal Value Theorem predicts how animals should choose between patches and the central place foraging hypothesis predicts how much food an animal should take back to the central place.

If an animal is behaving optimally within the framework of both theories, it should exploit patches according to Marginal Value Theorem rules until it has achieved its optimal prey load according to the Central Place Foraging hypothesis (the Target prey load), then return to the central place.

Unfortunately it is difficult to make precise tests of optimal patch use hypotheses with unmarked Herons in the field because most individuals cannot be followed continuously during a foraging trip. As a consequence variables such as the travel time to the colony and between patches, and even the quality of alternative patches available to each individual, are often unknown. In this situation it is not possible to test the predictions of the central place foraging hypothesis. It is possible however, to make some broad predictions about the relationship between patch residence time and prey intake rate which are consistent with the Marginal value Theorem outlined above, and which can be tested against field results when other variables are unknown. Those predictions which can be tested against observed foraging patterns are outlined below:

1) If patches vary in quality we would not expect birds to forage for the same period of time in each patch nor would we expect birds to forage until they have caught a fixed quantity of food in each patch.

2i) We would generally expect birds which experience high prey intake rates to remain in patches for longer periods than birds with low prey intake rates. This relationship between prey intake rate and patch residence time will hold only if birds are catching prey which individually only make small contributions to the final target prey load. (This is because birds catching single large prey which fulfill or exceed target prey load requirements will immediately leave the patch and the prey intake rate up to the point of capture of the large prey will have little or no bearing on the patch leaving decision.)

2ii) As a corollary to the above we would expect birds which remain in a patch until they have achieved their target prey load, to have higher prey intake rates and longer patch residence times than birds which leave a patch before they have achieved their target prey load (birds catching large prey excepted).

3) If resource depression occurs i.e. if the density of available prey falls as a result of the action or presence of the predator, and birds are following Marginal Value Theorem rules, we would expect them to leave patches when their prey intake rate falls below the average for the whole habitat.

4) If birds remain in a patch to attain their target prey load the time spent foraging in the patch will be inversely proportional to the rate of biomass intake. Under these circumstances the relationship between prey intake rate and time spent in the patch should follow a negative exponential curve.

It is also possible to make some broad tests of how birds assess their prey intake rate within a patch. Krebs (1974) and Krebs et al. (1978) suggested that birds might use a fixed giving up time (G.U.T.) to measure prey intake rate, and leave the patch when the inter-capture interval between successive prey exceeds this fixed limit. This hypothesis has been criticised because in real foraging situations prey are often encountered in an unpredictable way. This has led to the Stochastic Sampling theories of Oaten (1977), Green (1980) and McNamara (1982).

Stochastic sampling theories assume that animals acquire information about prey availability while foraging and predict how long animals should sample before rejecting patches. It is not possible to test Stochastic Sampling theories without accurate information about travel times between patches and the variability of reward rate in alternative patches. We can however, test the predictions of the fixed G.U.T. model, which are outlined as prediction 5 below. The final prediction (see 6 below) is also concerned with sampling and tests the hypothesis that birds which remain in patches are basing their decision to stay on some measure of prey intake rate. This may appear to be intuitively obvious if the predictions 2i and 2ii are fulfilled, but it allows us to test if birds remain in patches because they have consistently higher prey intake rates than birds which leave patches before attaining their target prey load.

5) If birds are using a fixed G.U.T. when deciding to leave patches we would expect the time interval between the capture of the last prey and leaving the patch to be longer than previous prey intercatch intervals and that within the range of feeding sites used by each heron, the G.U.T. should be constant and independent of biomass intake rate.

6) If birds are using some measure of prey intake rate to make patch-leaving decisions we would expect birds which remain in patches until they have achieved their target prey load, to have consistently higher prey intake rates during their whole foraging period, than birds which leave patches before attaining their target prey load.

2.2 METHODS.

Observations were made on the patch residence times and biomass intake rates of Grey Herons in the field in order to test the predictions outlined above. Data were collected between 01/04/86 and 03/07/86 on birds using three adjacent feeding areas regularly used by herons from the neighboring colonies of Carrelet, Les Bruns and Paty de la Trinite. Foraging areas 1 and 2 were basins stocked with fish on the Carrelet fish farm, the third, feeding area 5, was a semi flooded pasture adjacent to basin 2 (see fig 1.2). Observations on feeding birds were carried out from portable hides or cars using binoculars and 25-60x zoom telescopes. Only data from full adult birds which were observed continually whilst they were in a patch were included in the analyses. In total 41 complete sets of patch residence data were collected during more than 200 hours of observation.

In basins 1 and 2 birds foraged in discrete shallow water areas (<30cms.) around the perimeter of the deeper parts of the basins. Most birds foraged within discrete areas of about 400 square metres and birds which made flights of greater than 100m. were considered to have left the patch. In foraging area 3 the water levels were shallow over the entire marsh and as a consequence the birds were more mobile while foraging than in the other sites.

In this marsh birds which made flights longer than 150m. into a different area of the marsh, or which left the marsh completely were considered to have left the patch. The time of arrival and departure of each bird was recorded as well as the time of capture, size and, where possible, species of all prey caught. Prey length was estimated in fractions of bill length (mean Grey Heron bill length = 120mm, Moser 1984). The biomass intake from each prey was calculated using the prey length/dry wt. formulae of Moser (1984). A mean length/dry wt. value from all similar prey types was used when species identification was not possible. All aggressive interactions and non-feeding behaviours were recorded and the duration of these was removed from the patch residence time to give the total foraging time of focal birds.

It was not possible to determine if all focal birds were breeding or were collecting food for chicks, but the foraging sites chosen for observation were all within 0.5 kms. of a Grey Heron colony. Only adult birds were observed and the period over which observations were collected coincided with the period of the breeding cycle when most adult Grey Herons have chicks. Observations made on the two colonies adjacent to the feeding areas confirmed that these areas were frequently used by breeding birds.

Since most birds could not be observed returning to the colony after they had finished a foraging bout, I have used a minimum target prey load to distinguish birds which probably left the patch because they had obtained sufficient food to feed nestlings (successful foragers) from those birds which left the patch to continue feeding elsewhere (unsuccessful foragers). Birds which caught a minimum of 22 g. (approx 3.3g dry wt) of prey in a patch were considered to have caught enough food for a minimum target prey load. Twenty two grams was chosen since it was the lightest recorded prey load delivered to any brood in the Carrelet colony in 1985 (see Chapter 4). It was necessary to distinguish between these two groups of birds because they left patches for different reasons and thus the relationship between patch residence time and biomass intake rate will be different within each group.

The use of a minimum target prey load to distinguish between these groups is open to error, for example some birds may arrive in patches with prey that they had caught in a previous patch. Some of these birds may have caught sufficient prey in previous patches to achieve their target prey load requirements without catching 22 g. of prey in the patch where they were observed. Thus they would be classed as unsuccessful foragers when they were actually leaving the patch because they had achieved target prey load requirements.

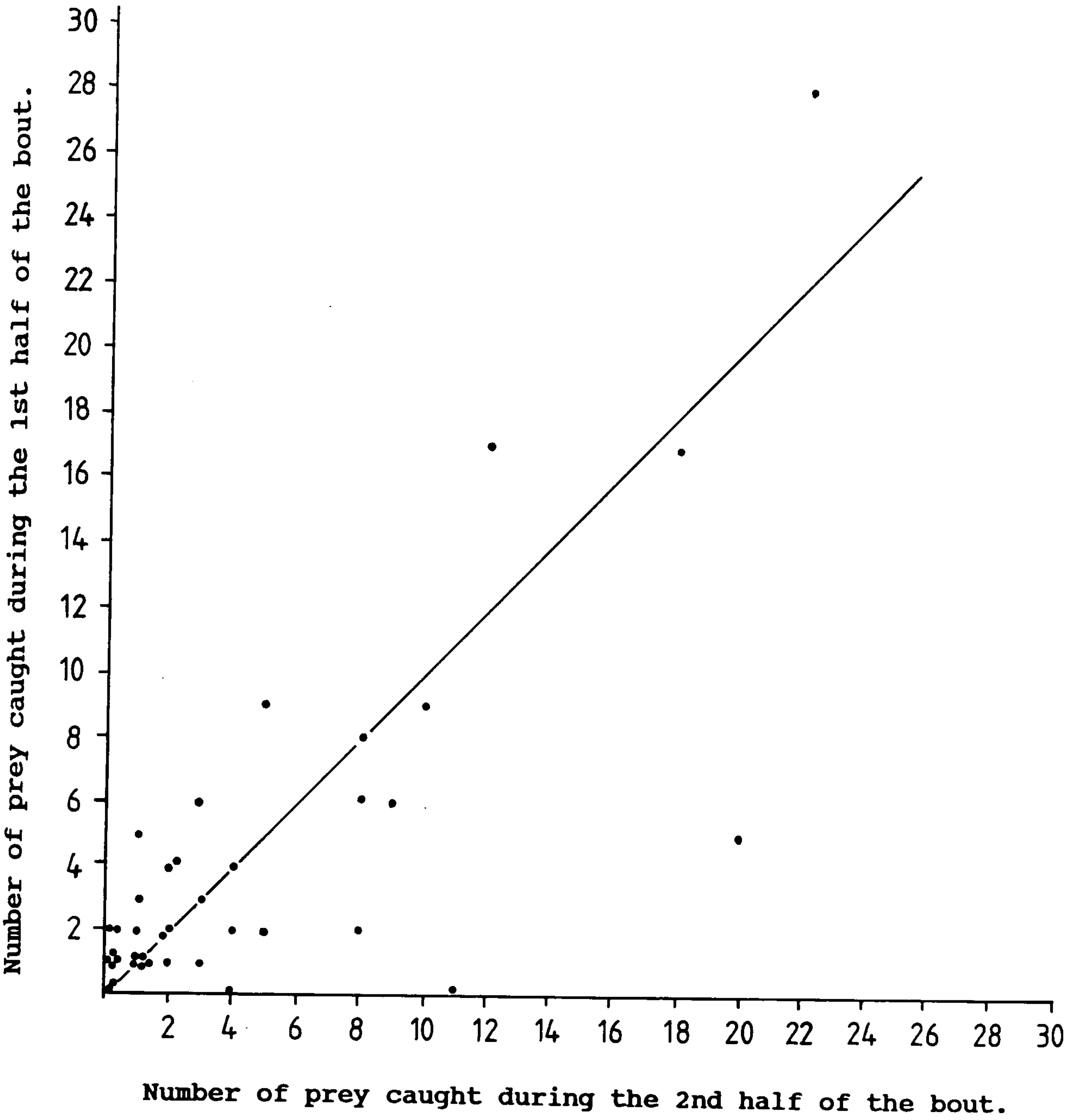
2.3 RESULTS.

2.3.1 Patch Quality.

A comparison between the number of prey caught during the first and second halves of each of the 41 foraging bouts (see figure 2.1) shows that there was no significant tendency for the frequency of prey capture to either increase or decrease during the foraging period ($z = 0$ $p= 0.5$ sign test).

The time intervals between prey captures were very variable. In some patches birds caught more prey during the first half of the foraging bout than in the second half whilst in other patches this trend was reversed. Such variability in the prey capture rate was observed, at different times, for the same bird in the same patch and for different birds in different patches within all three feeding areas. This strongly suggests that in these patches prey were a renewable resource and that the quality of patches was being controlled, in the short term, by random movements of prey into and out of the patch. Measured on the gross time scale of a foraging bout there was no evidence that resource depression and/or prey depletion had a consistent effect on biomass intake rate, since there was no consistent decrease

FIGURE 2.1 Number of prey caught during each half of the 41 observed foraging bouts.



Note: The line represents equal numbers of prey caught during both halves of the bout.

in the rate of biomass intake during the foraging bouts of focal birds.

On a shorter time scale resource depression and prey depletion may or may not have been occurring. The data collected do not however permit a test of this.

Table 2.1 shows the diet composition of the focal birds. Most of the small prey (<3cms) were aquatic insect larvae and the majority of the fish were commercial hybrid carp Cyprinus carpio. Because prey also varied in size there was no significant correlation between the weight and number of prey captured by the birds (r= 0.0658 d.f.36 p>0.1 see figure 2.2).

The foraging success of birds in a patch was therefore dependent on both the size and quantity of prey in the patch. Basins 1 and 2 were both stocked with carp of all sizes (see table 2.1). However since larger fish tend to prefer deeper water (Helfmann 1978 and Crivelli pers comm.) and Grey Herons usually forage in water less than 30 cms. deep it is not surprising that large fish were numerically unimportant in the diet. The large fish were all caught in shallow water (< 30cms.) and these captures probably occurred when large fish strayed from their preferred habitat.

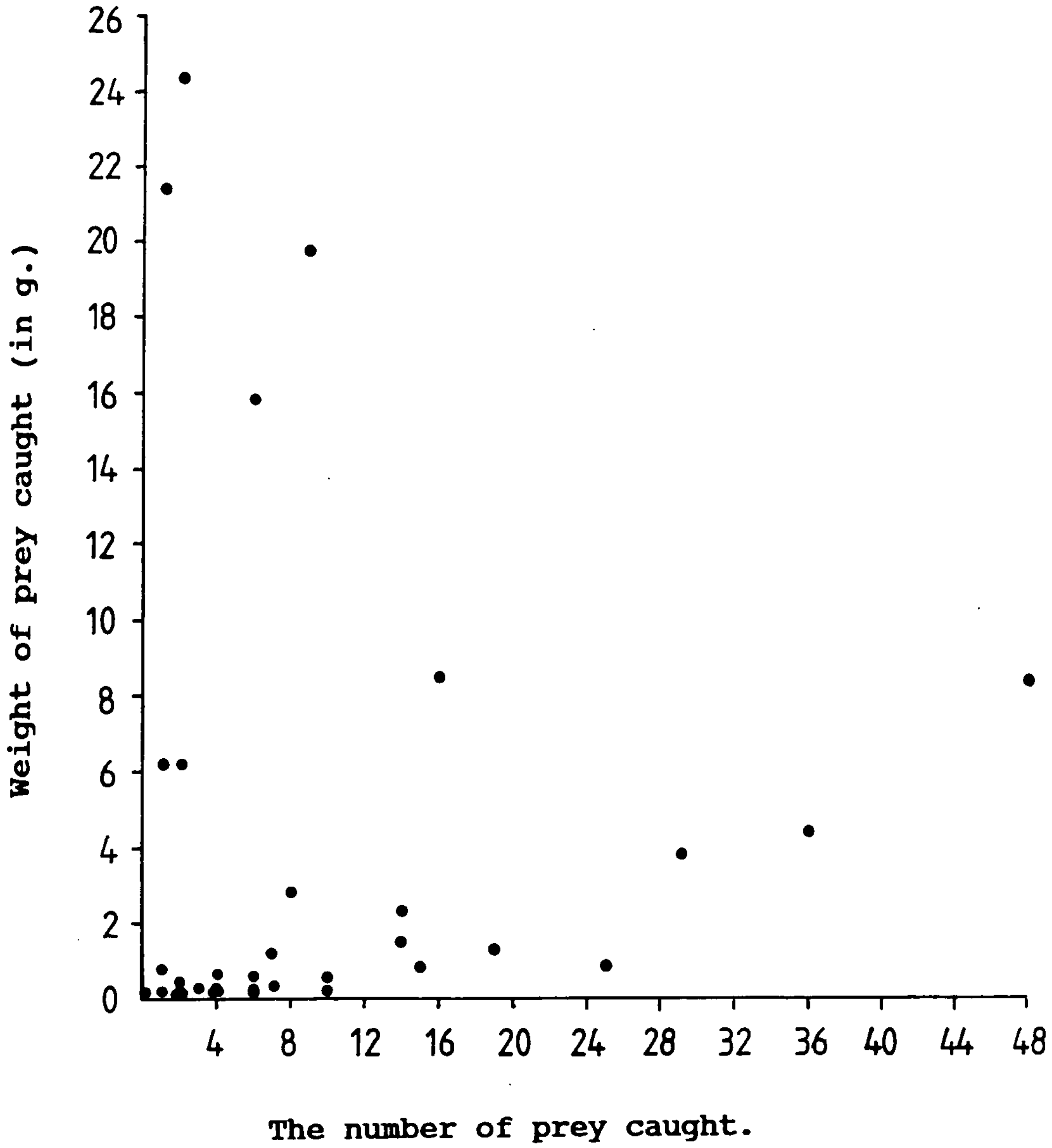
TABLE 2.1 Diet composition, in percentage dry wt. and percentage frequency, of prey captured by focal birds.

Prey type	% Frequency	% dry wt
Insects (all < 3cm.)	60.0	5.1
Fish ≤ 3 cm.	21.8	4.9
Fish >3 ≤ 6 cm.	12.2	9.5
Fish >6 ≤ 9 cm.	0.3	2.0
Fish >9 ≤12 cm.	0.6	9.5
Fish >12 cm.	0.9	47.9
Frogs (all 3-6 cm.)	4.2	21.1

Total Prey Items = 335

Note: See Chapter 4 for a definition of % frequency in diet and % dry weight in diet.

FIGURE 2.2 The correlation between the number and biomass of prey caught by individual herons during each foraging bout.



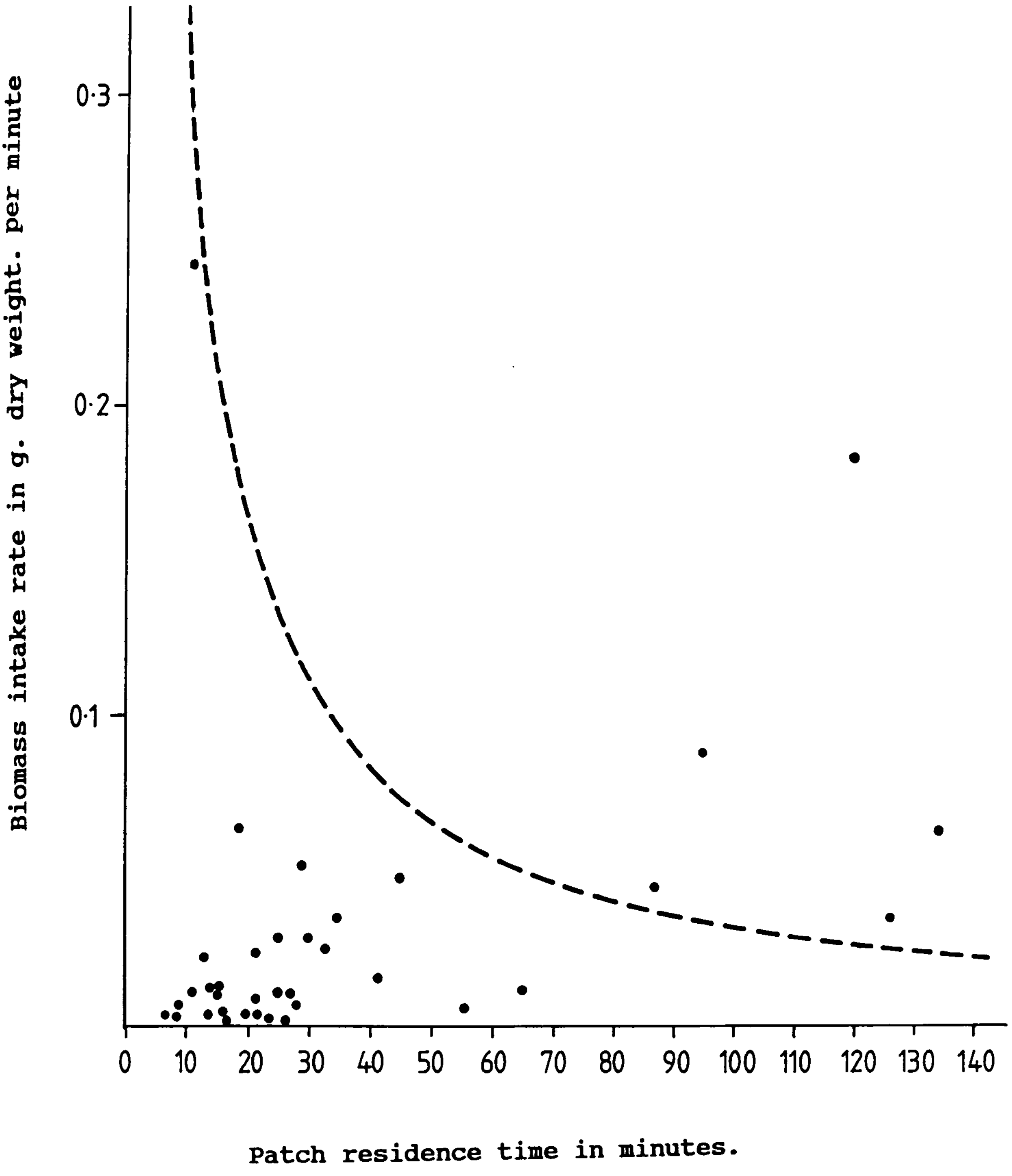
These results show that the prey intake of birds varied considerably during the course of a single foraging bout within a patch. Variations in prey intake rate were probably the result of changes in the number and size and species of prey present in the patch during the foraging bout.

2.3.2 Patch Choice by Grey Herons.

Figure 2.3 shows that there was a weak but significant parametric correlation between the patch residence time of focal birds and their mean biomass intake rate (the 5 birds catching large prey with a biomass exceeding the minimum target prey load have been excluded from the analysis) $r = 0.3423$ d.f.= 34 $p < 0.05$). In fact there is no a priori reason to expect a linear relationship between these variables, and the non parametric Spearman rank correlation for these data shows a more significant result ($r_s = 0.4006$ d.f.=34 $p<0.025$).

Birds which remained in a patch for sufficient time to catch enough prey to provide the minimum recorded biomass in a prey load (successful foragers), had significantly higher biomass intake rates ($t= 2.66$ d.f.= 34 equal variance $p<0.025$) and significantly longer patch residence times (t=

FIGURE 2.3 The relationship between the mean biomass intake rate and patch residence time of birds feeding at Carrelet.



Note: The dotted line represents the minimum target prey load threshold. Points to the right of this line represent birds whose final prey loads exceed minimum target prey load requirements.

9.363 d.f.= 5 unequal variance p<0.001) than birds which left the patch with less food (unsuccessful foragers), see table 2.2 for details. This analysis excludes birds which caught single prey exceeding the minimum target prey load. These results support predictions 1, 2i and 2ii and show that birds tended to favour foraging in patches which afforded high prey biomass intake rates. Presumably therefore, they rejected patches in which their biomass intake rate was low.

Five additional observations were made on birds which caught, as their first prey or after only a few prey, a single large fish which exceeded the minimum target prey load. In all cases the birds left the patch after the large prey had been caught. Even including these observations in the above analyses, successful foragers still had significantly longer patch residence times (t= 2.687 d.f.= 9 unequal variance p<0.025) and significantly higher prey intake rates (t= 2.284 d.f.= 9 unequal variance p< 0.05) than unsuccessful foragers (see table 2.3).

There was a significant negative correlation between biomass intake rate and patch residence time (rs = - 0.8545 n=10 p<0.02 Spearman Rank Correlation) for all birds which left the patch after they had exceeded the minimum target prey load (see fig. 2.4). This analysis includes birds which

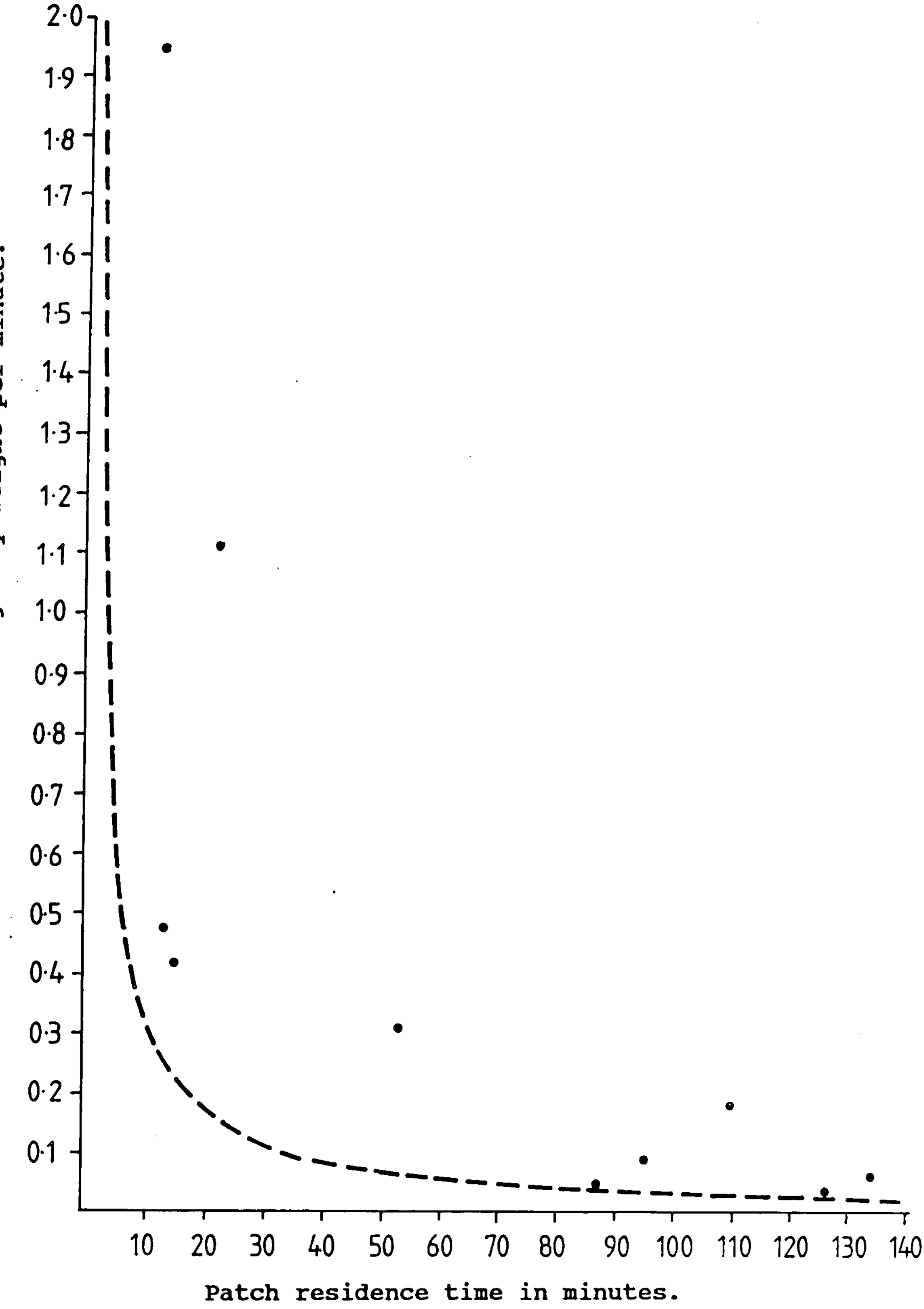
TABLE 2.2 Mean prey intake rate and patch residence time of successful and unsuccessful foragers. (Excluding birds which caught single prey exceeding the minimum target prey load)

	Prey intake rate g. dry wt. ± S.E.	Patch residence time, mins ± S.E.	
Successful foragers	0.083 ± 0.026	110.4 ± 8.90	n=5
unsuccessful foragers	0.024 ± 0.008	23.98 ± 2.44	n=31

TABLE 2.3 Mean prey intake rate and patch residence time of successful and unsuccessful foragers. (Including birds which caught single prey exceeding the minimum target prey load)

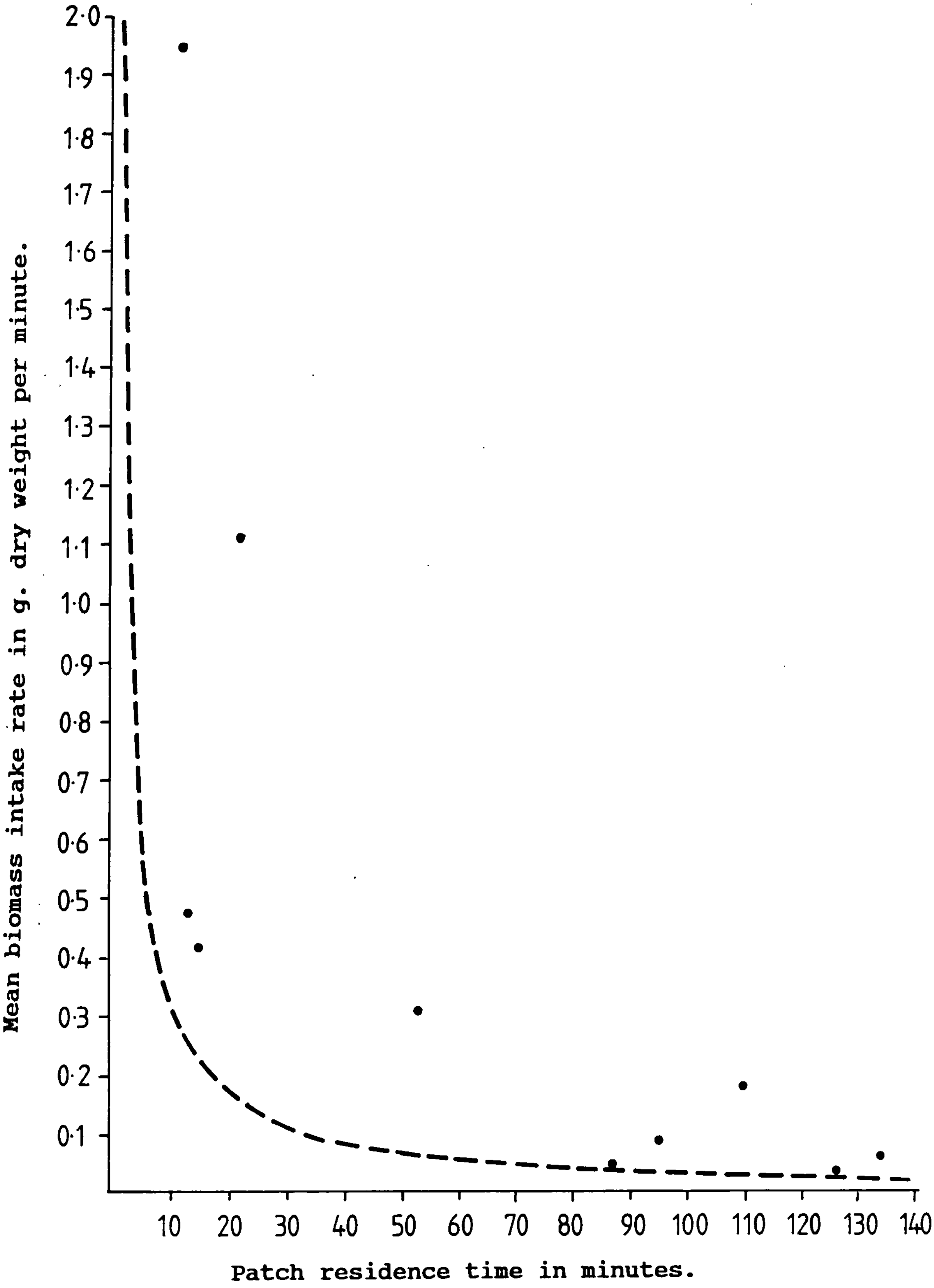
	Prey intake rate g. dry wt. ± S.E.	Patch residence time, mins ± S.E.	
Successful foragers	0.468 ± 0.194	66.50 ± 15.64	n=10
unsuccessful foragers	0.024 ± 0.008	23.98 ± 2.44	n=31

IGURE 2.4 The biomass intake rate and patch residence time of birds whose final prey loads exceed the minimum target prey load.



ote: The dotted line represents the minimum target prey load threshold. Points to the right of this line represent birds whose final prey loads exceed minimum target prey load requirements.

FIGURE 2.4 The biomass intake rate and patch residence time of birds whose final prey loads exceed the minimum target prey load.



Note: The dotted line represents the minimum target prey load threshold. Points to the right of this line represent birds whose final prey loads exceed minimum target prey load requirements.

caught single large prey exceeding a minimum target prey load. The relationship between patch residence time and biomass intake rate for these birds follows the typical negative exponential curve that would be expected if birds left the patch when they achieved a fixed prey load.

This supports the previous assumption that birds which caught over 22 g. wet weight (3.3 g. dry wt.) of prey left the patch because they had achieved their target prey load, see prediction 4. These bird have therefore been excluded from further tests of the predictions concerning patch leaving decisions.

2.3.3 Patch leaving decisions of unsuccessful foragers.

Within the unsuccessful foraging group there was no significant relationship between biomass intake rate and patch residence time (rs = 0.1658 d.f.=29 p > 0.1 Spearman Rank correlation, data from fig 2.3). This shows that unsuccessful foragers with relatively high biomass intake rates had similar patch residence times to unsuccessful foragers with low biomass intake rates. Similarly there was no significant correlation (rs = 0.129 d.f.= 29 p > 0.1 Spearman rank correlation) between the biomass intake rate during the first 24 mins. of foraging (mean patch residence time of unsuccessful foragers) and the total patch residence time of unsuccessful foragers (see fig. 2.5). This shows that unsuccessful foragers which experienced relatively high rates of biomass intake during the first part of the foraging period within a patch, still did not forage for longer periods than unsuccessful foragers with low initial biomass intake rates. Birds which left the patch before 24 mins. have been included in the analysis.

Fig 2.6 shows that within the unsuccessful foraging group there were 13 birds which showed a rise in biomass intake rate and 13 showed a fall in biomass intake rate, between the two halves of the foraging bout. This shows that there were no consistent trends for biomass intake to either rise or fall between the first and second halves of the foraging bout. The mean patch residence time of birds with biomass intake rates which were lower during the second half of the foraging bout (mean= 23.17 mins. ± 3.147 S.E. n= 12) was not significantly different (u= 107.5 $p > 0.05$ Mann Whitney u test) from that of birds with biomass intake rates which did not fall (mean= 24.51 mins. ± 3.509 S.E. n= 19). Thus, regardless of whether biomass intake rate was rising or falling, unsuccessful foragers were leaving patches after similar patch residence times.

FIGURE 2.5 The relationship between the mean biomass intake rate (measured over the first 24 minutes of foraging) and the patch residence time of unsuccessful foragers.

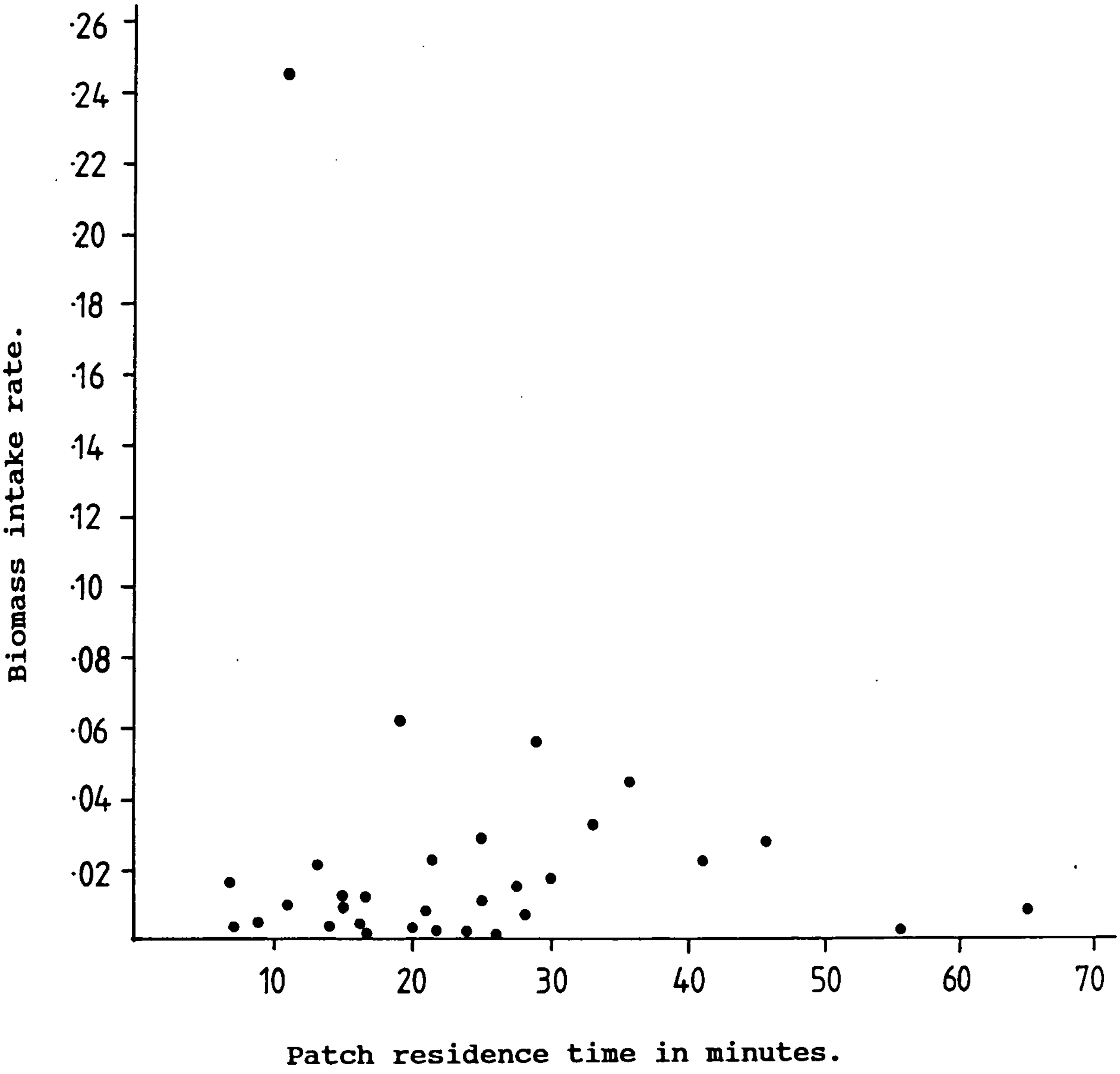
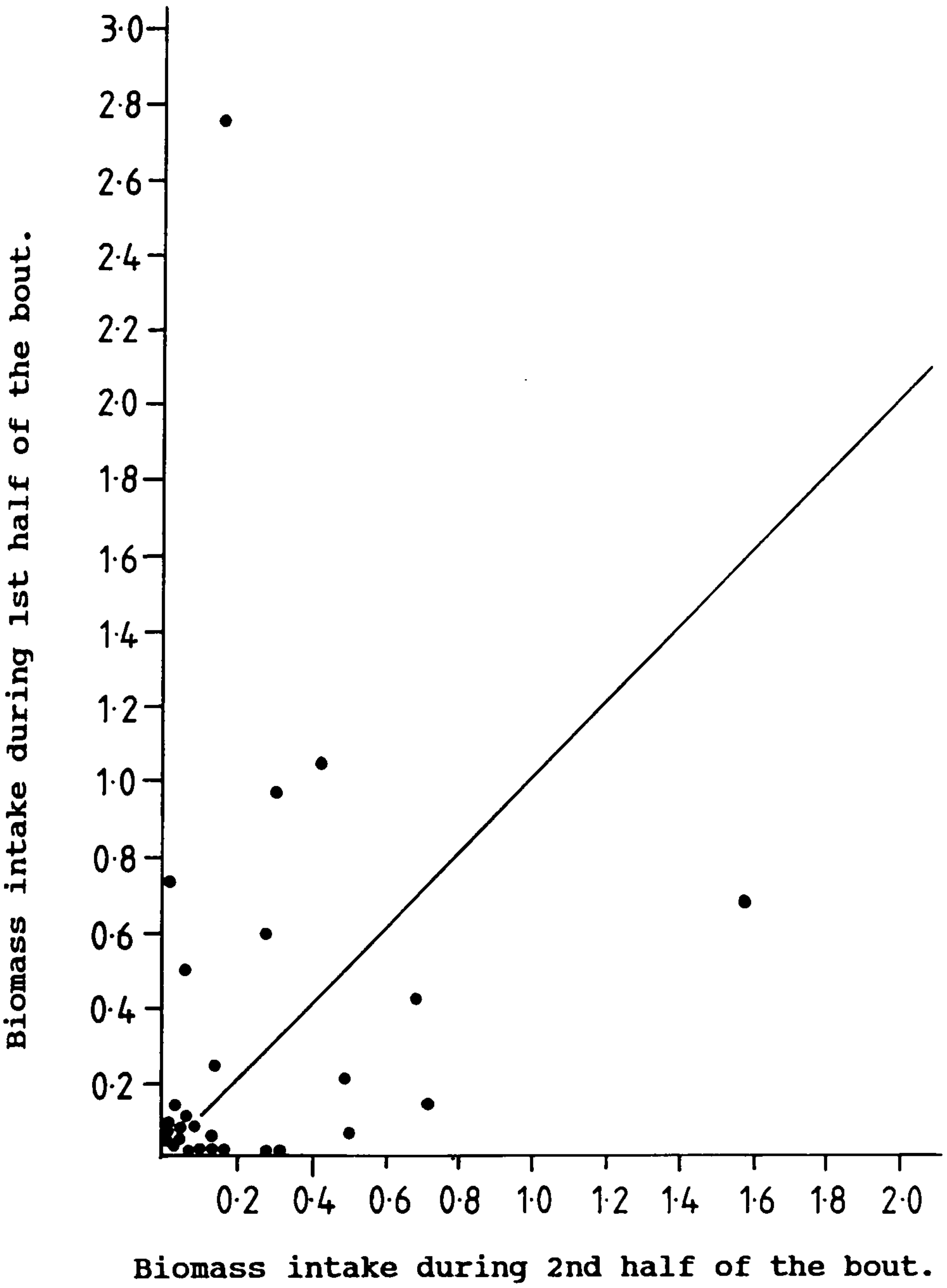


FIGURE 2.6 Biomass intake (in g. dry weight) of unsuccessful foragers during the 1st and 2nd halves of their foraging bout.



Note: The line represents an equal biomass of prey caught during both halves of the bout.

Foraging theory (including the Marginal Value Theorem) predicts that birds should reject all patches with gain rates lower than a critical rate, after some form of initial sampling. Within the range of unacceptable gain rates, biomass intake rate should have no affect on the patch leaving decision. The results presented so far show that unsuccessful foragers had significantly lower biomass intake rates than successful foragers and within the unsuccessful foraging group, patch residence time was not affected by absolute biomass intake rate measured over the whole foraging bout or by changes in the rate of biomass intake rate between the first and second halves of the bout. It is therefore possible that unsuccessful foragers rejected patches because the rate of biomass gain during the initial sampling period was lower than the critical rate required for efficient patch use, whilst successful foragers had biomass intakes higher than this rate and remained in patches to achieve their target prey load. If this is true the relationship between patch residence time and biomass intake rate shown in fig. 2.3 should not be linear but a step wise function with birds accepting or rejecting patches after an initial fixed sampling period.

2.3.4 Sampling Patch Quality.

Table 2.4 compares the G.U.T. (time from the capture of the last prey until leaving the patch) of unsuccessful foragers with the mean prey intercatch interval that they experienced during a foraging bout within a patch. There was no significant trend for G.U.T. to be either longer or shorter than the mean inter-catch interval ($z = 0.00$ $p = 0.5$ sign test). Thus there was no support for prediction 5 (that if birds were using a fixed G.U.T. strategy to make patch leaving decisions their G.U.T. should be longer than the mean prey intercatch interval).

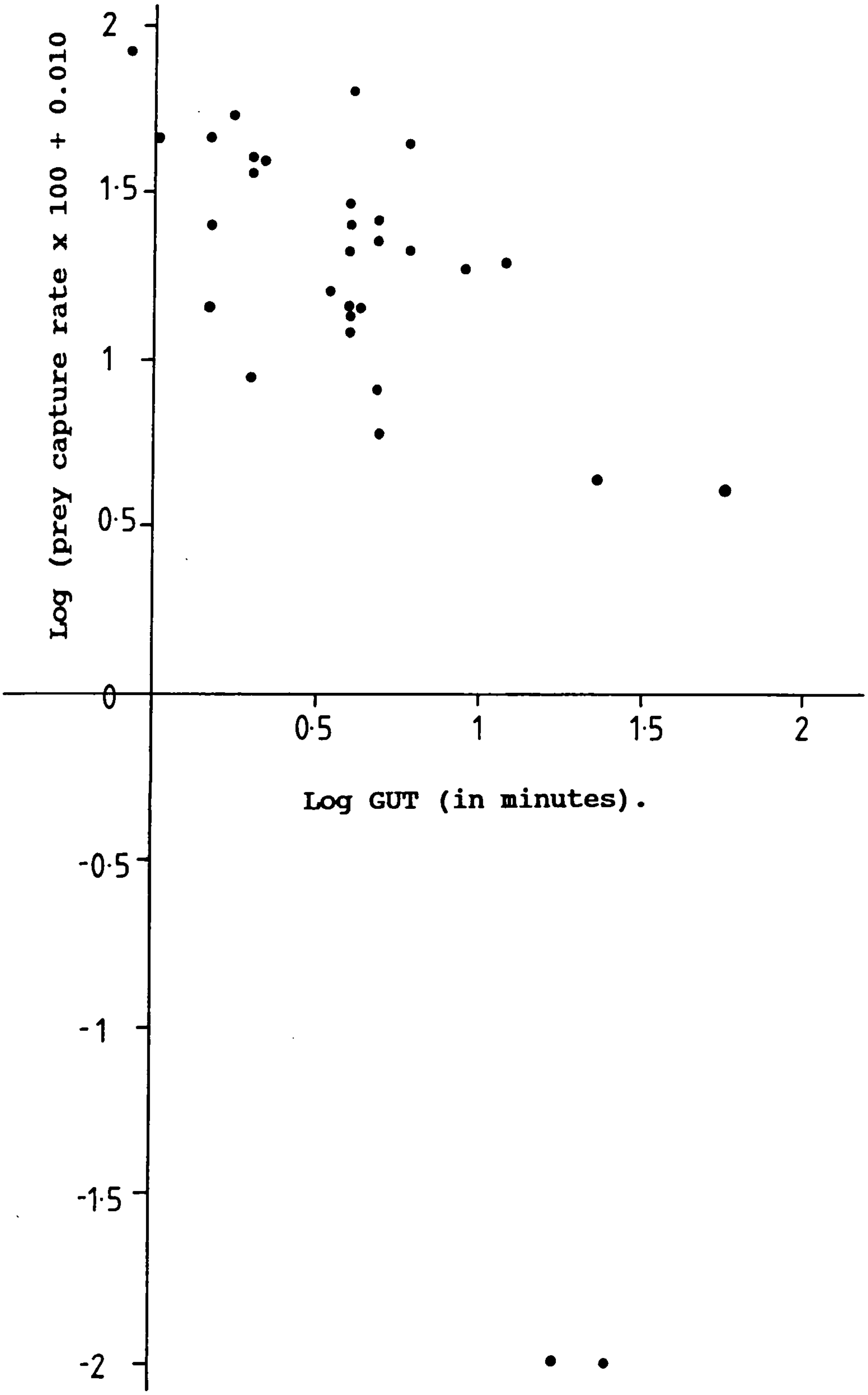
Fig. 2.7 shows that the G.U.T of unsuccessful foragers was negatively correlated with prey capture rate ($rs = - 0.6036$ $n = 31$ $p < 0.02$. Spearman rank correlation (Data have been transformed using log [(I.R.* 100)+ 0.01] and log [G.U.T.] to give a linear relationship). This shows that birds which had high prey capture rates had long G.U.T.'s whilst birds with low rates had short G.U.T.'s.

This strong negative correlation between the two variables suggests that unsuccessful foragers were not leaving patches after the intercatch interval exceeded a fixed limit, but supports the previous suggestion that these birds were leaving patches after a fixed period of sampling. This is

TABLE 2.4 The mean intercatch interval (I.I) between prey, the total number of prey caught and the G.U.T. for each observed unsuccesful foraging bout (time intervals are given in mins. +/- S.E.).

foraging bout.	mean I.I	G.U.T.	Total prey caught
1	14.9 ± 18.8	5.0	4
2	6.5 ± 8.1	1.5	6
3	2.2 ± 3.2	2.0	6
4	5.5 ± 2.8	4.0	2
5	1.2 ± 1.6	0.8	25
6	1.7 ± 1.6	4.0	4
7	0.0	26.0	0
8	0.0	23.0	1
9	3.6 ± 0.9	12.0	2
10	0.0	16.8	0
11	5.5 ± 6.4	4.0	2
12	1.0 ± 0.9	4.0	8
13	3.0 ± 2.2	4.0	14
14	5.0 ± 0.0	4.0	2
15	0.0	4.0	1
16	2.1 ± 2.1	6.0	6
17	3.8 ± 3.1	6.0	6
18	10.0 ± 4.2	2.0	2
19	2.5 ± 1.7	5.0	4
20	1.8 ± 1.7	1.8	19
21	2.3 ± 1.8	1.0	15
22	3.7 ± 3.1	1.5	7
23	10.0 ± 8.5	5.0	2
24	2.0 ± 2.1	1.5	10
25	2.7 ± 0.6	5.0	3
26	2.5 ± 2.4	2.0	4
27	2.0 ± 1.4	4.0	2
28	5.5 ± 8.6	3.5	10
29	0.0	15.0	1
30	7.9 ± 10.8	9.0	4
31	2.6 ± 2.7	2.0	7

FIGURE 2.7 The relationship between the GUT. and prey capture rate (in minutes) of unsuccessful foragers.



best explained by comparing the predictions of the two models which are described below.

Sampling Period Model. In the sampling period model, birds forage for an initial fixed sampling period which is sufficiently long to allow birds to predict the quality of the patch. If biomass intake rate is below a critical limit birds reject patches after sampling. If biomass intake is higher than this, birds continue to forage, possibly using a "sliding window" sampling period (Krebs et al. 1978), until biomass intake rate falls below the critical rate or until they achieve their target prey load. They then leave the patch. The model predicts a fixed patch residence time within the range of unacceptable biomass intake rates. The model also predicts a negative correlation between prey capture rate and G.U.T. within the range of patches which are rejected, see Fig 2.8.

Fixed G.U.T. Model. With a fixed G.U.T. patch-leaving strategy, birds continue to forage until the interval between prey captures exceeds some fixed limit (the fixed G.U.T.), after which they leave the patch. The model predicts that patch residence time should be correlated with prey capture rate (measured over the whole foraging period) and also predicts a fixed G.U.T. which, within the range of rejected patches, should be independent of prey capture

FIGURE 2.8 **Hypothetical model showing the relationship between patch residence time, G.U.T. and prey capture rate (PCR), for birds in good and poor patches, using a non specified measure of prey intake rate measured over a sampling period.**

In this example the critical capture rate (C.R.) is set at 0.5> C.R. <0.33.   * denotes prey capture.

Intake rate starts above critical limit.

```
* * * * * * * * * * * * * * * * * * * extend foraging * * 1
<--------------------------><-------- until target-------->
1_____________________________________preyload.__________1


* * * * *   *    *     *    *1.1 reject       G.U.T. 1
------<--------------------------> patch after
_________________________________1 extended sampling.
```

Intake rate below critical limit.

```
 *   *   *   *   *   *   *1.1 reject patch.      G.U.T. 1

<---------------------------->                   PCR 0.233
1___________________________1

 *      *       *       *1..1 reject patch       G.U.T. 2

<---------------------------->                   PCR 0.133
1___________________________1

    *              *1......1 reject patch.       G.U.T. 6

<---------------------------->                   PCR 0.067
1___________________________1

1...........................1 reject patch.       G.U.T. 27

<---------------------------->                   PCR 0.000
1___________________________1
   initial sampling period

1____1 = patch residence time, including sampling period.

1....1 = G.U.T.    <----> = sliding sampling period.
```

FIGURE 2.9 Hypothetical model showing the relationship between patch residence time, G.U.T. and prey capture rate (PCR), for birds in good and poor patches, using a fixed G.U.T. patch leaving strategy.

In this example G.U.T. = 3.
* denotes prey capture.

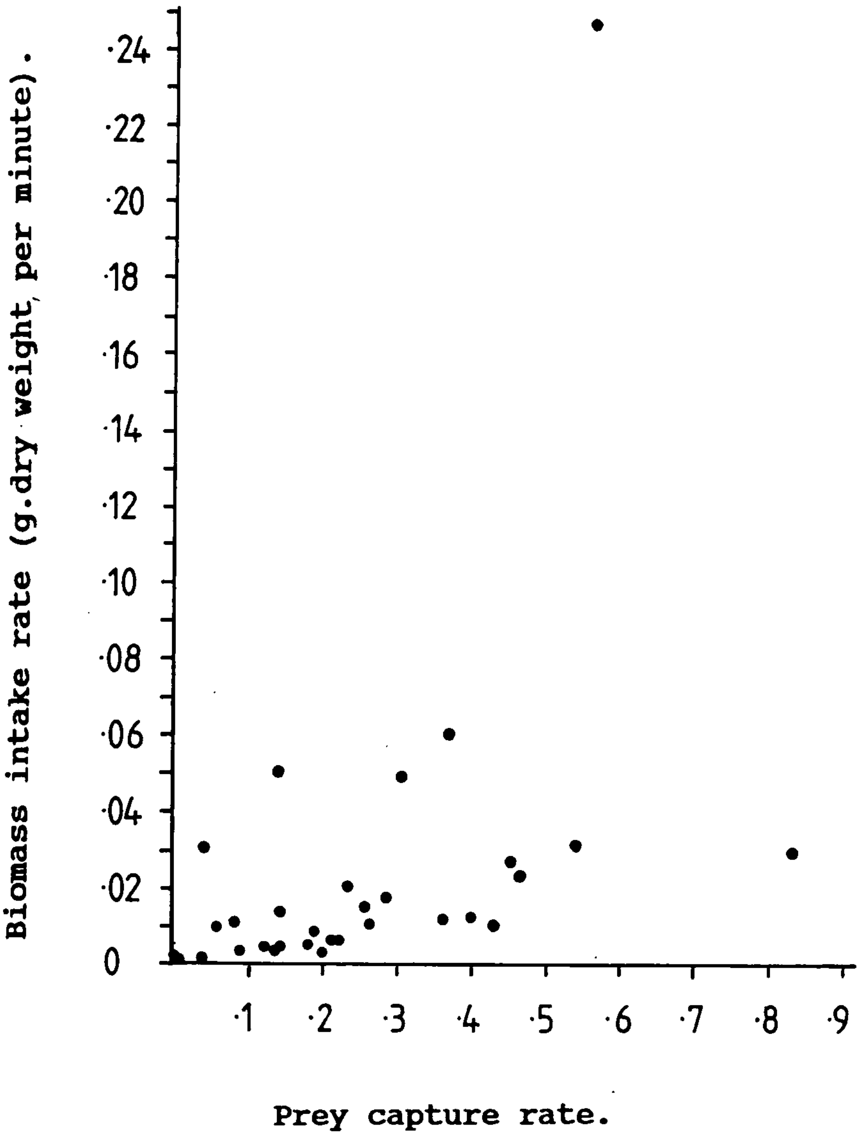
```
 * * * * * * * * * * * * * * * * * * * extend foraging until
1_____________________________________ till target prey load

 **** * * * * * *  *1...1 reject patch    G.U.T. 3
1______________________1                  PCR 0.455

  * *1...1 reject patch                   G.U.T. 3
1________1                                PCR 0.200

   *1...1 reject patch.                   G.U.T. 3
1_______1                                 PCR 0.111

1...1 reject patch.                       G.U.T. 3
1___1                                     PCR 0.000

1...1 = G.U.T.     1___1 = patch residence time.
```

rate; this is shown in Fig 2.9.

Both the models described above assume that biomass intake rate is proportional to prey capture rate. Fig 2.10 shows that for unsuccessful foragers, there was a significant positive relationship between these variables ($r_s = 0.6408$ $n = 31$ $p < 0.02$ Spearman rank correlation). The predictions of the models can therefore be tested against the observed relationships between biomass intake rate and patch residence time and between prey capture rate and G.U.T. shown by unsuccessful foragers. Since the biomass intake rate of unsuccessful foragers had no affect on patch residence time, and since their G.U.T.'s were negatively correlated with prey capture rate and were not consistently longer than the mean intercatch intervals, there was no support for the fixed G.U.T. model. These results are however consistent with the predictions of the fixed sampling period model and therefore provide some support for the hypothesis that unsuccessful foragers rejected patches because of low biomass intake rates measured over a fixed sampling period.

If the birds were making patch leaving decisions on the basis of biomass intake rate during sampling we would expect that birds which stayed in patches to achieve a minimum target prey load, would have higher biomass intake rates

FIGURE 2.10 The Biomass intake rate (in g. dry weight per minute) and Prey Capture rate of unsuccessful foragers.



during sampling than birds which left patches with less prey (prediction 5). Using the mean patch residence time of unsuccessful foragers (24 mins.) as the mean sampling period, we can test this prediction by comparing the mean biomass intake rate of successful foragers with that of unsuccessful foragers during the sampling period.

Since some unsuccessful foragers left before 24 mins whilst others left after this time, I have assumed that each bird was using a slightly different sampling period. I therefore used the total patch residence time of each unsuccessful forager as its sampling period to calculate the mean biomass intake rate of unsuccessful foragers during sampling. Biomass intake rates of successful foragers were calculated over a 24 minute sampling period. Table 2.5 shows that during this first sampling period successful foragers had significantly higher biomass intake rates than unsuccessful foragers. This supports the hypothesis that successful foragers were remaining in patches because they experienced high biomass intake rates during the initial sampling period.

If birds were continuing to sample we would also expect successful foragers to have higher biomass intake rates than unsuccessful foragers during subsequent sampling periods. Table 2.5 shows both the episodic and cumulative biomass

TABLE 2.5 **Comparison between the mean biomass intake rate (± S.E.) of successful foragers during each 24 min. period of the foraging bout and unsuccessful foragers during their entire foraging period. (Figures are g. dry wt per min.)**

	Sampling period	Episodic Intake rate.	Cumulative intake rate.
Successful foragers n=5	1	*** 0.121 ± 0.032	0.121 ± 0.032 ***
	2	0.112 ± 0.074	0.116 ± 0.047 ***
	3	0.018 ± 0.008	0.084 ± 0.030 **
	4	** 0.080 ± 0.039	0.083 ± 0.032 **
Unsuccessful foragers n=31		0.024 ± 0.008	

*** p<0.002 ** p<0.01 Mann Whitney U test.

intake rates of successful foragers during subsequent sampling periods. Episodic intake rates were calculated as the mean biomass intake rate for all birds during each sampling period whilst cumulative rates were calculated from the start of the foraging bout until the end of the current sampling period. Episodic biomass intake rate was significantly higher only in sampling period 4. During 24 min. periods 2 and 3 there were no significant differences between the mean biomass intake rates of the two groups. However variance amongst birds was high and sample sizes very small. Cumulative rates of biomass intake were however significantly higher for successful foragers than for unsuccessful foragers in all sampling periods. It is therefore possible that birds were using measures of cumulative gain rather than episodic gain to make patch leaving "decisions". These results provide further support for the hypothesis that patch leaving decisions were based on some measure of biomass intake rate measured over a sampling period and it is possible that successful foragers were remaining in patches to achieve a minimum target prey load because they had consistently high cumulative biomass intake rates during their entire foraging bout. Birds which caught single large prey have again been excluded from these analyses, since their patch leaving decision was not based on prey intake up to the point of capture of the last prey.

2.4 DISCUSSION.

The results provide broad evidence that the temporal and spatial availability of food within the environment affects the foraging site choice of Grey Herons. This is consistent with other field studies on large wading birds which demonstrate the role of food availability in the dynamics of foraging site use (Krebs 1974, Kushlan 1976, Hafner and Britton 1983 and Richner 1986). In the present study, birds which experienced high biomass intake rates tended to forage at the same site for longer periods than birds with low intake rates (see Fig 2.3 & Tables 2.2 & 2.3). This supports predictions 1,2i and 2ii outlined in the introduction and shows that birds were making patch choice decisions which would tend to increase their biomass intake rate during a foraging trip. Biomass intake rate affected the foraging time of birds within a patch in two ways:

a) When biomass intake rate was high birds remained in patches to achieve at least a minimum target prey load. The relationship between biomass intake rate and patch residence time for these birds followed a negative exponential curve (see Fig 2.4). This supports prediction 4 and strongly suggests that these birds left patches because they had achieved their actual target prey load requirements.

b) When biomass intake rate was low birds left patches before capturing a minimum target prey load. Within the range of biomass intake rates shown by this group there was no evidence that intake rate, whether measured over the first part of the bout or over the entire bout, had any affect on patch residence time (see Figs 2.3 & 2.5).

Within the group of birds that rejected patches before capturing a minimum target prey load (unsuccessful foragers) there was no evidence that the birds were consistently leaving patches when their biomass intake rate was falling (see Fig 2.6) or that their initial biomass intake rate had any affect on their patch residence time (see Fig 2.5). These results appear to contradict the Marginal Value Theorem which normally predicts that predators with high initial biomass intake rates should forage for longer periods than those with low initial rates, and that predators should leave patches when their biomass intake rate is falling.

However, the results from section 1 indicate that although birds showed changes in prey intake rate during a foraging bout, there was no consistent trend for prey intake rate to fall (see Fig. 2.1). It is therefore possible that the birds were foraging in patches which, although they showed short term fluctuations in the availability of prey had, in the long term, relatively constant levels of prey availability and could therefore be classed as either "good" or "poor". Under these conditions (i.e. where biomass gain curves are linear) the Marginal Value Theorem predicts that predators should reject poor patches and continue foraging in the best patches. As outlined in the results the data are consistent with this aspect of the Theorem which predicts a step-wise relationship between biomass intake rate and patch residence time with birds either accepting or rejecting patches after sampling the quality of the patch. This may be the reason that the non-parametric correlation between these variables in Fig 2.3 shows a higher level of significance than the parametric correlation. However, it was not possible to determine whether unsuccessful foragers were actually rejecting patches because they had biomass intake rates which were lower than the critical rate required for "optimal" patch use because this critical rate could not be calculated with the data collected during the study. The reasons for this are given in the introduction.

The results were not consistent with prediction 5, that birds rejecting patches should have G.U.T's which were longer than their mean prey intercatch interval (see Table 2.4). Thus there was no evidence that birds were using a fixed G.U.T. strategy to assess their biomass intake rate.

The strong relationship between G.U.T. and prey capture rate (see Fig 2.7) and the lack of correlation between biomass intake rate and patch residence time for unsuccessful foragers does however suggest that these birds were rejecting patches after a fixed sampling period (see results for details). Krebs et al. (1978) showed that where the average prey intake rate (measured over all the patches which are visited) is high the G.U.T. is shorter than when the average rate is low. In this study however birds were moving freely between feeding areas so we would expect birds to be using relatively similar G.U.T. throughout the whole of their feeding range. I therefore do not interpret the strong negative correlation between G.U.T. and prey capture rate, shown in Fig. 2.7, as evidence for the fixed G.U.T. strategy for patch sampling. Evidence for a fixed G.U.T strategy has been found in other Heron species (Great Blue Heron *Ardea herodias* Krebs 1974, Snowy Egret *Egretta thula* and the Great Egret *Casmerodius albus* Erwin 1985). It is therefore possible that under different situations birds use different methods to assess biomass intake rate.

Predators would only be expected to use a fixed G.U.T. strategy when prey intake varies in a predictable way. The results from section 2.3.1 show that encounters with prey were highly discontinuous, prey in the same patch varied considerably in size and biomass intake rate was probably controlled by random movements of prey within and between patches. Under these circumstances biomass intake would vary in an unpredictable manner and one would expect the birds to use some form of stochastic sampling method to assess prey availability (Oaten 1977, Green 1980, Iwasa et al. 1981 and McNamara 1982).

The results also show that, measured over sampling periods of 24 mins (the mean patch residence time of unsuccessful foragers) the mean cumulative biomass intake rate of successful foragers was consistently higher than the mean intake rate of unsuccessful foragers measured over the duration of their entire foraging bout (see Table 2.5). This supports the previous suggestion that successful foragers remained in patches because they had high biomass intake rates, whilst unsuccessful foragers left patches because they had low biomass intake rates. The results do not tell us how birds were sampling biomass intake rate but they are consistent with the hypothesis that birds were making patch leaving decisions on the basis of cumulative biomass intake rate measured over successive sampling periods.

Although the results are consistent with unsuccessful foragers leaving patches after a fixed sampling period there was considerable variation in patch residence time of these birds (range = 7-65 mins. see Figs. 2.3 & 2.5). This variation possibly reflects inter-bird variation in foraging experience within a patch which could considerably alter the time required to sample the patch. As suggested in chapter 1, birds visiting a patch for the first time may need to sample prey intake for a long period before being able to accurately assess variations in the availability and the size of prey within the patch. Whereas birds with some previous experience within the patch may be able to determine its quality and thus its relative profitability after a little or no sampling.

Other factors may also affect the degree of sampling between patches. Krebs et al. (1978) showed that when meal times were long, Great tits Parus major spent more time sampling between patches before making a final choice, than when meal times were short. It is possible that Herons with limited time budgets make patch choices more quickly than birds which have low time budget constraints. In the Camargue some Grey Herons start breeding in early February whilst the latest start in May (pers obs). This as well as inter-pair differences in brood size may result in considerable variation in time budget constraints between birds foraging in the same areas and may give rise to inter bird differences in sampling behaviour.

Alternatively the variation in the patch residence time of unsuccessful foragers may be the result of individual birds following different "optimal" strategies. In chapter 1, I showed that each heron from the colony at Carrelet, used a different set of foraging sites. Thus each bird will have different travel times between alternative patches and each bird will be making patch choice decisions within a different range of patches of different quality.

The critical value of biomass intake rate below which each individual should reject patches may therefore be different for each bird. Some birds may be foraging in depleting patches whilst others may be using non-depleting patches. The "optimal" patch use behaviour of each bird may therefore be different and dependent on the type and quality of patches within its home range.

Looking for optimal patch use trends, using the data combined from many different birds (as I have done in this study) may disguise some of these individual "optimal" patch use strategies and cause considerable variance in the grouped data set. This is emphasised by the results of Richner (1986) who looked at the foraging site movements of Grey Herons in winter. He used the mean biomass intake rates of birds feeding in a river and estuarine system (where the biomass intake of birds varied with the tidal cycle) to predict how birds should move between different foraging areas in order to maximize their prey intake rate during the day. The observed patch changes by most birds followed the predicted pattern. Some birds however, remained faithful to individual foraging sites even though they could have increased their prey intake rate by moving to a different area. Although Richner could not explain why some birds did not follow the predicted pattern of foraging site changes, his results however, clearly show that individual birds sometimes follow different patch use strategies, some of which may appear to be "sub-optimal" when compared with the strategies shown by other birds feeding in the same area.

Variation in the foraging patterns of different birds (and thus possible variations in patch use behaviours) may be the result of several different factors. In the discussion of the previous chapter I suggested that each bird may use only a limited number of patches to facilitate the learning of foraging site characteristics thus enabling birds to make more rapid foraging decisions. The importance of learning in determining feeding behaviour and choice of feeding site is demonstrated by the atypical foraging sites chosen by juvenile herons (Kushlan and Kushlan 1975) and by the lower foraging efficiency of young birds when compared to older conspecifics using the same feeding sites (Recher and Recher 1969 and Cook 1978).

Social dominance interactions have also been shown to affect the foraging site use of Herons (Recher and Recher 1969). Subordinate birds may not have access to the best foraging sites and may show patterns of patch use that appear to be "sub-optimal" when compared to competitively superior birds.

Limited time budgets may also affect choice of foraging site. During the pair formation, nest building and mate guarding periods Herons often reduce the time spent foraging (Burger 1978, Van Vessem and Draulans 1987). Van Vessem and Draulans showed that during this period Grey Herons foraged nearer to the colony than at other periods. It is therefore possible that time budget costs associated with non feeding activities cause birds to use poor feeding sites close to the colony during breeding, which they do not use when they have more time for foraging.

Time budget constraints may also affect exploratory behaviour. The value of exploratory behaviour (to discover alternative patches) must be assessed in terms of the amount of time required to find a new site and the amount of sampling required to learn new site characteristics. Thus birds may avoid looking for new patches if they have limited time budgets and if the time required to find and assess the quality of new patches is likely to be long. When time budgets are less restricting birds may become more exploratory and visit a wider range of foraging sites.

Taking all these factors into account there may be considerable differences in the patch use of different individuals and some birds may use patches that appear to be "sub-optimal" when compared to other individuals within the same foraging mosaic. The only way to discover whether each bird is making "optimal" patch choices within the spatial and temporal constraints imposed upon it would be to follow each bird throughout the range of patches that it visits and to test the affects of inter-bird competition and time budget constraints on patch choice behaviour. As outlined in the introduction this was impossible within the scope of this study, and indeed would be difficult for most Heron species under field conditions.

The results of this study show that, despite the considerable variation between individuals, breeding Grey Herons showed a significant tendency to reject patches where their biomass intake rate was low and continue foraging in patches where they experienced consistently high intake rates. This is consistent with some aspects of the Marginal Value Theorem and indicates that birds were responding to the quality of patches in a way which would tend to increase their intake rate of food during a foraging trip. Thus in the short term (duration of a foraging trip) food intake rate appeared to be an important factor in determining foraging site choice.

Because of the difficulty in locating and following marked birds in the field this study examined foraging decisions only during individual foraging trips. It was not possible to assess how birds made long term decisions about which part of the foraging habitat to use when foraging. However it is possible that patch quality may be an important factor governing individual bird's decision whether or not to return to a particular patch on subsequent foraging trips. This is an important area of research that needs to fully examined if the foraging patterns of herons are to be fully understood. It is unlikely, however, because of the large home ranges and frequent foraging site changes shown by individual Grey Herons in the current study, that such a study could be undertaken in the Camargue. Such a study would need to be undertaken in an area where it was easier to follow individual birds throughout their home ranges and also in an area where birds made less frequent foraging site changes.

2.5 SUMMARY

1) Biomass intake did not consistently fall during foraging bouts, suggesting that prey were a renewable resource and that measured over the duration of a foraging bout, prey depression and depletion, if they were occurring, had no consistent affect on biomass intake rate.

2) Variations in biomass intake rate during foraging bouts were probably the result of changes in the number, size and species of the available prey within patches.

3) There was a significant positive correlation between biomass intake rate and patch residence time showing that birds with high biomass intake rates tended to forage within a patch for longer periods than birds with low intake rates.

4) The relationship between patch residence time and biomass intake rate for successful foragers followed a negative exponential loading curve, suggesting that all these birds were leaving patches when they had achieved target prey load requirements.

5) Within the unsuccessful foraging group there was no significant correlation between patch residence time and biomass intake rate. Within this group, birds with low biomass intake rates were leaving patches after a similar residence time to birds with higher biomass intake rates. This suggests that these birds were rejecting patches after a fixed foraging period.

6) Unsuccessful foragers were, in general, not leaving patches because biomass intake rate was falling.

7) The G.U.T. of unsuccessful foragers was not consistently longer than their mean prey inter-catch intervals. There was considerable variation in the G.U.T. of unsuccessful foragers and G.U.T. was negatively correlated with prey capture rate. This suggests that birds were not using a fixed G.U.T. strategy to make patch leaving decisions. These results however, support the hypothesis that unsuccessful foragers were leaving patches after a fixed sampling period.

8) Measured over the mean residence time of unsuccessful foragers, successful foragers had higher biomass gain rates then unsuccessful foragers. During subsequent "sampling" periods successful foragers had higher cumulative rates of biomass intake than unsuccessful foragers. This suggests that birds were leaving patches when their biomass intake rate was lower than some critical rate during sampling and that birds remained in patches when their cumulative biomass intake during sampling was higher than this critical rate.

CHAPTER 3

COLONIALITY IN THE GREY HERON:

AN ADAPTATION FOR THE EXPLOITATION OF UNPREDICTABLE FOOD RESOURCES ?

3.1 INTRODUCTION.

The results from chapter 1 show that, in the Camargue, many breeding Grey Herons make frequent foraging site changes during the breeding season. The results from chapter 2 suggest that many foraging site changes may be the result of short term changes in the availability of food at the feeding site, although there was also evidence that some site changes were the result of the seasonal drying up of temporary marsh systems.

In a foraging environment where prey availability changes in an unpredictable way one would expect the birds to have developed strategies to maximise their chances of locating unpredictable or temporary food resources. Chapter 2 examined how individual birds might locate and exploit patches on the basis of patch sampling whilst this Chapter explores the hypothesis that, in addition to exploring for patches as individuals, Grey Herons might also use the breeding colony as a centre to locate and exploit the feeding sites used by other colony members.

There are currently two hypotheses which suggest how colonies could be an adaptation for the exploitation of unpredictable food resources. These are the Information

Centre Hypothesis (Ward and Zahavi 1973) and the Flock recruitment hypothesis (Evans 1982 and Bayer 1982). These two hypotheses are outlined below:

The Information Centre Hypothesis (ICH). Ward and Zahavi proposed that roosts and breeding colonies of birds evolved primarily as centres of information transfer so that individuals which are unsuccessful at finding food can follow successful individuals to their good feeding areas. According to the hypothesis the advantage of nesting in a colony would be to enhance opportunities for following if and when necessary. The relationship between leaders and followers would usually be parasitic. Leaders would not be expected to advertise their departure in such a relationship (Evans 1982). Followers benefit from being led to good feeding areas and even if a follower is excluded from the leader's feeding site it may still benefit "from having located the profitable habitat type of which the leader's territory is a part" (Scott Forbes 1986). Leaders could suffer costs from being followed, such as those incurred by territorial defence or interference in feeding resulting from the presence of the follower (Bertram 1978), and indirect costs related to leading a follower to a good feeding area and thereby increasing the fitness of a potential competitor. If leaders incur costs from leading, then it is necessary to show that they can benefit in some other way from the information centre function of the colony before this hypothesis can be accepted (this is discussed below). This is of course only necessary if leaders do not benefit from colonial nesting in some other way for example from communal defence against predators.

The Flock Recruitment Hypothesis (FRH). Proponents of this hypothesis suggest that colonies are an adaptation to facilitate the formation of flocks. Flocking may increase the chances of locating unpredictable food resources by social facilitation (Rand 1954, Fisher 1958, Krebs et al. 1972, Lazarus 1979), enhance feeding efficiency (Anderson et al. 1986), enable other types of resource to be located e.g. thermals (O'Maley and Evans 1982) or provide defence against predators. According to this hypothesis the relationship between leaders and followers is cooperative, and both benefit from leaving the colony together. In a cooperative relationship leaders would be expected to advertise departures to potential followers (Evans 1982).

These hypotheses are not mutually exclusive. Even if cooperative benefits arise for flock foragers, individual birds may still use the colony as an information centre. The ability of birds to use the colony in this way depends upon the duration for which prey remain available in the newly discovered patch (Bayer 1982). A short lived patch lasting less than the duration of the foraging trip, can be exploited only by those members of the foraging groups which find it and the colony cannot function as a centre for the transfer of information about the location of the patch. Long-lived patches exploitable over several feeding trips could be detected by other colony members which follow birds from the original foraging group as they return to the patch after a visit to the colony. If there are benefits from cooperative feeding in long lasting patches, then birds returning to the colony after a visit to one of these patches would be expected to attempt to recruit followers for the return visit. In this case information exchange about the location of the patch would occur in a cooperative manner between leader and followers and the colony is functioning as both an information and flock recruitment centre.

Scott Forbes (1986) suggested that the potential for following by colony members may be related to the rate of departures from the colony. This is because followers have to wait in the colony for a leader to depart. When the rate of departures is low followers will, on average, have to spend longer waiting for a leader than when the rate of departures is high. If a follower has to wait too long for a leader, the cost of waiting (measured in lost foraging time) may exceed the costs incurred from leaving the colony to search for a feeding site on its own. Thus when the rate of departures from the colony is low, many potential followers may leave to find patches of food without waiting for a leader and the proportion of departures which are followed will be lower than when the rate of departures from the colony is high. This hypothesis should be equally true whether the relationship between leaders and followers is parasitic or mutually beneficial.

If the relationship between leaders and followers is parasitic and leaders suffer costs when followed then we need to find other benefits to explain why leaders should join the colony and suffer costs. Ward and Zahavi (1973) suggested that leaders join a colony as an insurance against the need to follow on some occasions during the breeding season. I suggest two other ways that leaders might benefit from the information centre function of a colony, even if they do not become followers themselves:

1) The costs and benefits to members of a leader/follower group may not only affect the actual participants but may at times also affect the survival of their nestlings and thus to some extent may be shared between parents. Direct costs from leading (e.g. lowered biomass intake rates resulting from competition with followers at the

feeding site) are likely to lower brood survival while benefits to a follower (e.g. the discovery of a good feeding site and thereby an increase in its biomass intake rate) may increase the survival of its brood. Leaders may sometimes benefit from the information centre function of the colony, through increased brood survival when its partner follows. We would expect potential leaders to nest in a colony if the costs it incurs by leading are less than the benefits it derives through its partner following.

2) Fledgling Grey Herons have an extended period of dependence on their parents for up to a week after they first leave the nest. During this period the fledglings forage on their own but also return to the colony to receive food from their parents. Whilst foraging, young birds are often excluded by older conspecifics from the better feeding areas (Burger 1978) and are probably ignorant of the location of many of the alternative feeding sites that are within foraging range of the colony. It is possible that fledglings use the colony as an information centre to locate feeding sites during this period and this may increase their post fledging survival. Parents whose fledglings follow may therefore benefit from an increase in brood

survival (and thus lifetime reproductive success). Leaders may nest in a colony if the costs they suffer from leading are less than the benefits they derive from their fledglings being followers.

In order to test that the colony functions as a centre for the exploitation of unpredictable food resources, in addition to any anti predator function that it may confer, it is necessary to obtain data to test the predictions o the Information Centre and/or Flock Recruitment hypotheses.

Both hypotheses require that the feeding areas are unpredictable in location or duration of availability. However the information centre hypothesis is relevant only if foraging areas can be exploited for periods lasting longer than a foraging trip. Both hypotheses predict that the departure intervals between birds should be closer together than predicted by a random model, and that birds leaving the colony together should go to the same feeding area more often than birds which leave the colony successively but at long inter-departure intervals. However, the Information centre hypothesis predicts that the relationship between leaders and followers is normally parasitic, leaders would not be expected to advertise their departure to followers and the number of birds leaving the colony together for the same feeding area would be expected to be small. The Flock foraging hypothesis predicts that leaders would always advertise their departures to potential followers and following groups would be expected to be large.

Also the Information centre hypothesis predicts that birds which have been unsuccessful at foraging should follow successful birds to their foraging areas but the flock foraging hypothesis predicts that solitary individuals should be less successful than groups in the location or exploitation of some resource.

This Chapter tests the predictions of the flock recruitment and information centre hypotheses using field data collected from two different colonies of Grey herons.

3.2 METHODS

Observations were made in 1985 and 1986 on two Grey heron colonies in the Camargue area of the Rhone delta S. France. The colonies were at Carrelet in 1985, a colony of 63 pairs nesting in trees on the Carrelet fish farm near Albaron (see chapter 1), and Roustan in 1986 a colony of 25 pairs of herons nesting in trees near They de Roustan, Port st Louis at the mouth of the Grand Rhone (see Fig 1). All data refer to the Carrelet colony unless otherwise stated.

Data were collected on the time of departure and destination of birds leaving a colony from observation platforms placed near the colony. Details of the colony, hide and observation procedures used at Carrelet are given in chapter 1. At Roustan observations were made from the roof of a landrover parked on an access road near to the colony.

At both colonies, birds leaving the colony were observed through binoculars until they landed on the feeding grounds or disappeared from view. Two or more observers were used during each observation period so that simultaneous departures from the colony could be recorded. Birds were classified as followers if they went to the same feeding area as the previous departing bird or if they disappeared

from view in the same direction as the previous bird.
At Carrelet (1985) the whole colony was visible and some nests and individual birds could be recognised (see chapter 1). At this colony, whenever possible, departing birds were assigned an identity either at the pair or individual level (see chapter 1 for details).

3.2.1 Analysis of data.

The data were analysed in a number of different ways in order to test the predictions of the Information Centre and Flock Recruitment Hypotheses outlined in the introduction. Details of the different analyses, relevant to the different predictions, are given below:

1) Predictability of the feeding grounds.

The inter-feeding area and foraging site movements of individual birds described in chapters 1 & 2 suggest a high degree of unpredictability in the quality of feeding areas. To give a better overall view of these movements, by all colony members, I have grouped all departure observations from the colony for three different periods of the breeding season (the season was arbitrarily divided into 3 periods during each of which 9 full days of observations were collected). The degree that the colony members moved between feeding areas was determined using a χ^2 table of contingency to test the heterogeneity of use of feeding areas on different days, during each of the three seasonal periods (period 1: 26/03/85 to 21/04/84; period 2: 23/04/85 to 09/05/85; period 3: 13/05/85 to 04/06/85). The feeding areas outlined in chapter 1 were combined into four groups to give sufficient data for analysis. Groupings were as follows:

Group 1 = Feeding areas 1,2 & 3
Group 2 = Feeding area 5
Group 3 = Feeding areas 6 & 8
Group 4 = Feeding areas 4,7,9,10,11 & 12

2) Daily and Seasonal rate of departures from the colony.

To show seasonal as well as daily changes in departures from the colony the mean rate of departures was calculated for each hour after dawn during the same seasonal periods as section 1.

To compare differences in the number of departures during different periods of the day, data were combined from daily time periods when the rate of departure was relatively constant between days (within each seasonal period). The daily time periods chosen for analysis were 0-2 and 3-11 hours post dawn. The rate of departures during these 2 different time periods (within each seasonal period) were compared using a t test.

To compare the number of departures from the colony during different seasonal periods, data were grouped to calculate the mean daily number of departures between 1-12 hours post dawn for each seasonal period. This daily time period was chosen to compare between seasonal periods because it provided the longest, most continuous data set for days within each period. Grouped data were again compared using the t test.

3) Timing and non-independence of departures from the colony.

If birds were leaving the colony in groups more often than we would expect by chance, then the observed number of short time intervals between departures (inter-departure intervals) would be significantly higher than predicted from a random Poisson distribution. To test this the inter-departure intervals between successive departures from the colony were calculated. It is possible to compare the observed distribution of inter-departure intervals with a random predicted distribution only if the distribution pattern is calculated from periods of the day when the number of birds leaving the colony is relatively constant. Therefore this analysis was carried out on data grouped within two daily time periods (0-2 and 3-11 hours post dawn). Within these daily time periods the number of birds leaving the colony were approximately the same each day (see above). Days were combined within each seasonal period to give sufficient data for analysis.

The predicted distribution of inter-departure intervals for each daily time period, within each seasonal period, was calculated from the random (Poisson) distribution generated from the equation of Andrzejewski and Wierzbowska (1961) see also Krebs (1974) and Scott Forbes (1986). A chi2 test of goodness of fit corrected for the Poisson distribution (n-2 d.f.) was used to compare the observed and predicted distributions. The distribution of inter-departure intervals, within each daily time period, was compared between seasons using the Kolmogorov Smirnov test to determine how the distribution of inter-departure intervals changed during the season.

To test whether grouped departures were flying to the same feeding area, the data were analysed to determine the relationship between departure interval and destination of successive departures from the colony. For this analysis data were grouped for all hours during the day within each seasonal period. Days with less than 10 hours of observations were included in the analyses. The grouped data were compared, using the chi^2 test, to test the frequency of following (successive departure going to the same feeding area) for different inter-departure intervals.

The Scott Forbes hypothesis (see introduction) predicts that when the rate of colony departures is low the proportion of followers should be lower than when the rate of departures is high. This hypothesis was originally proposed to qualitatively predict proportions of followers in colonies of different size. However, it can be tested by looking for changes in the proportion of followers in the same colony when there are changes in the rate of departure. The data were compared, between the two different daily time periods (0-2 & 3-11 hours post dawn) and between the different seasonal periods, using the chi^2 test to test how the proportion of followers changed with the rate of departures from the colony.

4) The relationship between leaders and followers.

During the observation periods data were collected on the behaviour of birds leaving the colony. This and the data on behaviour on the foraging grounds presented in chapter 3, were examined for evidence on the relationship between leaders and followers.

5) Benefits to leaders that nest colonially.

The data were examined to determine whether there was any evidence that leaders became followers, that leaders had partners that followed or that leaders had fledglings which followed.

3.3 RESULTS.

The results are presented in subsections related to the predictions outlined in the introduction.

3.3.1 Predictability of the feeding grounds.

Daily departures from the colony to the four grouped feeding areas are shown for the three seasonal periods in Table 3.1 (only days with greater than 10 hours of observations have been included in the analyses). The table shows that during seasonal periods 1 & 2 there was a significant tendency for colony members to use different feeding areas on different days (Seasonal period 1, $Chi^2 = 51.8$ d.f.= 24 $p < 0.001$; Seasonal period 2, $Chi^2 = 52.9$ d.f.= 24 $p < 0.001$). During period three this tendency was not significant ($Chi^2 = 25.2$ d.f.= 24 $p > 0.3$).

As outlined in chapters 1 and 2, many of the foraging sites used by birds at Carrelet were within temporary water bodies which dry out during the summer and which may also show short term changes in quality as prey move between sites. I therefore interpret the data in table 3.1 as showing that the birds were making frequent switches between those

TABLE 3.1 The number of daily departures to four different groups of feeding areas during three seasonal periods.

FEEDING AREAS	Observation Days									SEASONAL PERIOD
	1	2	3	4	5	6	7	8	9	
1)	10	13	24	24	16	9	8	20	9	PERIOD 1
2)	15	21	5	18	20	21	8	8	12	26/03/85-
3)	17	23	19	20	9	16	11	15	21	21/04/85
4)	23	17	11	25	17	14	6	21	29	
1)	7	5	13	17	16	14	27	9	10	PERIOD 2
2)	6	0	5	9	8	7	8	6	6	23/04/85-
3)	10	7	13	18	11	7	17	11	13	09/05/85
4)	10	6	6	7	2	1	8	24	11	
1)	11	6	10	14	11	7	6	7	9	PERIOD 3
2)	7	16	10	17	16	10	11	7	5	13/05/85-
3)	13	19	10	10	14	9	11	4	4	04/06/85
4)	10	10	18	18	12	8	12	13	11	

foraging areas which exhibited unpredictable changes in prey availability. Late in the season most temporary marshes are dry and it is possible that the lack of significant switching between feeding areas from day to day in seasonal period 3 was due to the birds having moved from temporary feeding areas to more permanent marshes with stable prey availability. It should be noted however that there was no consistent trend for individual birds to use fewer or a less dispersed range of foraging sites during the latter part of their breeding cycle (see chapter 3).

3.3.2 Daily and Seasonal rate of departures from the colony.

The numbers of birds leaving the colony during each hourly period after dawn are shown in fig 3.1. Data have been grouped from the same days and within the same seasonal periods as section 1. This is to show seasonal as well as daily changes in departure rate from the colony.

Table 3.2 shows the mean hourly rate of departures from the colony during the early morning (0-2 hours post dawn) and late (3-11 hours post dawn) periods of the day. The data are grouped to compare the rate of departures during each daily time period, within the 3 seasonal periods. Table 3.2 also

FIGURE 3.1 The mean number of Grey Herons leaving the Carrelet colony each hour after dawn during three different seasonal periods.

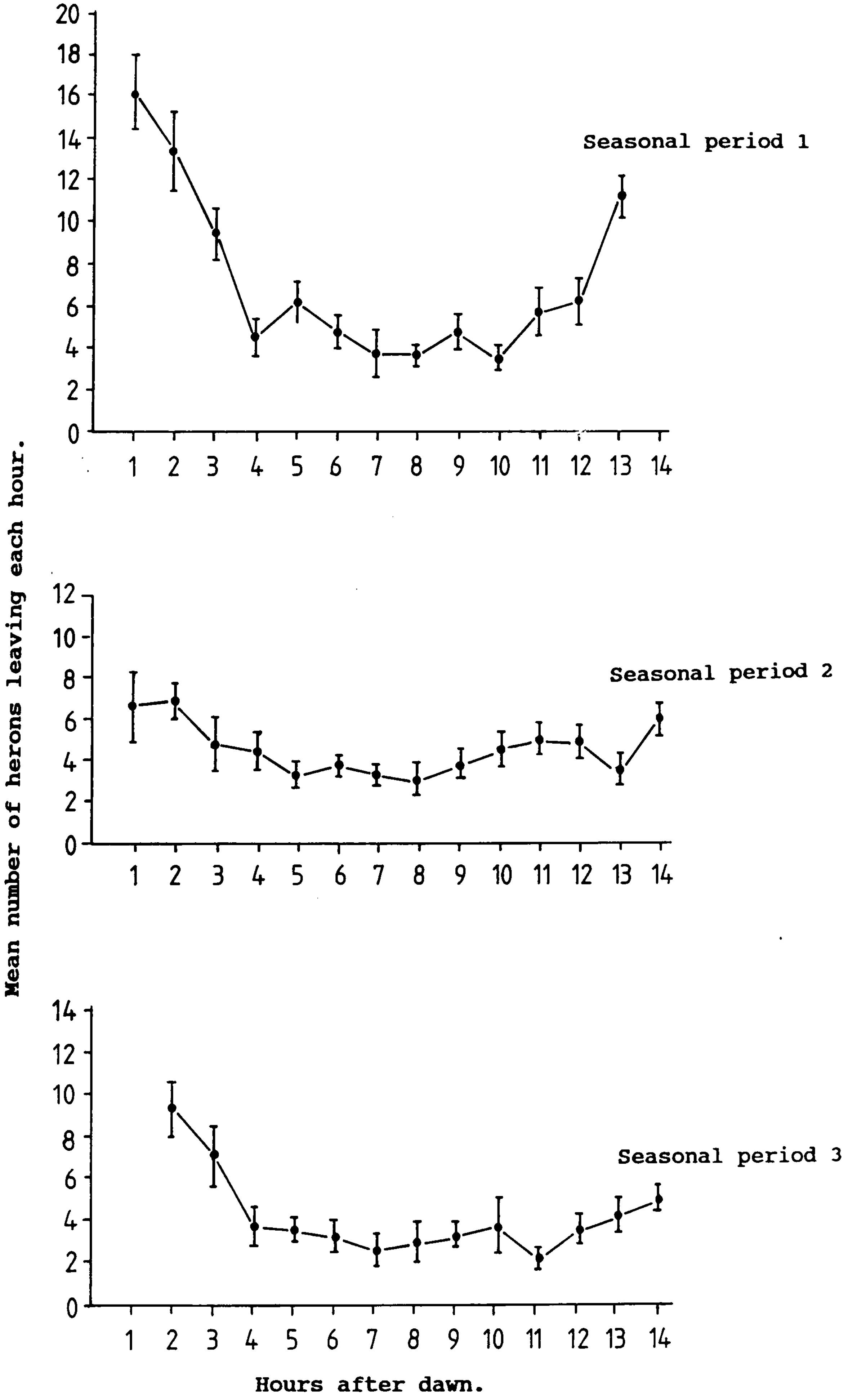


TABLE 3.2 The mean hourly rate of departures (± S.E.) from the colony during 2 daily time periods (0-2 & 3-11 hours post dawn) within each seasonal period and the mean total number of departures (± S.E.) from the colony between 1-12 hours post dawn during each seasonal period.

DAILY PERIOD (hours post dawn)	SEASONAL PERIOD PERIOD 1	 PERIOD 2	 PERIOD 3
0-2	14.77 ± 1.38 (18)	6.69 ± 0.85 (13)	9.83 ± 1.44 (8)
3-11	4.69 ± 0.33 (72)	3.82 ± 0.25 (71)	3.15 ± 0.28 (72)
1-12	66.6 ± 4.90 (9)	46.3 ± 4.36 (7)	45.5 ± 5.22 (8)

Note: Figures in parentheses are sample sizes (number of hourly or 1-12 periods per seasonal period).

gives the mean daily number of departures between 1-12 hours post dawn for each seasonal period.

In all three seasonal periods the mean hourly rate of departure was significantly higher in the 0-2 hour post dawn daily time period than in the 3-11 hour post dawn period (Seasonal period 1, $t = 7.100$ d.f.=19 $p<0.01$; seasonal period 2, $t = 3.246$ d.f.=14 $p<0.01$; seasonal period 3, $t = 4.244$ d.f.=8 $p<0.01$; unequal variance in all cases). There was also a seasonal decline in the number of departures from the colony, during the daily time period 1-12 hours post dawn. This seasonal decline was significant only between seasonal periods 1 and 2 and between seasonal periods 1 and 3 ($t = 3.04$ d.f.=14 $p<0.01$ and $t = 2.952$ d.f.=15 $p< 0.01$, periods 1/2 and 1/3 respectively, unequal variance in both cases). There was no significant decline between seasonal periods 2 and 3 ($t = 0.116$ d.f.=13 $p> 0.10$ unequal variance).

3.3.3 Timing and non-independence of departures from the colony.

The distribution of inter-departure intervals over the two daily time periods (0-2 and 3-11 hours post dawn) are shown separately for the three seasonal periods in Figs. 3.2 &

FIGURE 3.2 The Distribution of interdeparture intervals over the early (0-2 hours post dawn) daily period during the 3 different seasonal periods.

Note: Shaded bars represent the expected (random) distribution of interdeparture intervals. Clear bars represent the observed distribution.

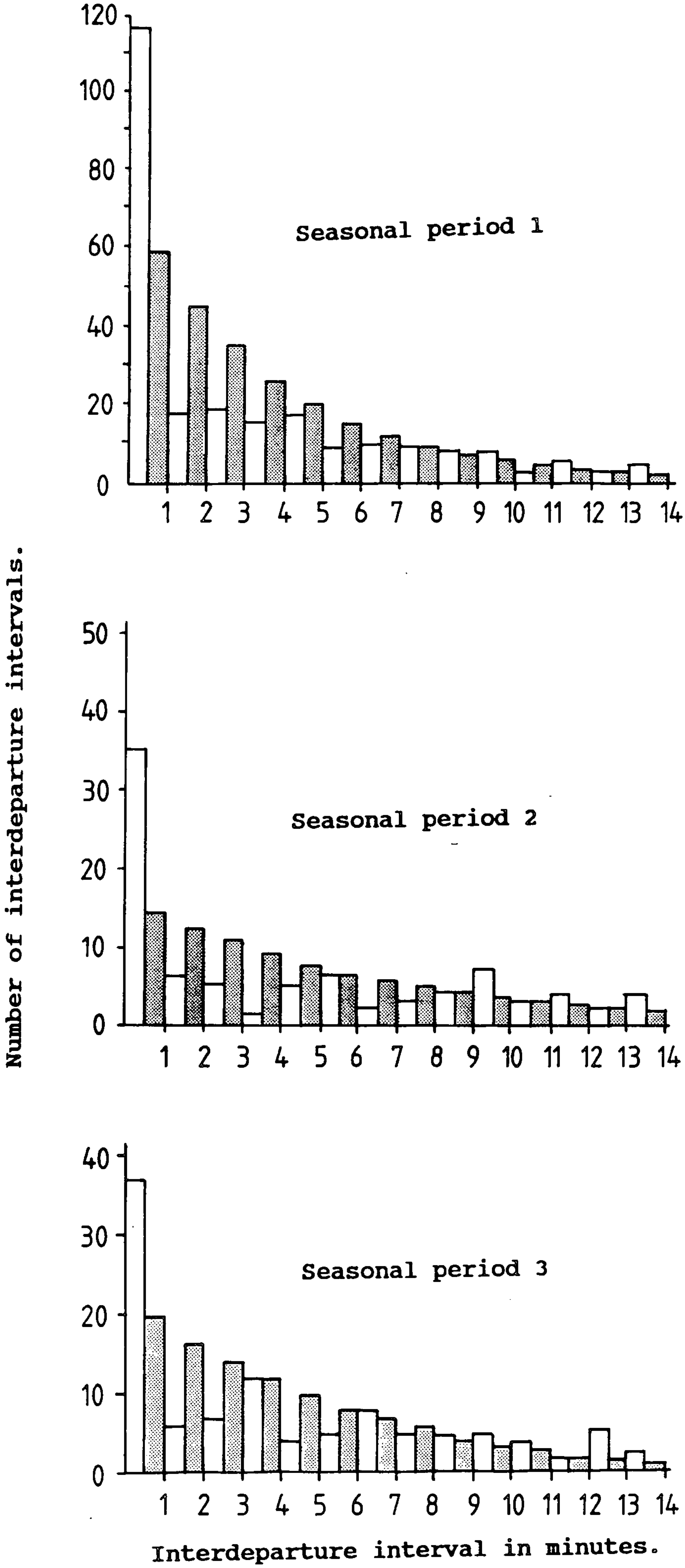
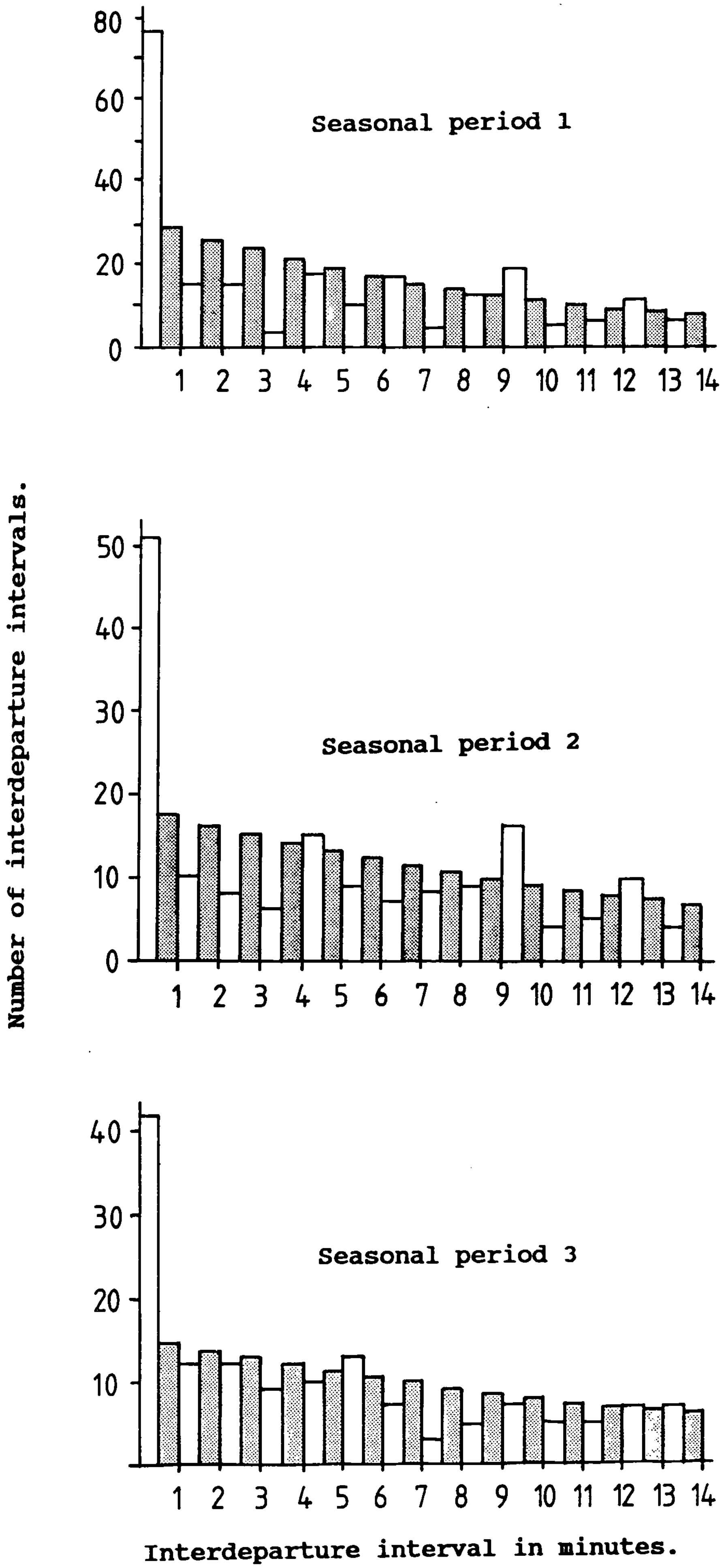

Seasonal period 1
120
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Seasonal period 2
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Seasonal period 3
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Number of interdeparture intervals.
Interdeparture interval in minutes.

FIGURE 3.3 The Distribution of interdeparture intervals over the late (3-11 hours post dawn) daily period during the 3 different seasonal periods.

Note: Shaded bars represent the expected (random) distribution of interdeparture intervals. Clear bars represent the observed distribution.


Seasonal period 1
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Seasonal period 2
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Seasonal period 3
40
30
20
10
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Number of interdeparture intervals.
Interdeparture interval in minutes.

3.3. The figures show both the observed and the predicted distributions for each daily time period and seasonal period.

A chi^2 test of goodness of fit corrected for the poisson distribution (n-2 d.f.) was used to compare the observed and predicted distributions. The results clearly show that the observed inter-departure intervals were biased towards the 0-1 minute inter-departure interval when compared with the random model. The results depart significantly from random during both daily time periods and in all seasonal periods (Daily time period 0-2 hours post dawn: $chi^2 = 95.26$ d.f.=10 $p< 0.001$ seasonal period 1, $chi^2 = 50.67$ d.f.=9 $p< 0.001$ seasonal period 2 and $chi^2 = 41.07$ d.f.=10 $p< 0.001$ seasonal period 3. Daily time period 3-11 hours post dawn: $chi^2 = 136.6$ d.f.=23 $p< 0.001$ seasonal period 1, $chi^2 = 107.52$ d.f.=24 $p< 0.001$ seasonal period 2 and $chi^2 = 72.37$ d.f.=23 $p< 0.001$ seasonal period 3).

The distribution of inter-departure intervals changes with season. The bias towards the 0-1 minute inter-departure interval at dawn (0-2 hour post dawn daily time period) was significantly greater in seasonal period 1 when compared to either seasonal periods 2 or 3 ($D = 0.2236$ $p< 0.005$ seasonal period 1 vs. seasonal period 2; $D = 0.2006$ $p< 0.005$ seasonal period 1 vs. seasonal period 3; $n1 = 249$, n2

= 101, n3 = 122; Kolmogorov Smirnov test for both comparisons). There was no significant difference between the inter-departure interval distributions of seasonal periods 2 or 3, (D= 0.0811 p> 0.1 Kolmogorov Smirnov test).

There was, however, no significant seasonal change in the distribution of inter-departure intervals in the 3-11 hour post dawn period (D = 0.1022 p>0.1 seasonal period 1 x seasonal period 2; D = 0.0542 p>0.1 seasonal period 2 x seasonal period 3; D = 0.0979 p>0.1 seasonal period 1 x seasonal period 3 Kolmogorov Smirnov test). To summarise, departures from the colony occur much closer together than we would expect if they occurred at random. The degree of grouping of departures however decreases between the 0-1 and 3-11 hour periods and between the first two seasonal periods.

To determine whether the unexpectedly high proportions of birds leaving the colony within one minute of each other were likely to go to the same feeding area more often than birds leaving the colony successively but at greater inter-departure intervals, the destinations of successive departures were compared for inter- departure intervals less than and greater than 1 minute. The results are presented in Table 3.3.

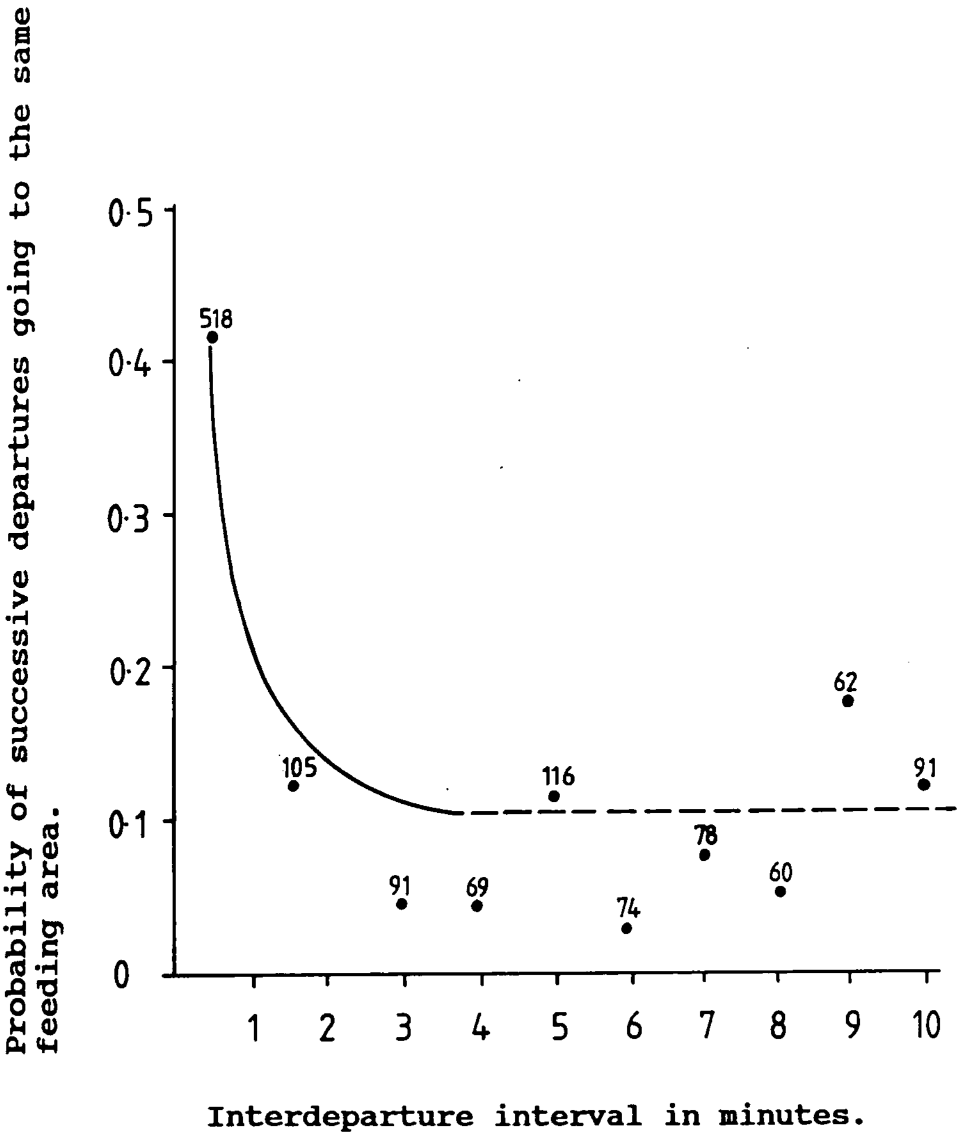
TABLE 3.3 **Destination of birds leaving the colony at interdeparture intervals greater than and less than 1 minute, in relation to the destination of the preceding departure.**

		Destination in relation to previous departure		
		Same	Different	
Departure Interval (mins.)	0-1	121	158	Seasonal period 1
	> 1	55	462	
	0-1	47	74	Seasonal period 2
	> 1	45	372	
	0-1	61	67	Seasonal period 3
	> 1	46	398	

The results show that within each seasonal period birds leaving the colony within 1 minute of each other went to the same feeding area significantly more often than birds leaving the colony at greater inter-departure intervals ($chi^2 = 110.8$ d.f.=1 $p<0.001$ period 1, $chi^2 = 50.1$ d.f.= 1 $p< 0.001$ period 2 and $chi^2 = 68.2$ d.f.= 1 $p<0.001$ period 3). Figure 3.4 shows the probability, for different inter-departure intervals, that successive colony departures went to the same feeding area; data are from all observations combined.

Only birds leaving the colony within 1 minute of the previous departure appeared to be influenced by the destination of the preceding bird. Herons leaving the colony at intervals greater than 1 minute after the previous departure probably could not see the previous bird which would already have been about 0.7 km. away from the colony after one minute (mean flight speed of the Grey Heron = 40.6 km./h. Marion 1984). It is therefore probable that birds which followed the preceding colony departure, to the same feeding area, at inter-departure intervals greater than 1 minute were random followers, i.e. birds which were going to the same feeding area but which were not influenced by the previous birds departure.

FIGURE 3.4 The probability, for different interdeparture intervals, that birds leaving the colony successively, went to the same feeding area.



Note: Figures represent the number of observations at each interdeparture intervals. Curve drawn by eye.

The Scott Forbes hypothesis, which predicts that when the rate of colony departures is low the proportion of followers should be lower than when the rate of departures is high, was tested by comparing the proportion of followers between periods when the rate of departures from the colony changed. The results presented above show that there is a decline in the rate of departures from the colony between the two daily time periods and between the three seasonal periods.
If the Scott Forbes hypothesis is correct we would expect both a daily and seasonal decline in the proportion of following from the colony.

However, before this can be tested the data must be corrected for changes in the number of random followers as the rate of departures from the colony changes. As the rate of departures rises there will be more shorter inter-departure intervals as compared with longer time intervals. There will therefore be an increase in the number of random followers in the short inter-departure intervals. The proportion of random followers, using the definition derived from the results earlier in this section, is the proportion of birds which follow in departure intervals greater than one minute. At Carrelet this proportion was 10.3% see fig 3.4 (this proportion should remain constant regardless of the rate of departure). The results have therefore been corrected for a 10.3 % proportion of random followers.

The numbers of "true" followers (corrected for 10.3% random following) leaving from the colony are shown for the two daily time periods and three seasonal periods in Table 3.4 (all random followers have been included as "other departures"). In all three seasonal periods there was a significant reduction in the proportion of followers between the two daily time periods 0-2 and 3-11 hours post dawn (chi^2= 8.631 d.f.= 1 $p<0.01$ seasonal period 1, chi^2= 5.31 d.f.= 1 $p<0.05$ seasonal period 2 and chi^2 = 10.09 d.f.= 1 $p<0.01$ seasonal period 3). This shows that as the daily rate of departures fell there was a significant decline in the proportion of followers from the colony. Similarly within the 1-12 hour post dawn period there was a significant reduction in the proportion of followers between seasonal period 1 and seasonal period 2 (chi^2 = 4.3 d.f.= 1 $p< 0.05$) and between seasonal period 1 and seasonal period 3 (chi^2 = 7.153 d.f.= 1 $p< 0.01$). There was, however, no significant difference between the proportion of followers in seasonal periods 2 & 3 (chi^2 = 0.2889 d.f.= 1 $p> 0.1$). These results show that, as the seasonal rate of departures fell, there was also a corresponding reduction in the proportion of followers from the colony.

TABLE 3.4 The number of Followers (F) and Non-followers (NF) from the colony, for 3 different daily time periods (0-1, 3-11 and 1-12 hours post dawn) and 3 seasonal periods.

	SEASONAL PERIOD					
	PERIOD 1		PERIOD 2		PERIOD 3	
DAILY PERIOD	F	NF	F	NF	F	NF
0-1	46 (41.3)	203 (207.7)	17 (15.2)	84 (85.8)	21 (18.8)	101 (103.2)
3-11	28 (25.1)	281 (283.9)	19 (17.0)	238 (240.0)	12 (10.8)	213 (214.2)
1-12	77 (69.1)	445 (452.9)	31 (27.8)	301 (304.2)	23 (20.6)	275 (277.4)

NOTE: Figures in parentheses are the numbers of followers and non-followers corrected for 10.3 % random following.

3.3.4 The relationship between leaders and followers.

Advertisement of departures. An almost complete absence of vocal signalling by leaders and followers was observed throughout the season. Birds leaving the colony for the feeding grounds did so directly, they were never seen circling the colony or attempting to attract followers with visual displays in any way. This suggests that leaders were not advertising their departures to potential followers.

Flock size. 87% of the observed departures from the colony (n= 1889) were not followed by another bird leaving for the same feeding area within one minute i.e. most birds left the colony for the feeding areas singly. When grouped departures did occur, the mean number of birds leaving the colony together for the same feeding site within one minute of each other, was 2.28 S.E.= 0.077 n= 78 (data from seasonal period 1 only). This indicates that when group departures were made, groups usually consisted of two birds and not of large flocks. Larger (up to 30 birds) flocks of birds were, however, seen on the foraging grounds.

Degree of sociality on the foraging grounds. The foraging sociality of birds has already been discussed in chapters 1 & 2. However to summarise; many birds fed solitarily and appeared to defend temporary feeding territories. However some birds also fed in loose flocks. Birds within flocks were occasionally aggressive towards each other. There was no evidence of dense flocks of birds. I believe that such dispersed aggregations of herons could not act as an effective cooperative fishing group, because between each bird there were large areas of unexploited habitat where prey could take refuge. Birds in flocks and territories used low mobility, stalking tactics to capture prey. This suggests that flock members were not attempting to drive prey towards each other, on the contrary these behaviours would tend to minimise disturbance to the prey. Birds which did not find food in a patch left the feeding area singly, at no time were flocks of herons seen searching for new feeding areas together, this suggests that the birds were not using cooperative mechanisms to find new feeding areas.

Birds in both territories and in flocks, were attracted to other birds which had caught prey (pers obs, not quantified). However this usually involved kleptoparasitic attacks. Where this occurred, intruders often attempted to feed near a bird which had successfully caught a prey. Most birds (whether they were handling prey or not) were aggressive to other birds which attempted to land or feed near them.

Two other studies, Marion (1984) and Van Vessem et al. (1984) have also shown that Grey Herons are both aggressive and territorial on the feeding grounds during the breeding season.

3.3.5 Benefits to leaders that nest colonially.

To examine the hypothesis that leaders could potentially derive benefits from becoming followers or having partners which followed data were collected from birds leaving individually marked nests at the Carrelet colony. Because observations were also being collected on the foraging patterns of individual birds (see chapter 1), observations were heavily biased towards identifying leaders and the identity of most followers could not be determined.

In total, leaders were seen leaving from 21 individually recognisable nests. Followers were observed leaving 4 recognisable nests and leaders and followers were seen leaving, at separate times, from a further 6 nests. Followers were never seen to follow their own partners. Unfortunately the identity of the individual leaders and followers which were seen leaving the same nest could not be determined. However the observation that leaders and followers left at different times from the same nest indicates that either some leaders became followers and, or, that some leaders had partners which followed. In either case, despite the costs of leading, leaders could also derive benefits from the information centre function of the colony.

To test the hypothesis that leaders could derive benefits from their fledglings following I have used data from the colony at They de Roustan 1986. The number of adults and fledglings following to the same feeding area as the previous bird which left the colony, were compared for different inter-departure intervals during two seasonal periods. The first period was between 10/04/86 to 02/06/86 and included six full days observations (minimum of 10 hours observations per day). The second period was between 20/06/86 and 04/07/87 and included 5 days observations. The results are shown in Table 3.5. In seasonal period 1 significantly more adults (chi2= 15.61 d.f.=1 p<0.001) and fledglings (p= 0.0096 Fishers exact probability) followed in the 0-1 min. inter-departure interval than if inter-departure intervals were greater than 1 minute. In period 2 no significant differences could be established for either adults or fledglings.

TABLE 3.5 **Destination of adults and fledglings leaving the colony at different interdeparture intervals, in relation to the destination of the preceding departure.**

		Destination in relation to previous departure		
Seasonal Period 1		Same	Different	
Departure Interval. (mins.)	0-1	24	26	Adults
	> 1	58	233	
	0-1	5	2	Fledglings
	> 1	0	9	

Seasonal Period 2		Same	Different	
Departure Interval. (mins.)	0-1	8	23	Adults
	> 1	20	124	
	0-1	7	6	Fledglings
	> 1	14	21	

These results support the results from Carrelet (see section 3.3.3 above) and show that birds leaving the colony within 1 minute of each other were much more likely to go to the same feeding area than birds leaving at greater inter-departure intervals. The results also show that, during the first seasonal period, some of the fledglings were following the previous departure to the same feeding site. The results also provide further evidence for seasonal changes in following behaviour. These results therefore show that some leaders could, during certain periods of the season, derive benefits from their fledglings following other birds to the feeding grounds.

3.4 DISCUSSION.

The results show that birds left the colony in groups much more often than would be expected at random (see Figs. 3.2 & 3.3), and that birds leaving the colony within one minute of each other were going to the same feeding areas significantly more often than birds which left after intervals greater than one minute (see Fig.3.4). These results are consistent with both the information centre and the flock recruitment hypotheses. It is also possible that the birds were leaving the colony in groups for other reasons, such as predator avoidance or detection. However I consider this unlikely since adult Grey Herons have few natural enemies and if flocking conferred an anti-predator advantage, the majority of birds leaving the colony would be expected to do so in flocks. Since most birds left the colony for the feeding grounds alone this was clearly not the case.

It has been suggested that grouped departures may result from synchronisation between birds, arising when birds leave the feeding areas in groups (Bayer 1982). During the current study it was not possible to collect sufficient data on the direction of arrivals at the colony and therefore I was unable to test this. However observations on the feeding areas gave no indications of grouped departures of birds leaving for the colony.

The above argument is in fact circular since grouped departures from the colony may synchronise birds so that they also arrive at the colony in groups. Scott Forbes (1986) found that Great Blue Herons leaving the colony at the same time went to the same feeding area significantly more often than birds leaving at greater inter-departure intervals. He did not, however, find any significant tendency for successive arrivals at the colony to have come from the same area.

I therefore interpret the evidence presented in this chapter as support for the hypothesis that the birds were using the colony as a centre to exploit unpredictable food resources. As outlined in the introduction there are two ways in which they can do this ie. through information transfer at the colony and by using the colony as a flock recruitment centre. However the absence of advertisement by departing leaders and the small size of departing groups suggest that the relationship between leaders and followers was parasitic and that the birds were not using the colony as a flock recruitment centre (see section 3.3.4). The results therefore provide support for the hypothesis that birds were using the colony as an information centre to locate new feeding areas. Evidence for the use of the breeding colony as an information centre for the location of unpredictable food resources by herons, has also been provided by Krebs (1974), Scott Forbes (1986) and Brown (1986).

It was not possible to test the hypothesis that unsuccessful birds were following successful leaders. This is difficult to test in herons which store food for chicks in the oesophagus and stomach (see Chapter 1) and therefore show no external signs of their foraging success. An attempt was made to use electronic nest balances to weigh the prey loads of foragers when they returned to the colony to feed chicks, however these did not work properly and no data were collected. In addition to using balances in future studies, it might be possible to use chick begging as an indicator of their hunger and therefore an indirect measure of the amount of food fed by a parent, as suggested by Krebs (1978). Evidence that followers were birds that had been unsuccessful at foraging and that they followed leaders that were successful on previous foraging trips was shown by Brown (1986). However, Brown was studying Cliff swallows (Hirundo pyrrhonata) which store food in the bill and throat where it is visible to an observer. Brown could therefore easily distinguish between successful and unsuccessful birds, as could other swallows !

The daily and seasonal trends in the rate of departure from the colony and the corresponding trends in following behaviour shown in Table 3.4 provide support for the hypothesis that the proportion of following is related to the rate of departures from the colony as suggested by Scott Forbes (1986). They are however open to other interpretations.

It is possible that the colony was used as a night roost by non breeding birds who exploited it as an information centre when they left in the morning. Van Vessem _et_ _al_. (1984) have shown that, early in the season, non breeders visit the colony to roost and will occasionally follow breeding birds to their feeding areas. Since non breeders do not visit the colony in the day (they have no chicks to feed) this may account for the observed changes in the proportion of followers during the day in the present study. However non-breeding birds stop visiting the colony when chick hatching starts (Van Vessem _et_ _al_. 1984 and pers obs). At Carrelet chick hatching was almost complete by the end of seasonal period one, therefore daily changes in the proportion of followers in seasonal periods 2 & 3 cannot be due to non breeders which follow. The seasonal reduction in the daily proportion of followers could, however, be a consequence of seasonal changes in the proportion of non-breeding birds visiting the colony.

At Carrelet all observations on immature birds were left out of the data set, so some (immature) visiting followers have already been removed from the analysis. Observations on the feeding grounds showed no apparent diurnal changes in social or foraging behaviour, nor were there any apparent diurnal changes in the prey types caught (see chapter 4), so it is unlikely that birds needed to follow out more at dawn. I therefore suggest that the daily decrease in the proportion of following is a consequence of the falling rate of departures and consequent reduced opportunity for following.

The seasonal decline in following behaviour may have been due to the seasonal decline in the rate of colony departures. However it may have also have been due to a seasonal change in the predictability of the feeding areas used by the birds. As shown in table 3.1 there was no significant tendency for birds to use different feeding areas on different days in period 3 and if birds were not switching feeding sites we would not expect them to follow. It is probable that no single explanation can fully account for the seasonal decline in following behaviour.

Information about the location of food resources can be transferred at several levels. At the lowest level the follower may follow the leader only for a short period and obtain information about the general location of a feeding area. At higher levels the follower may follow the leader to its foraging site and gain information about the location of food at the micro-patch level. Since most of the birds at Carrelet appeared to hold temporary feeding territories (see chapter 1) it is unlikely that followers derived immediate benefits from feeding at the leaders foraging site. Followers may, however, have foraged within the leaders territory after the leader had returned to the colony or, more probably, fed near to the leader and benefited from exploiting part of the feeding area that the leaders territory was within. In some feeding areas the birds fed in loose flocks (see chapter 1) and followers to these areas may have benefited directly from foraging at the leaders site. In these areas however, levels of aggression between birds were sometimes very high and birds within the flocks were frequently supplanted. It is therefore possible that only dominant followers could ever benefit from feeding at a subordinate leaders foraging site.

Most temporary marshes in the Camargue dry out during the summer and therefore have unpredictable levels of prey availability measured over the period of a season. However, since water levels do not change rapidly until mid to late summer, most marshes have levels of prey availability which are relatively predictable on a day to day basis. The availability of prey at the 'Macropatch' or marsh level is therefore probably stable enough to be detected at the colony by information transfer. The results from chapter 2 suggest that in some foraging sites (micro-patches within a feeding area) prey availability may vary over the duration of a foraging trip. At the micro-patch level therefore the availability of prey may not remain stable long enough for information about patch quality to be transferred at the colony. However over long periods of time the prey availability in a micropatch may be predictable, as prey repeatedly enter and leave the patch. Some birds caught prey in the same micropatch during their entire foraging trip (chapter 2). This indicates that prey availability in some micropatches is of a sufficient duration for the patch to be located by birds following a leader on its return trip. Some herons in the colony were seen to visit the same small feeding area in a large marsh, during several consecutive foraging trips (chapter 1) and this seems to support the idea of long term predictability in the quality of some micro-patches. It therefore seems likely that the Carrelet birds were foraging in macro and micro-patches which exhibited patch quality characteristics of sufficient duration to be detectable at the colony by followers.

The results from section 3.3.5 show that leaders could derive benefits from the information centre function of a colony through either becoming followers themselves and/or by having partners which followed (leaders which became followers could not be distinguished from leaders which had partners that followed). Reverse role benefits for leaders (where leaders sometimes became followers) was also shown for Cliff swallows by Brown (1986). Other potential benefits for leaders, through fledgling following, were also shown in the current study (see Table 3.5). Thus potential leaders do not necessarily suffer only costs through information transfer when they breed in a colony.

Although the results from the current study strongly suggest that the Grey Herons at Carrelet were using the colony as an information centre to locate new foraging sites, this does not mean that in other colonies Grey Herons do not use the colony as a flock recruitment centre, or indeed that at other sites Grey Herons use the colony as an information centre. Other bird species certainly hunt in flocks and the colonies of such species have been shown to act as flock recruitment centres Anderson et al. (1981). It is therefore possible that in areas where Grey Herons feed predominantly in flocks, they also look for new feeding areas in flocks and that they use the colony as a flock recruitment centre.

Van Vessem _et_ _al_. (1984) and Van Vessem & Draulans (1987) found little evidence that Grey Heron colonies acted as centres for the transfer of information about food resources. However these authors also found that the majority of birds that they studied held permanent feeding territories for most of the breeding season. Where birds hold permanent feeding territories they would not be expected to use the colony as an information or flock recruitment centre. It is possible that in species, such as the Grey Heron, which show intra-specific variation in social foraging strategies the use of a colony as a flock recruitment or foraging centre is dependant on the type of foraging sociality shown by the colony members. In such species foraging sociality is dependant on factors such as the spatial and temporal availability of prey and the defendability of patches around the colony (Kushlan 1978). Where the availability of prey in patches varies in an unpredictable manner and where patches are not economically defendable we would expect less territorial behaviour on the feeding grounds and we would also expect the birds to use the colony as an information centre or a flock recruitment centre, or possibly both simultaneously (see introduction to this chapter). Where the availability of prey in patches is predictable and where patches are economically defendable we would expect birds to hold territories and we would not expect birds to use the colony as an information or flock recruitment centre. Studies on the Great Blue Heron, which exhibits a wide range of foraging tactics including holding permanent territories (Bayer 1978), switching between intertidal and terrestrial foraging (Krebs 1974) and showing temporal variability in feeding site use around a colony (DesGranges 1979), have revealed differences in the synchrony of departures at different colonies Scott Forbes (1986), Pratt (1980), Bayer (1981), Krebs (1974) and DesGranges (1979). Although some of the differences in following behaviour from these studies may be due to differences in colony size (i.e the Scott Forbes hypothesis), they may also be due to differences in the foraging sociality of the birds in different areas, which in turn may be due to differences in prey distribution, defendability of territories etc..

3.5 SUMMARY

1) There was a significant tendency for colony members to use different feeding areas on different days during the earlier parts of the breeding season. During the late part of the season the birds tended to use the same feeding grounds every day. This suggests that during the earlier parts of the season, the location of the feeding areas was unpredictable.

2) There was a significant tendency for more birds to leave the colony during the early morning than at other periods of the day. Similarly the rate of departures from the colony was greater during the earlier part of the season than the later part.

3) The birds left the colony in groups more often than would be expected from random. The bias towards grouped departures was greatest during the early part of the day and during the early part of the breeding season.

4) Birds leaving the colony together went to the same feeding area more often than birds leaving the colony successively but at greater time intervals.

5) Following behaviour was affected by the rate of departures from the colony. When the rate of departures was high there was more following than when the rate was low.

6) An absence of vocal or other forms of signaling between leaders and followers, and the small size of leader/follower groups suggests that the relationship between leaders and followers was parasitic and that birds were using the colony as an information centre rather than a flock recruitment centre.

7) There was evidence that leaders could potentially offset some of the costs of leading through their partners or fledglings using the colony as an information centre.

CHAPTER 4

THE FOOD OF THE GREY HERON IN THE CAMARGUE.

4.1 INTRODUCTION.

The Grey Heron is an opportunistic carnivore which feeds mainly in aquatic habitats where water levels are shallow enough to enable birds to stand or wade, although they can plunge dive, and swim for prey in deeper water (Lowe 1954, and pers obs). The birds also occasionally feed on land or fish from land into water which is too deep for normal foraging techniques. Previous studies have shown that the principal aquatic prey are fish. On land the birds feed on small mammals, reptiles, insects and even earthworms. Grey Herons sometimes feed on fresh carrion, especially fish, and will also steal prey from other birds which use the same feeding areas. There are great variations in diet between different areas which are dependent on both foraging habitat and season. These are reviewed by Cramp & Simmons (1977) see also Hancock & Kushlan (1984) and Moser (1984).

Large and highly mobile prey are subdued and often killed with repeated stabs from the bill followed by mandibulation, before ingestion but most small prey are eaten alive (pers obs) and ingested almost immediately after capture. Prey of all sizes are usually manipulated to ensure that they are ingested head first probably to prevent scales, fins and appendages from damaging or catching in the oesophagus.

Catfish (Ictalurus nebulosus) possess sharp spines which they erect when attacked, and I have observed birds repeatedly stabbing these fish for up to 10 mins. before eating them. This was presumably to break the spines allowing the bird to swallow the fish without injury. It is possible, however, that the spines fold down when the fish is dead and extended stabbing is required to ensure this. This behaviour has also been observed by Krebs (1974) in Great Blue Herons (Ardea herodias) feeding on Staghorn Sculpin (Leptocottus armatus) a fish which possesses similar defensive spines.

Young herons are altricial and parents feed their young at the nest until they fledge. The diet of chicks may therefore reflect that of their parents. However, because of handling constraints small chicks cannot eat some of the larger prey caught by their parents (Moser 1984). Moser suggested that because of this, parents may actively select a diet containing small prey during the early stages of chick rearing. He has shown that chicks older than 30 days can eat most size classes of prey eaten by their parents. Therefore if this diet selection hypothesis is correct we may expect parents with older chicks to have a different diet to that of parents with younger chicks. It is also possible that younger chicks have different dietary requirements to older chicks and this may also result in differences in the diets of chicks of different age.

Because the diet of parents is likely be strongly affected by the availability of suitable prey types in the feeding areas this is also likely to influence the diet of their chicks. Moser (1984) also suggested that the diet of chicks may be affected by optimal foraging constraints on parents. For example he suggested that the relative profitability of the different prey types available to foraging parents at the feeding site could affect the diet of parents and that in turn this may affect the diet of nestlings.

There has been considerable confusion in the literature as to whether Grey Herons feed chicks directly from the bill or regurgitate onto the floor of the nest. Milstein et al. (1970) concluded from their own observations that parents normally regurgitate prey onto the nest. Most chicks in the brood therefore obtain some food from the prey load of the parent, although because of differences in the competitive abilities of individual chicks (see chapter 5), the distribution of food between the chicks may not always be even.

This chapter describes the diet of nestling Grey Herons in the Camargue, and examines how diet varies with time of day, age of chicks and between individual parents foraging at different sites. I have not examined how the availability or relative profitability of prey at the parental feeding site affected the diet of parents or nestlings because it was not possible to effectively sample the relative availability of prey on the feeding grounds.

Scientific names of all prey items in the diet are given in Appendix 1.

4.2 METHODS.

Three non destructive methods of sampling the diet of water birds, are available, ie. analysis of regurgitates (Owen 1955, Moser 1984), direct observations of prey taken by adults (eg. Cook 1978) and analysis of food pellets (eg. Giles 1979). The first method, analysis of regurgitates, was considered to give the greatest sample sizes with the fewest biases. Differences in the digestibility of different prey types is likely to introduce large biases in diet determined by the analysis of food pellets (which consist of only the indigestible remains of prey) and the diet determined from feeding observations on focal birds is likely to be biased heavily towards the diet obtained in those feeding areas where feeding observations are easiest (Moser 1984). For conservation, moral and legal reasons it was not considered appropriate to examine the diet of the Camargue birds by killing specimens and examining stomach contents. This study therefore concentrated on the analysis of dietary data obtained from the analysis of chick regurgitates although this has inherent biases since chicks cannot eat all the prey size classes eaten by their parents (Moser 1984).

Food samples were obtained by collecting chick regurgitates from different colonies. Young heron chicks often regurgitate their last meal when approached by a predator. Chick regurgitation is presumed to be an anti predator mechanism to make chicks lighter and therefore more mobile when escaping attack and also to provide an alternative source of food to distract the predator (Temple 1969). Many chicks regurgitated when they were approached but if not, they were stimulated to eject their last meal by gently massaging the stomach after the methods of Moser (pers comm.). It was possible to tell if a chick had recently been fed by feeling its abdomen and no attempt was made to take regurgitates from birds with obviously empty stomachs. In most cases prey were identified, weighed and measured on the nest and fed back to the chicks, but where samples could not be identified or when a large number of regurgitates were being collected during the same visit to the colony, they were stored in plastic bags with 50 % alcohol for identification in the laboratory.

Wherever possible data from regurgitates taken simultaneously from a brood were combined to avoid biases resulting from prey selection by different sized chicks within the brood. Where comparisons between the diet of chicks of different ages are made, I have used data from the whole prey load and the age of the oldest chick on the nest.

Regurgitates from each brood were assumed to be part of a single prey load from one parent. This assumption is probably correct only when chicks are still being guarded by their parents, since one parent is usually feeding at any one time. After the guarding period chicks may sometimes be fed in quick succession by both parents (pers obs). The figures for estimated number of prey loads analysed are therefore minimum values.

Diet studies were carried out in two colonies in the Camargue in 1984 and 1985. Details are given below:

1) Couvin 1984 (11 pairs nesting in reeds).
Regurgitates were repeatedly taken from 7 nests between 24/05/84 and 05/7/84 although the majority of regurgitates were taken between 07/06/84 and 29/06/84. Nests were visited twice a week until parents stopped guarding (chicks 28 days old). After this visits were more frequent. No individual parents could be recognised.

2) Carrelet 1984 (140 pairs nesting in trees).
Regurgitates were collected from as many chicks as possible during four visits to the colony: 0800 hrs. and 1700 hrs. on 27/06/84 and at the same times 6 days later (03/07/84). All regurgitates were

stored in alcohol for analysis in the laboratory.

3) Carrelet 1985 (63 pairs nesting in trees). Regurgitate collection was restricted to 3 broods with marked parents. The foraging sites of the parents were monitored regularly during the breeding season (see Chapter 1 for details). Regurgitates were collected several times a week between 17/06/85 and 02/07/85, immediately after a known parent fed the brood. All regurgitates were analysed on the nest and fed back to the chicks. In addition to regurgitate collection from these three nests, observations were made of adults feeding chicks of all ages from as many other nests as possible. Observations were made using binoculars and a 15 x 45 zoom telescope from a tower hide 75 m. from the colony. The size of all prey items seen was estimated using the parents bill as standard measure. Feeding observations were also carried out on individually marked birds in the field.

Whenever regurgitates were collected the time of collection and the age of the chicks was recorded. Chick ages were estimated by the development of feathers, limbs and bill at Carrelet in 1984 and by hatching and fledging dates at

Couvin 1984 and Carrelet 1985. Data on the foraging site use by parents were used in conjunction with data on nestling diet and field observations to determine where different prey types were caught.

Following the methods and definitions of Moser 1984, four measures of prey abundance were used in analyses of chick diet:

1) Percentage wet weight (% wet wt.). This indicates the proportion of a particular prey type expressed as a percentage of the total biomass of all prey loads.

2) Percentage occurrence (% occ.). This indicates the proportion, as a percentage, of all prey loads that contained that prey type.

3) Percentage items (% item.). This indicates the proportion, as a percentage, of the total number of prey items examined that were of that prey type.

4) Mean proportion (wet weight) of prey type in regurgitate. The proportion (wet weight) of each prey type in each regurgitate was used to calculate the mean proportion of different prey types in

regurgitates. Data were arc-sine transformed for the calculation of mean proportions and standard deviation. The transformed data were used in tests of significance between different samples.

The data were analysed to compare the diet of chicks from different colonies, diurnal changes in diet, dietary differences between different broods within the same colony and changes in prey type and prey size with chick age. Details are given below:

4.2.1 The diet of birds from different colonies.

The diet of nestling herons from the two different colonies was compared qualitatively by looking at both the % weight and % occurrence of all the different prey species. Quantitative comparisons were made using a t test to test differences in the mean proportion (by weight) of the most important prey types in regurgitates from the two colonies. Data were arcsine transformed for the calculation of mean proportion and standard deviation.

4.2.2 Diurnal changes in diet.

Diurnal changes in diet were examined by comparing the % occurrence of prey items from regurgitates taken before and after 0800 hours. These time periods were chosen because most of the birds which fed chicks before 0800 will have been feeding at night. Broadly speaking therefore, this compares the diet of birds feeding at night with that of birds feeding during the day. This qualitative comparison was to determine the most important prey types caught during the two daily periods. A t test was used for a quantitative comparison of the mean proportion (by weight) of the most important prey types found in regurgitates during both periods. Data from each time period were grouped within each colony and were arcsine transformed for the calculation of the mean proportion of the different prey types.

4.2.3 Dietary differences between different broods within the same colony

Dietary differences between individual broods within each colony were qualitatively compared using the percentage wet weight of the most important prey types taken from each brood. Unfortunately it was not possible to quantitatively test the differences in diet between broods and parents because the variance in the mean proportions (% wet weight) of dietary items within each group was too great.

Field observations on individual birds were used to explain the differences in diet between different broods.

4.2.4 Changes in diet with chick age.

The diet of chicks from three different age classes was compared qualitatively using percentage occurrence, percentage weight and percentage prey items of all the different prey types found in regurgitates from the two different colonies. Quantitative differences in the mean proportion (by weight) of the most important prey types in the diet of the different age groups were compared using a 1 way Analysis of Variance (1 way ANOVA). The results from the two colonies and from all broods from within each age class were combined to give sufficient data for analysis. Data were arcsine transformed for the calculation of mean proportion and standard deviation.

4.2.5 Prey size classes fed to chicks of different age.

Measurements of prey items taken from regurgitates were used to compare the occurrence of different prey size classes in regurgitates taken from chicks of different age. Field observations were used to determine if there were changes in the feeding behaviour of chicks with chick age.

4.3 RESULTS.

4.3.1 How the chicks were fed.

Observations at Carrelet 1985, where 118 feeding bouts were observed between parents and chicks ranging from 1 to 65 days old, confirm the conclusions of Milstein et al. (1970), that parents regurgitate prey for their chicks onto the floor of the nest. On all but three occasions parents regurgitated directly onto the nest after being stimulated by vigorous bill grasping from the chicks. The exceptions were when a 45 day old chick managed to catch the regurgitate as it left the parents bill, and twice parents were observed catching a fish next to the colony and returning to the nest with the fish in their bills. In the latter cases the adults did not ingest the prey which was dropped onto the nest for 29 & 38 day old chicks.

4.3.2 The diet of birds from different colonies.

The diet of nestling herons from the two colonies over the study period is shown in table 4.1 (the Latin names of all prey are given in Appendix 1). Most regurgitates contained several prey types although a few contained a single large

TABLE 4.1 Composition of the diet of nestling Grey Herons from two heronries during the study periods.

	Couvin 1984		Carrelet 1984		Carrelet 1985		total	
	% occ.	% wt.	% occ.	% wt.	% occ.	% wt.	% occ.	% wt.
Carp	44	38	46	21	35	33	52	33
Eel	46	39	54	32	10	14	41	32
Sunperch	21	10	13	6	10	13	19	10
Tench	7	5	10	7	1	+	6	4
Bream	1	1	4	3	1	+	2	1
Rudd / Roach	2	+	4	3	0	0	2	1
Mullet	0	0	6	5	0	0	2	1
Atherine	11	1	10	3	0	0	8	1
Gambusia	9	1	13	+	3	+	9	1
Stickleback	7	+	4	+	0	0	4	+
Catfish	4	2	8	5	0	0	4	2
Pike	3	+	0	0	0	0	1	+
Pipefish	9	+	0	0	0	0	4	+
Flounder	1	+	0	0	0	0	+	+
Aq.insect Larvae	24	1	62	13	35	40	49	13
Insect imago	7	+	15	+	0	0	8	+
Frogs	4	+	15	+	5	+	9	+
Amphibian Larvae	3	+	2	+	0	0	2	+
Crayfish	0	0	2	+	0	0	+	+
Crab	0	0	2	+	0	0	+	+
Snake	6	1	10	+	2	+	6	1
Shrimp	11	1	8	+	0	0	7	+
Mammal	3	+	0	0	0	0	1	+
Total prey loads	70		52		50		172	
Total prey weight	8303 g		3102 g		3373 g		14778 g	

Note: + denotes less than 1% .

TABLE 4.2 **The mean proportion (in % wet weight) of the most important prey types in regurgitates from Couvin and Carrelet in 1984.**

	Couvin	Carrelet
Carp	22.45 ± 8.06	9.29 ± 2.38
Eel	27.50 ± 4.42	27.02 ± 4.35
Sunperch	3.90 ± 2.02	1.14 ± 1.54
Aq.insect larvae	0.31 ± 0.33	8.99 ± 2.05
prey loads	65	42

Note: Data were arcsine transformed for the calculation of mean proportion and standard deviation. Data have been retransformed to show mean proportions in % wet weight ± S.E. rather than in angular degrees.

prey item or several prey of the same species.

The most important prey species in both % weight and % occurrence were Carp, Eels, Aquatic insect larvae and Sunperch. The mean proportion (by weight) of the most important prey types in regurgitates from the two colonies are compared in table 4.2. Data are from 1984 only (there were insufficient data to compare the regurgitates obtained from Carrelet in 1985 with the regurgitates obtained from both colonies in 1984).

There was no significant difference in the mean proportions of carp, eels or sunperch in the regurgitates from the two colonies (carp $t = 1.855$ $p> 0.05$ unequal variance, eel $t = 0.649$ d.f. = 105 $p> 0.05$, sunperch $t = 1.234$ d.f. = 105 $p> 0.05$). The mean proportion of aquatic insects in regurgitates from Carrelet was, however, significantly greater than that from Couvin ($t = 4.077$ $p> 0.001$ unequal variance). This shows that there were significant dietary differences between the two colonies.

4.3.3 Diurnal changes in diet.

Table 4.3 shows the composition of regurgitates taken before and after 0800 hours. The data are from 119 prey loads consisting of 1603 prey items collected from both Carrelet and Couvin in 1984. Regurgitates taken from chicks early in the morning must have contained prey delivered by parents which had been feeding at dawn or even at night, whereas prey in chick regurgitates taken later in the day will have come from parents feeding in normal daylight conditions. Although the percentage occurrence of the different prey species in the diet changed between the two periods, there were no important prey types which were caught exclusively during either period. To test whether any of the dietary changes were significant, I compared the mean proportion (by weight) of the most important prey types (carp, eels, sunperch and aquatic insects) in regurgitates, between the two daily periods. The results from the two colonies are shown in table 4.4.

In both colonies there were no significant changes in the mean proportion (by weight) of any of the important prey types, between the two daily periods (Couvin: carp $t = 0.99$ d.f.= 63 $p > 0.05$; eel $t = 0.07$ d.f.= 63 $p > 0.05$; sunperch $t = 1.96$ d.f.= 63 $p > 0.05$; aquatic insect larvae $d = 0.39$ $p > 0.05$ unequal variance) (Carrelet: carp $t = 1.49$ d.f.= 40 $p >$

TABLE 4.3 Percentage occurence of different prey items in the diet of nestling Grey Herons from two different daily periods.

	Couvin		Carrelet	
	Pre 0800	Post 0800	Pre 0800	Post 0800
Carp	46	46	39	54
Eel	50	43	48	65
Sunperch	38	13	17	12
Tench	4	11	13	7
Bream	4	0	7	0
Rudd / Roach	4	2	4	4
Mullet	4	0	7	4
Atherine	13	11	22	0
Gambusia	17	4	13	15
Stickleback	21	0	4	0
Catfish	4	4	7	7
Pike	8	0	0	0
Pipefish	13	7	0	0
Flounder	0	2	0	0
Aq.insect Larvae	37	17	78	54
Insect imago	8	7	22	7
Frogs	0	7	4	27
Amphibian Larvae	4	2	0	4
Crayfish	0	0	0	4
Crab	0	0	0	4
Snake	13	2	13	0
Shrimp	25	4	7	7
Mammal	4	2	0	0
Total prey loads	24	46	23	26

TABLE 4.4 **The mean proportion (in % wet weight) of the most important prey types in the diet of nestling Grey Herons from two different daily periods**

	Couvin		Carrelet	
	Pre 0800	Post 0800	Pre 0800	Post 0800
Carp	14.1 ± 5.0	27.2 ± 5.9	3.8 ± 2.4	14.2 ± 3.6
Eel	25.7 ± 4.7	28.5 ± 5.5	22.4 ± 7.1	30.3 ± 5.7
Sunperch	9.1 ± 3.7	1.3 ± 1.6	0.6 ± 1.2	1.6 ± 2.7
Aq ins larvae	0.2 ± 0.1	0.4 ± 0.6	8.8 ± 2.6	9.1 ± 3.1
prey loads	22	43	17	25

Note: Data were arcsine transformed for the calculation of mean proportion and standard deviation. Data have been retransformed to show mean proportions in % wet weight ± S.E. rather than in angular degrees.

0.05; eel $t = 0.49$ d.f.= 40 $p > 0.05$; sunperch $t = 0.50$ d.f.= 40 $p > 0.05$; aquatic insect larvae $t = 0.04$ d.f.= 40 $p > 0.05$).

4.3.4 Dietary differences between different broods within the same colony

Table 4.5 shows the differences in the proportions of the most important prey types in the diet of chicks from 7 different broods at Couvin in 1984. It was not possible to distinguish between regurgitates from different parents at Couvin. The diet of each brood shown in the table therefore represents the combined diet of both parents. At Carrelet in 1985 it was possible to distinguish between some birds and table 4.6 shows the composition of regurgitates brought back to the nest by individual parents. The results presented in both tables clearly show that the composition of regurgitates from different broods and from different parents from the same colony can vary considerably. Unfortunately it was not possible to test the differences in diet between broods and parents because the variance in the mean proportions (% wet weight) of dietary items within each group was too great.

TABLE 4.5 Percentage wet weight of different prey types in regurgitates from 7 different broods at Couvin 1984.

NEST	A	B	C	D	E	F	G
Carp	65	5	20	25	7	42	62
Eel	6	87	65	45	48	30	21
Sunperch	18	3	0	12	7	10	9
Aq.insect larvae	0	1	6	6	2	1	+
Other	11	4	9	12	36	17	8
prey loads	14	12	5	7	10	7	16

TABLE 4.6 Percentage wet weight of different prey types in regurgitates fed to 3 separate broods by 5 individual parents at Carrelet 1985.

NEST	A		B		C
Parent	(f)	(c)	(l)	(g)	(m)
Commercial Carp	32	0	20	17	0
Wild Carp	19	1	1	35	26
Eel	29	0	0	4	31
Sunperch	6	12	19	28	0
Aq.insect larvae	13	86	60	16	39
Other	1	1	0	0	4
prey loads	11	5	12	6	8

Note : letters in parentheses indicate the identity of the bird as used in Chapter 1.

The results from chapter 1 show that each of the individual birds from Carrelet in 1985 and included in table 4.6 were feeding in a different set of foraging sites and, taken together, these observations suggest that the diet of individual parents differed according to where they were foraging. However, the possibility of individual specialization on particular prey types cannot be ruled out.

Field observations at Carrelet in 1985 showed that bird (f) from nest A foraged at the fish farm and in several temporary marshes nearby. Analysis of regurgitates showed that the prey species caught by this bird varied unpredictably from day to day and usually consisted of either Commercial carp alone, Commercial Carp and aquatic insect larvae, or non-commercial fish and aquatic insect larvae. On only one occasion were both wild and commercial carp found in the same prey load. Field observations showed that on the fish farm herons caught commercial carp, sunperch and aquatic insects whilst in marshes outside the farm they caught a variety of prey including wild carp, eels, sunperch, catfish and aquatic insect larvae. The simultaneous presence of wild carp and commercial carp in the same regurgitate suggests that bird (f) occasionally used more than one foraging site during the same foraging trip. It is also possible that the bird was fishing at two different sites within the fish farm since on some occasions regurgitates contained only commercial carp and at other times they contained commercial carp and large numbers of aquatic insect larvae.

Both birds (l) and (g) from nest B also foraged on the fish farm and used temporary marshes nearby. The regurgitates from prey loads delivered by both these birds also varied between days. They sometimes contained commercial fish whereas on other days they contained only prey caught outside the fish farm.

Bird (c) from nest A and bird (m) from nest C were never observed on the fish farm and no commercial carp were found in regurgitates from these birds. Both birds used several different foraging sites and regurgitates from prey loads delivered by both birds showed variations in prey type. Regurgitates from bird (c) sometimes contained only aquatic insect larvae and on other occasions a variety of prey including wild carp, sunperch, frogs and aquatic insects. Regurgitates from bird (m) were more consistent and normally contained aquatic insect larvae and small wild carp; but one prey load was composed entirely of eels.

4.3.5 Changes in diet with chick age.

To test if parents feed different prey types to chicks of different age, I have separated the data from regurgitates taken from chicks of age classes 0-20, 21-30 and greater than 30 days old. Within each age class data have been grouped for statistical analysis (there were insufficient data to allow finer divisions within age classes to be made). Table 4.7 shows the composition of regurgitates taken from chicks of different ages and includes data from Couvin 1984 and Carrelet 1984 and 1985.

No important prey types were fed exclusively to any particular age class, and most of the small changes in diet composition probably result from the relatively small sample sizes in each age class.

To test whether any of the dietary changes between chick age groups were significant, I compared the mean proportion (by weight) of the most important prey types (carp, eels, sunperch and aquatic insects) in regurgitates, between the different age groups. The results, which combine data from within age groups from both colonies, are shown in table 4.8.

TABLE 4.7 Composition of regurgitates taken from different age classes of Grey Heron chicks from the two colonies during the study periods. (+ denotes less than 1%)

Age Class (in days)	0-20			21-30			>30		
	% occ	% wt	% item	% occ	% wt	% item	% occ	% wt	% item
Carp	43	26	17	50	33	17	58	40	38
Eel	48	31	8	39	34	5	41	34	6
Sunperch	21	12	9	20	8	3	17	7	4
Tench	10	8	1	5	5	+	5	2	+
Bream	0	0	0	0	0	0	5	1	+
Rudd / Roach	1	+	+	+	4	+	2	1	+
Mullet	7	5	3	0	0	0	1	+	+
Atherine	7	2	13	11	1	+	6	+	2
Gambusia	7	+	2	9	+	2	13	+	3
Stickleback	5	+	3	7	+	5	2	+	+
Catfish	2	2	+	4	+	+	6	2	+
Pike	0	0	0	2	+	+	2	+	+
Pipefish	0	0	0	7	+	+	2	+	+
Flounder	0	0	0	0	0	0	0	0	0
Aq insect Larvae	43	9	41	51	16	61	50	10	43
Insect imago	7	+	+	7	+	+	6	+	+
Frog	12	+	1	5	+	+	11	1	+
Amphibian Larvae	2	+	+	2	+	2	2	+	+
Crayfish	2	+	+	0	0	0	0	0	0
Crab	0	0	0	0	0	0	2	+	+
Snake	12	3	+	4	+	+	6	+	+
Shrimp	2	+	+	5	+	3	11	+	+
Mammal	0	0	0	2	+	+	2	+	+
Total prey loads	42			56			64		
Total prey No.	609			1390			1251		
Total prey weight	2919 g.			5508 g.			5825 g.		

TABLE 4.8 **Percentage wet weight of different prey types in regurgitates taken from different age classes of chicks during the study periods.**

Age Class in days	0-20	21-30	>30
Carp	10.96 ± 3.32	18.93 ± 4.18	28.76 ± 3.96
Eel	25.30 ± 5.33	20.36 ± 4.34	12.48 ± 3.82
Sunperch	5.62 ± 3.32	1.24 ± 1.19	2.80 ± 1.98
Aq insect Larvae	6.87 ± 3.20	11.14 ± 3.25	5.77 ± 2.23

Note: Data were arcsine transformed for the calculation of mean proportion and standard deviation. Data have been retransformed to show mean proportions in % wet weight ± S.E. rather than in angular degrees.

The were no significant changes in the mean proportion (by weight) of carp, eels or aquatic insect larvae in regurgitates taken from the three different age classes of chicks (Carp; F= 1.942 d.f.= 2,144 p> 0.05 1 way ANOVA: Eel; F = 0.978 d.f= 2,144 p> 0.05 1 way ANOVA: Aquatic insect Larvae; F = 0.620 d.f.= 2,144 p> 0.05 1 way ANOVA). It was not possible to test for differences in the proportion of sunperch in regurgitates taken from chicks of different age classes because the variance in the mean proportion between age classes was significantly different.

4.3.6 Prey size classes fed to chicks of different age.

It is not possible to give an accurate frequency distribution for carp sizes fed to chicks, since many of the larger fish were partially digested. However using only two size classes, small ($\leq$ 5 cms.) and large (> 5 cms.), showed that the majority of carp found in regurgitates from all age classes of chick were less than 5 cms. long (see table 4.9).

However, the four undigested carp weighing over 100 g. (i.e. over 18 cms.) found in regurgitates all came from chicks older than 20 days. The remains of digested carp of all sizes up to 250 g. (i.e up to 24 cms.),however, were found in chicks from all age classes.

TABLE 4.9 Occurence of carp of different size classes in regurgitates from different age classes of chick.

	Age class of chick (in days)		
	0-20	21-30	>31
carp < 5cm.	90	189	387
carp ≥ 5cm.	12	10	25
	n = 102	n = 199	n = 412

TABLE 4.10 Occurence of eels of different size classes in regurgitates from different age classes of chick.

Size Class of Eel	Age class of chick (in days)		
	0-20	21-30	>31
10-15 cm.	15	1	12
16-20 cm.	5	4	4
21-30 cm.	18	13	13
31-40 cm.	7	9	11
41 + cm.	0	3	3
	n = 45	n = 30	n = 43

Table 4.10 shows the occurrence of different size classes of eel in regurgitates from chicks from the three different age classes. The data were compared using a chi^2 table of contingency on data grouped within 2 prey size classes; small eels ($\leq$ 30 cms.) and large eels (> 30 cms.). Data were grouped to ensure that sample sizes were large enough for a chi^2 test.

There was no significant difference in the occurrence of large or small eels in regurgitates from the three different age classes of chick (chi^2 = 0.819 d.f. = 2 $p > 0.05$). These results clearly show that parents were not excluding small prey from their diet as their chicks increased in size.

4.3.7 Re-ingestion of prey: effects of prey size and quantity.

During observations on 118 feeding bouts between parents and chicks at Carrelet in 1985 parents were sometimes observed re-ingesting prey from the regurgitate either during the period that the chicks were feeding from it or after the chicks had finished feeding. Data on hatching and fledging dates were used to calculate the age of the broods involved in 99 of these feeding bouts (see chapter 1 for details on the calculation of chick age). Prey re-ingestion was observed by parents with chicks that ranged from 1 to 47 days old. However, the behaviour was not evenly distributed between broods of all ages. During the 32 feeding bouts observed between parents and chicks of 25 days or younger, parents were observed re-ingesting prey 26 times whereas during the 67 feeding bouts observed between parents and chicks older than 25 days parents were seen re-ingesting prey only 8 times. This difference is significant at the $p < 0.01$ level ($chi^2 = 43.1$ d.f.= 1).

Comparing the size of prey re-ingested by parents with chicks of different age showed that on 24 of the 34 occasions when parents were observed re-ingesting prey, the re-ingested prey were too large for the chicks to eat.
This difference between the frequency of reingestion of prey either too large or small enough for the chicks to eat is significant at the $p< 0.05$ level ($chi^2 = 4.97$ d.f.= 1). Prey were classified as being too large for the chick if the chick was observed being unable to swallow it or if the length of the prey (compared against the parents bill) exceeded the maximum size eaten by chicks of that age class; data on maximum prey size eaten by chicks of different age from Moser (1984).

Parents usually waited until the chicks attempted to eat the prey, but if the prey were obviously too large for the chicks, the parent sometimes re-ingested them immediately. Taken together these observations show that parents tended to re-ingest prey from the nest when they had younger chicks and that the prey that they re-ingested were often too large for the chicks to eat.

On four occasions parents were observed re-presenting prey that chicks had not been able to eat, after a further period of digestion, although it was not possible to see if the chicks then ate the prey. Four different adults were observed breaking up partially digested large prey with their bills, when they were feeding small chicks. The chicks then ate pieces off the nest or from the parents bill.

Further evidence that parents sometimes fed chicks with predigested large prey came from regurgitates taken from two separate broods. On both occasions pieces of the same large fish were found in regurgitates from different chicks on the same nest. This shows that the fish had been predigested into separate pieces before being fed to the chicks. In both cases the chicks were too small to have eaten the intact prey without predigestion by the parent. These observations show that parents were not excluding large prey from their diet when they had small chicks and indicate that predigestion of prey by parents allows chicks to consume large prey that they would not normally be able to eat.

When chicks were small, parents occasionally regurgitated too much food onto the nest. This was observed on three occasions when parents re-ingested prey of a suitable size for their chicks after the chicks had finished eating. Three parents were observed re-ingesting small prey which their chicks could have eaten, whilst the chicks were still feeding and were obviously still hungry. This suggests that parents sometimes regurgitate prey which were not intended for the chicks and it is possible that parents cannot control how much food they regurgitate.

4.4 DISCUSSION.

The observation that parents feed chicks by regurgitating onto the nest has important implications for diet studies on Grey Herons. It means that while foraging, parents do not have to select only prey sizes suitable for their chicks since chicks can leave any prey size classes that they cannot eat (this is considered later in the discussion). It is also possible that chicks could select prey types or size classes from the regurgitate on criteria other than the maximum size that they can eat. For example they could select prey on relative profitability to ensure that they maximise their prey intake rate whilst feeding (this is examined in greater detail in chapter 5) or they could select prey types from the regurgitate to meet some nutritional requirement. Such potential biases may have affected the results from this study, or from other similar studies which examine the diet of a bird species through the prey regurgitated by their chicks.

The diet of the Grey Herons nestlings recorded from the two colonies in this study consisted mainly of carp and eels (see Table 4.1). Carp were more important (% weight) than eels at Carrelet in 1985 whereas eels were more important than carp in regurgitates from Carrelet and Couvin in 1984.

The third most important prey item (by weight) in Couvin in 1984 was sunperch. In Carrelet in both 1984 and 1985 aquatic insect larvae were the third most important prey type and sunperch were the fourth and fifth most common important prey respectively in the two years.

This agrees very well with the diet reported by Moser (1984) for the same parts of the Camargue and confirms that Grey Herons in this part of France are highly specialised, taking mainly carp and eels. However, in the present study, Mullet were very rare whereas they were the third most important prey in Moser's study. In addition aquatic insect larvae (Coleoptera and Odonata) were particularly important dietary components at Carrelet in both 1984 and 1985 whereas they were rare in regurgitates from Couvin in 1984 (see Table 4.1) and in regurgitates taken by Moser. Mosers work was carried out in 1979 and 1980 in colonies situated within a few kilometers of those used in the present study. Mullet are found in brackish and saline water including marshes rivers and the sea, therefore the birds studied by Moser must have been foraging in these types of habitat. Table 4.1 shows an almost total lack of prey from brackish and saline water (except for a few Pipefish and Atherene and a single small Flounder) suggesting that very few of the birds from Carrelet and Couvin were feeding in saline or brackish water. This suggests that the birds in the different studies were foraging in different feeding areas and that the differences in diet reflect spatial differences in foraging site use between the different colonies rather than long term changes in prey availability within the Camargue basin, although this may change from year to year.

Moser never found Catfish in regurgitates although they are very common in the Camargue, and he suggested that adults may avoid taking these prey because of their exceedingly long handling times. The presence of Catfish in the present study indicate that Grey Herons do sometimes take these prey. Field observations on an individually marked breeding bird (bird i, see chapter 1) from Carrelet 1985 (the only bird from which sufficient feeding observations were obtained to determine its diet by this method) which fed in the same feeding area throughout the breeding season showed that approximately 83% (by weight) of its diet were catfish, whereas they occurred only occasionally in the diet of birds feeding elsewhere. This suggests that the availability of catfish may vary considerably between foraging areas in the Camargue.

The differences between the diets measured in the Camargue and those reported for other countries (Moltoni 1936 & 1948, Vasvari 1951 and Owen 1955 see also reviews by Cramp and Simmons 1977 and Hancock and Kushlan 1984) are greater.

Other studies show Herons taking large numbers of fish other than carp although the presence of Eels in different studies is fairly general. This shows that, apart from the general trends towards aquatic prey, the diet of the Grey Heron is fairly catholic and suggests that the diet is probably strongly influenced by the availability of prey in the foraging areas.

Owen (1955) showed that the diet at individual nests and at separate colonies was often different and the results from the current study show very similar trends (see Tables 4.5 & 4.6). The present study also shows that the diet of birds changes as they move between feeding areas. This suggests that, in general, individual birds did not restrict themselves to foraging in a particular habitat type or to catching a limited range of prey species. Grey Herons in the Camargue show a tendency to move between different foraging sites during the breeding season (see chapter 1) in contrast to breeding Herons in other areas which often show extreme area-restricted foraging Marion (1984) and Van Vessem et al. (1984). The diet of individual Herons in the Camargue may therefore vary much more than in other areas of Europe. Although chapter 2 suggests that many of the changes in foraging site by herons may have been the result of changes in prey availability, there may have been other reasons why birds moved between sites and thus experienced a change in diet. For example carp contain thiaminase, an enzyme which destroys vitamin B1 and this is known to cause nutritional problems in some piscivorous animals Kear (1973). It is therefore possible that some birds made foraging site changes when only carp were available at the foraging site they used first.

It was interesting to note that there were no diurnal changes in the occurrence of the most important prey species in the diet (see Tables 4.3 & 4.4) since there were clear diurnal changes in the rate of departure of birds from the colony to the feeding grounds (see chapter 1). Indeed one would expect the availability of different prey types to be affected in different ways by factors such as light and darkness, temperature, oxygen levels within the water column etc. All these factors are known to show quite extreme diurnal changes in different water bodies.

If the diurnal changes in rate of departure from the colony are related to the availability of prey then the observation that the importance of different prey types in the diet does not change with time of day suggests that the availability of all prey types changes in the same way during the day. It is possible that the importance of prey types other than carp, eels, sunperch and aquatic insects, in the diet, does change over the daily period, however there were insufficient data within the current study to test this. It is also possible that daily time period chosen to distinguish between early and late regurgitates (0800) was not sufficiently near dawn to distinguish between regurgitates composed of prey taken entirely at night and those taken entirely during daylight hours, although many of the regurgitates taken before 0800 were taken within 1 hour of dawn. Again there were insufficient data to test this. Future studies should take such factors into account when looking for diurnal changes in diet.

The lack of changes in the proportion of different prey types in regurgitates taken from chicks of different age (see Tables 4.7 & 4.8) strongly suggests that parents were not selecting particular prey species for chicks of different age. It also shows that the chicks of different age were not selecting different prey species or different proportions of different prey types from the parental regurgitate. Similarly the results suggest strongly that neither parents nor chicks excluded small prey from their diet as the chicks got older (see Tables 4.9 & 4.10). The observations on the re-ingestion of large prey from regurgitates presented to small chicks also suggests that the parents of small chicks were not excluding large prey from their diet.

Herons do not possess a crop and food is stored in the oesophagus before entering the stomach for digestion. The presence of parentally digested food in chick regurgitates indicates that parents were regurgitating food from the stomach as well as the oesophagus. Similar observations have been made by Owen (1955) and Marion (1984). Since parents are capable of regurgitating predigested food it is possible that some parents can feed chicks without catching prey that their chicks can handle. This means that parents do not necessarily have to catch small prey for small chicks.

The need to catch small prey was suggested by Gross (1923) for the Night Heron (Nycticorax nycticorax) and Moser (1984) for the Grey Heron. Predigestion of prey does incur a time budget penalty since parents must wait until large prey are sufficiently broken up before feeding the chicks. However, adult Herons have exceedingly efficient digestive systems (Vinokurov 1960) and most fish are completely digested after several hours. Since parents which return to the colony to feed small chicks remain at the nest to guard the brood until relieved by the partner, there is probably ample time to predigest prey without affecting the normal time budget patterns. Parents guard chicks until they are about four weeks old and after this age, chicks would be able to eat most prey without predigestion. Parents normally share guarding but on occasions I observed a bird flying off immediately after regurgitating whilst its partner remained guarding the chicks. On several occasions I observed the bird which remained on the nest, ingesting large prey fed by its partner, and which the chicks could not eat. On two occasions these birds re-regurgitated the partially digested prey for the chicks several hours later. Although this is a form of food stealing and some partners never attempted to re-present the prey to the chicks it also shows that parents can share the work of predigesting prey.

The wide range of prey sizes caught by birds feeding chicks of all ages suggests that at Couvin and Carrelet there were sufficient small prey in regurgitates to satisfy the requirements of young chicks without parents having to predigest prey. However in different feeding areas where there are a limited range of prey size classes available to parents, the predigestion strategy may become more important. There have been many observations that small chicks receive small prey (Milstein _et_ _al_. 1970, Moser 1984 and pers obs). However without data on the availability of different prey types in the environment, which is essential to determine how parents were selecting prey, it is not possible to demonstrate whether these prey were selected especially for the chicks or for other reasons. It is therefore not possible to judge the relative importance of prey selection and pre digestion strategies in parents feeding young chicks. The results do however show that predigestion is an alternative strategy available when parents do not catch suitably sized prey. If the relative importance of these two different strategies is ever to be tested it is essential that the prey selection processes of birds which are not catching food for chicks are fully understood. This would entail the collection of data not just on prey profitability but also accurate data on prey availability at the feeding site. Once established, the prey selection strategies of non-breeding adults could be compared with the prey selection strategies of breeding adults feeding different aged chicks.

Since large prey were being regurgitated for young chicks, but were being re-ingested by parents when the chicks could not eat them, it is possible that the proportions of the different prey types and size classes in prey loads obtained from chicks younger than 30 days (the age at which chicks can eat most prey size classes eaten by their parents, Moser 1984) were not a true reflection of the diet of their parents during this period. The proportions of prey in prey loads taken from broods older than 30 days probably gives the most accurate picture of the adult diet during the whole study. In this study the proportion of important prey items did not change with chick age but this was probably because the majority of important prey such as carp were very small (less than 5 cms.). In different study areas or in different colonies the availability of different size classes of prey may be different and parents might have to switch between different prey species in order to find sufficient small prey to feed their small chicks. Alternatively if insufficient small prey were available parents could switch to a pre-digestion strategy as outlined above.

4.5 SUMMARY

1) The diet in different colonies and from different broods within a colony appears to vary considerably and this probably reflects differences in feeding areas used by parents. However, this does not preclude the possibility that parents specialize in different prey or prefer to forage in different habitat types.

2) Individual parents brought back different prey types when they were foraging in different areas showing that if specialization in prey or habitat types occurs, there is some degree of variability in individual behaviour.

3) Regurgitates taken from older chicks contained some large size classes of prey that were not present in regurgitates from younger chicks. However, there was no evidence that parents excluded small prey from their diet when feeding older chicks.

4) Observations on feeding bouts between parents and chicks revealed that parents feeding young chicks often re-ingested prey that were too large for their chicks to eat. These were sometimes re-presented after a period of digestion by the parent. This indicates that parents were catching large prey even when they were feeding small chicks.

5) Regurgitates from small chicks sometimes contained prey that, had they not been broken up or predigested by the parent, would have been too large for the chicks to eat. The predigestion of large prey items by parents is an alternative strategy to the selection of small prey, that allows parents to feed chicks with size classes of prey that their chicks could not normally eat.

6) There were no marked changes in the range or proportions of different prey species in prey loads fed to chicks at different times of day or to chicks of different age.

CHAPTER 5

PREY SELECTION AND SIBLING COMPETITION: A FORAGING STRATEGY OF NESTLING GREY HERONS

5.1 INTRODUCTION.

The previous chapters dealt with the foraging patterns and foraging decisions of adult breeding Grey Herons. This chapter examines the foraging behaviour and foraging "decisions" of nestling Grey Herons when feeding on the food brought back to the nest by their parents.

The results from chapter 4 show that, when feeding chicks, adult Grey Herons regurgitate a bolus of mixed prey types onto the floor of the nest. The bolus may contain different numbers, species and size classes of prey in various states of digestion (see chapter 4 and also Owen 1955, Moser 1984, Milstein *et al*. 1970). The distribution of these prey items, which are simultaneously presented to all the brood, amongst the chicks is controlled by the individual abilities and behaviour of the chicks themselves. Yet this distribution is instrumental in determining which chicks will survive to leave the nest as fledglings.

Food appears to be a major factor limiting the breeding output of Grey Herons since it is common for some of the brood to die of starvation (Owen 1960, Moser 1984) or during bouts of intersibling aggression. In the Cattle Egret (*Bubulcus ibis*) aggression is caused by a reduction in the rate of food delivery to the nest Fujioka (1985).

Previous studies on the distribution of food amongst siblings of nesting Ardeids have shown that larger chicks have a competitive advantage over smaller chicks in gaining access to the parental regurgitate (Hafner 1978 & 1980, Mock 1984, Moser 1984, Fujioka 1985). The same authors have also shown that this frequently results in the death, by starvation, of smaller brood members. The size differences between Ardeid chicks is caused by asynchronous hatching of the eggs which results from asynchronous egg laying and commencement of incubation before the clutch is complete. Asynchronous hatching is considered to be a parentally-regulated "brood reduction strategy" to maximise the number of chicks fledged when food resources are unpredictable at the time of egg laying (Lack 1947; Owen 1960; Ricklefs 1965; O'Connor 1978; Moser 1984).

The size differences caused by asynchronous hatching govern the individual competitive abilities of chicks to obtain food. If all the chicks on a nest have access to the food delivered by their parents, then the rate of chick growth is dependant on individual prey intake rate. A chick with a foraging strategy which is superior to that of its siblings will grow faster than its nest mates and may thereby improve its competitive ability relative to its siblings. Such a chick would thereby improve its chance of surviving to fledging.

This competitive selection pressure could have led to the evolution of a foraging strategy which enables chicks to maximise their prey intake rate, thus ensuring that they gain the maximum amount of food during each meal. In some circumstances, however, it may not be an advantage for a chick to attempt to maximise its growth rate. If for example the smallest chick in the nest develops a strategy to forage more efficiently than its siblings then it may grow quickly until it is the same size as its nest mates. This would result in all brood members having similar competitive abilities and, if food availability is low at that time, may result in the starvation of the whole brood (O'Connor 1978). If, however, it grows to exceed the size of its nest mates before food becomes limiting it could survive even if the rest of the brood die. The evolution of a strategy to forage more efficiently would not be restricted in this way if it developed (in evolutionary time) before the asynchronous hatching strategy or if it arose in a larger member of the brood.

The "optimal foraging" behaviour required to maximise prey intake rate, when prey are simultaneously encountered by a predator, has been shown by Waddington and Holden 1979 (see also Krebs and McCleery 1984) to be the selection, at each choice, of the prey item which has the highest value of:

$$E/ht+t$$

where E = total energy value of food item.
ht = handling time.
t = travel time to the prey item.

It should be noted that unlike the classical sequential prey encounter models (MacArthur and Pianka 1966, Emlen 1966, Schoener 1971 and Krebs *et al*. 1977) the simultaneous encounter model predicts selection for a particular prey item regardless of the abundance of other prey items of that type or of the abundance of prey items of other types. Under most conditions the simultaneous encounter models also predict partial preferences for different prey types (Waddington and Holden 1979 and Waddington 1982). This is because the travel time to prey must be taken into account when calculating the benefit of eating any particular prey item. Sometimes a small prey item of low profitability (defined as E/ht) may be near enough to the predator to make the value of E/ht+t for that prey greater than E/ht+t for any of the more profitable prey. When this occurs the predator should eat the less profitable prey if it is to maximise its prey intake rate. However when the difference between the t values of all prey are small enough, such that E/ht+t for the less profitable prey is always smaller than E/ht+t for the most profitable prey, partial preferences are not predicted.

A Grey Heron chick "foraging" from a parental regurgitate on the nest will always encounter prey very close together. Since chicks 'travel' to prey using the darting stroke, which is a very rapid movement characteristic of most foraging herons, travel time differences between prey will be very small in comparison to prey handling times. Thus ht will almost be equal to ht+t; this means that the optimal behaviour for a Grey Heron chick selecting prey from a bolus within the nest will be selection for the prey item with the greatest profitability (E/ht). Partial preferences are not predicted.

A chick selecting and removing the most profitable prey from the available food each time it makes a choice will have a higher mean rate of intake (and will obtain more food) than a randomly foraging chick when they are feeding from the same food bolus. The randomly foraging chick sometimes wastes foraging time by eating sub-optimal prey which give it a lower reward rate than if it had chosen the most profitable prey available.

This chapter examines the feeding behaviour of nestling Grey Herons to determine whether they behave in a way that makes them forage more efficiently. The study is based on laboratory experiments which test the predictions of the Waddington and Holden simultaneous prey encounter model. The degree of prey selection made by the chicks is examined at different levels of availability of two prey types in artificial regurgitates and at different degrees of satiation of the birds.

5.2 METHODS

Five broods of Grey Herons, each containing 3 chicks from the same nest, were taken, under licence, from Heronries in the Rhone delta S. France. The broods were taken when the oldest chick in each nest was approximately 7 days old, and were housed on artificial straw nests in the aviary facilities at the Station Biologique de la Tour du valat, Camargue. The chicks were kept warm using infra red lamps until they could thermoregulate efficiently at about 20 days of age. When prey selection experiments were not in progress the chicks were fed to satiation three times a day on a mixture of chopped Eel (Anguilla anguilla), Carp (Cyprinus carpio), Bream (Abramis abramis) and other coarse fish according to availability. The diet was supplemented with vitamin and calcium solutions several times a week.

The captive broods were separated into two groups, broods 1,2 & 3 and broods 4 & 5. Different experiments were carried out on the two groups. These are outlined below:

5.2.1 BROODS 1,2 and 3.

These chicks were tested for their ability to select between two prey types with different profitabilities. The prey presented to each brood were always composed of two size classes of fish pieces large and small (the same species of fish, Bream, was used for both size classes so that both prey types were identical in calorific value and nutrient balance). Pieces of mean weight 9.02 ± 1.36 (S.D.) g. n = 50 (large) and 1.14 ± 0.23 (S.D.) g. n = 50 (small), were used in the experimental regurgitates.

The prey were placed randomly on a small piece of cardboard (approx 10 cm. square) in front of the chicks which were prevented, by means of a screen, from seeing the food until the start of the experiment. Differences in travel time to the prey were measured from video recordings made while the chicks were feeding and were found to be always less than 0.25 secs. These differences for both prey sizes used in the experiments, were small enough for a single optimal solution to be predicted by the Waddington and Holden model, namely selection for the most profitable prey item available.

Video recordings were made of the six chicks from broods two and three to measure the rate of prey intake of each individual bird when they were feeding to satiation on the two different types of prey. The mean prey intake of all the chicks was calculated for each 10 second period until they were satiated. This was to test the basic assumption of the optimality model, that the time taken to handle each prey item is the factor which controls the prey intake rate of each chick.

As birds remove prey from the regurgitate the abundance of the available prey types changes. This makes it difficult to distinguish between changes in selection caused by changes in availability of each prey type, and changes in the state of satiation of the birds. To overcome this problem the birds were presented with small meals, all with the same fixed initial frequencies of the two prey types. The experiment was then repeated until the chicks were satiated. The degree of selection for the most profitable prey type can then be determined within each small meal. By comparing the degree of selection between the different meals it is possible to determine if there are changes in the degree of selection at different stages of satiation.

The prey were presented at fixed initial frequencies of [3L,3S], [3L,6S] and [6L,3S]. Where L= large prey type and S= small prey type. The order in which the two prey types were eaten was recorded by the observer on a portable tape recorder and meal duration was measured with a stopwatch.

Chicks were colour marked with Ciba Geigy acrylic paints on the crown feathers, to facilitate individual recognition during the experiments. Each chick was tested for its ability to select an optimal diet (i) when feeding with another chick and (ii) when it was feeding alone.

The data from all birds were combined to determine the number of the most profitable and least profitable prey that were eaten whilst there were still prey of both types available on the nest. From this it is possible to determine the degree of selection for either prey type. Changes in the degree of selection caused by changes in the availability of prey and the state of satiation of the birds were compared using the chi^2 test.

5.2.2 BROODS 4 & 5

Broods 4 & 5 were tested for the ability to select an optimal diet (as for broods 1,2 & 3), except that they were given prey in a single fixed initial prey ratio [3L,6S], and chicks were tested only when feeding alone. Pieces of eel of mean weight 5.09 ± 0.44 (S.D.) g. and 1.18 ± 0.32 (S.D.) g. (n=72 large, n=48 small) were used as prey in the experimental regurgitates. The profitability of the large prey was then changed by inserting them into slots on a wooden board, the smaller prey were placed between the slots. The handling time of the large prey was therefore extended while that of the small prey remained unaffected. This resulted in a change of the relative profitability of the two prey types.

According to the predictions of the optimality model the chicks should eat the most profitable prey first, and therefore we would expect that before extending the handling time of the large prey, the chicks would eat the large prey before the small prey, but that afterwards they should select the small prey first.

The data from all birds were combined to determine the number of the most profitable and least profitable prey that were eaten whilst there were still prey of both types available on the nest. Changes in the selection for large and small prey, caused by changes in the relative profitability of the two prey types were compared using the chi^2 test.

As a further test to see if the behaviour of the chicks was influenced by prey size, the six chicks from broods 2 and 3 were individually given the choice between six small and a single large piece of fish, just too large for them to eat and of a size class that the chicks had not previously encountered. All prey used in the experiment were from the same species of fish (Bream) and were therefore identical in quality. The time that each chick spent in attempting to eat the large fish while there was still other food on the nest was recorded on tape by an observer. The experiment was repeated until the chicks were satiated.

The whole experiment was then repeated for four further meals. The data for each chick, within each meal, were combined to calculate the mean time spent by chicks on the large prey and the small prey. The mean time spent by the chicks on the different prey types was compared, between different meals, using a t test. Data were transformed using the equation Log(t+1) where t= time spent on large prey, to ensure a normal distribution for analysis using a t test.

5.3 RESULTS.

The results are presented in two sections relating to the different experiments as outlined in the methods.

5.3.1 EXPERIMENTS ON BROODS 1,2 AND 3.

The handling times, by chicks from broods 1,2 & 3, of the two different size classes of prey (large and small pieces of bream) are given in Table 5.1. This shows that the large prey were over 5 times more profitable than the small prey. Thus, according to the Waddington and Holden model the chicks would be expected to eat the large prey before the small prey regardless of the relative proportions of the two size classes of prey in the artificial regurgitate.

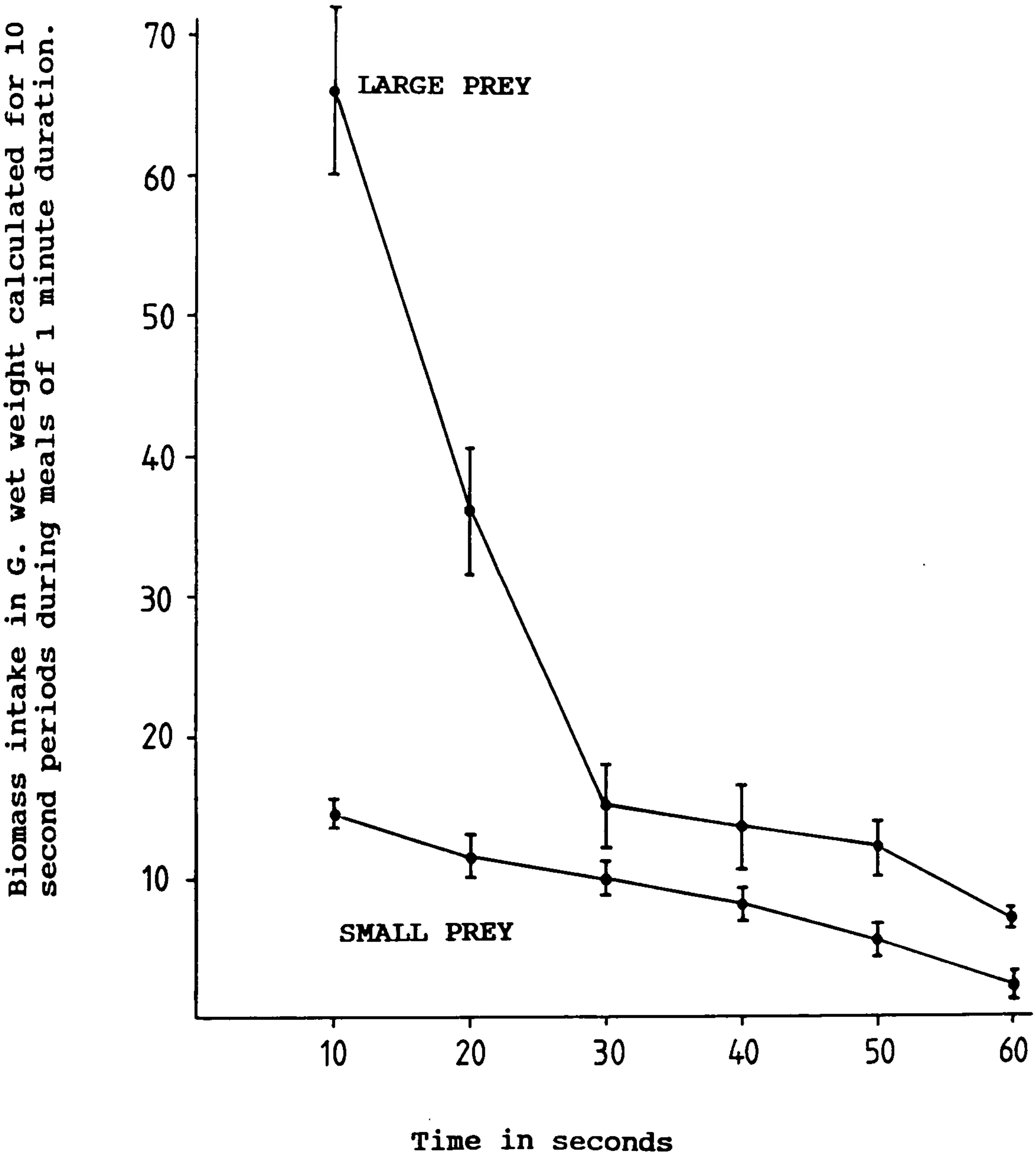
The mean biomass intake of the six chicks from broods 2 & 3, calculated during the first six 10 second periods, whilst feeding to satiation, on large and small prey (at different times) is shown in fig. 5.1. The figure clearly shows that the maximum rates achieved by each chick were very close to the value that would be expected for a prey intake rate limited by the handling time of the prey. Thus, when the chicks were hungry, the basic assumptions of the Waddington

TABLE 5.1 Mean Handling times (in secs. ± S.D.) and Mean Biomass (in g. wet weight ± S.D.) of the two sizes of prey presented to broods 1,2 and 3.

Prey Type	Handling Time		Biomass
Large	1.6 ± 1.12	n = 89	9.02 ± 1.4 g.
Small	1.1 ± 0.40	n = 178	1.14 ± 0.2 g.

Note: The relative profitability [E/ht(L)]/[E/ht(S)] of the prey was 5.44.

FIGURE 5.1 The mean Biomass intake (± S.E.) of chicks consuming large and small prey items whilst feeding to satiation.



and Holden optimality model were fulfilled. However, the figure shows that the intake of prey during subsequent 10 second periods fell. This arises because the chicks begin to pause between prey items as they become satiated. Thus their prey intake rate is affected not only by the handling time (a constraint imposed by the prey) but is also governed by some other factor. This suggests that hungry and partly satiated chicks may select prey in different ways. Since prey intake rate falls with satiation and since prey intake rate is related to the time taken to eat a meal, I have used the time taken to eat each small meal as an indication of the level of satiation of the chicks during the experiments.

5.3.1.i Selection for Prey Type; Chicks Feeding Alone.

The degree of selection made by chicks feeding alone on meals composed of different proportions of large and small prey and at different stages of satiation are shown in table 5.2.

The table clearly shows that when the chicks were presented with prey at an initial frequency of 3 Large and 3 small, they ate significantly more large prey, at all stages of satiation, than would be expected if they were choosing prey at random (meal times 0-10 secs. $Chi^2 = 107.93$ $p< 0.001$

TABLE 5.2 **The number of large (L) and small (S) prey eaten when both prey types were still available in the regurgitate. Chicks feeding alone.**

Initial Prey Availability	Prey Type	meal time (seconds) 0-10	11-20	21-50	>50
3L,3S	L	124***	53***	36**	128**
	S	5	10	12	78
3L,6S	L	-	47***	42***	115***
	S	-	19	21	117
6L,3S	L	-	77***	65**	63ns
	S	-	6	10	20

Note: The >50 secs. category includes all unfinished meals. Data from all chicks in broods 1,2 & 3 have been combined for analysis.

***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$ Chi^2 test for the observed frequency of Large & Small prey in the diet against expected (random) selection based upon relative abundance of prey, d.f.= 1 in all tests Further details are given in the text.

d.f.= 1; meal time 11-20 secs. $Chi^2 = 28.00$ $p < 0.001$ d.f.= 1; meal times 21-50 secs. $Chi^2 = 11.02$ $p < 0.01$ d.f.= 1; meal times >50 secs. $Chi^2 = 11.66$ $p < 0.01$ d.f.= 1).

Similarly at an initial prey presentation frequency of 3 Large prey and 6 Small prey, the chicks ate significantly more large prey, at all stages of satiation, than would be expected if they were choosing prey at random (meal time 11-20 secs. $Chi^2 = 40.93$ $p < 0.001$ d.f.= 1; meal times 21-50 secs. $Chi^2 = 30.02$ $p < 0.001$ d.f.= 1; meal times >50 secs. $Chi^2 = 26.85$ $p < 0.001$ d.f.= 1).

However, when prey were presented at an initial prey frequency of 6 Large and 3 small, the chicks ate significantly more large prey than would be expected from random, only during meals of 50 seconds duration or less (meal time 11-20 secs. $Chi^2 = 24.23$ $p < 0.001$ d.f.= 1; meal times 21-50 secs. $Chi^2 = 12.62$ $p < 0.01$ d.f.= 1). During meals of greater than 50 secs. duration the chicks took large and small prey in proportions not significantly different from random (meal times >50 secs. $Chi^2 = 2.78$ $p > 0.05$ d.f.= 1). This shows that at this initial prey presentation frequency and when the chicks were approaching satiation, they were tending to change from being selective to being non selective.

Comparing between the shortest and longest meal durations, Comparing between the shortest and longest meal durations, at all initial presentation frequencies, shows that there was a significant reduction in selectivity for the Large prey (3L,3S, Chi^2 = 47.43 $p<0.001$ d.f.= 1; 3L,6S Chi^2 = 8.83 $p<0.01$ d.f.= 1; 6L,3S Chi^2 = 7.71 $p< 0.01$ d.f.= 1). This confirms the previous result and shows that at all initial prey presentation frequencies, the chicks they were tending to become less selective as they became satiated.

The degree of selection for Large prey was also affected by the initial presentation frequencies of the two prey types. A comparison between the initial presentation frequencies 3L,6S and 6L,3S shows that at all stages of satiation the birds were significantly more selective for the large prey when the initial presentation frequency of these prey was higher than that of the Small prey (meal time 11-20 secs. Chi^2 = 10.75 $p< 0.01$ d.f.= 1; meal times 21-50 secs. Chi^2 = 6.75 $p< 0.02$ d.f.= 1; meal times >50 secs. Chi^2 = 16.85 $p< 0.01$ d.f.= 1). This contradicts the proposed model which predicts that the selection for the most profitable prey should not be affected by the relative abundance of either prey type.

5.3.1.ii Selection for Prey Type; Chicks Feeding Together

Table 5.3 shows the degree of selection made by chicks feeding with a competitor on meals composed of different proportions of large and small prey and at different stages of satiation.

When chicks were feeding together with a competitor at an initial frequency of 3 Large and 3 small, there was a tendency for the chicks to select larger prey more often than expected. However this trend was significant in only three of the four groups of meal durations (meal times 0-10 secs. $Chi^2 = 38.19$ $p < 0.001$ d.f.= 1; meal time 11-20 secs. $Chi^2 = 21.75$ $p < 0.001$ d.f.= 1; meal times >50 secs. $Chi^2 = 5.98$ $p < 0.02$ d.f.= 1). At meal times of between 21 and 50 secs. there was a similar trend for selection for large prey, however this trend was not significant ($Chi^2 = 3.06$ $p > 0.05$ d.f.= 1).

At an initial prey presentation frequency of 3 Large prey and 6 Small prey, the chicks ate significantly more large prey, at all stages of satiation, than would be expected if they were choosing prey at random (meal time 0-10 secs. $Chi^2 = 25.52$ $p < 0.001$ d.f.= 1; meal times 11-20 secs. $Chi^2 = 33.12$ $p < 0.001$ d.f.= 1; meal times 21-50 secs. $Chi^2 = 19.59$ $p < 0.001$ d.f.= 1; meal times >50 secs. $Chi^2 = 29.26$ $p <$

TABLE 5.3 The number of large (L) and small (S) prey eaten when both prey types were still available in the regurgitate. Chicks feeding together.

Initial Prey Availability	Prey Type	meal time (seconds) 0-10	11-20	21-50	>50
3L,3S	L	102***	67***	12 n.s.	52*
	S	30	22	4	29
3L,6S	L	33***	67***	24***	63***
	S	15	46	10	45
6L,3S	L	48***	60**	17 n.s.	55***
	S	0	9	5	6

Note: The >50 secs. category includes all unfinished meals. Data from all chicks in broods 1,2 & 3 have been combined for analysis.

***= p< 0.001, **= p< 0.01, *= p< 0.05 Ch i2 test for observed frequency of L & S in diet against random expected selection based upon relative abundance of prey, d.f.= 1 in all tests.

0.001 d.f.= 1). There was a similar trend when prey were presented at an initial prey frequency of 6 Large and 3 small, however, the trend was significant only within the first two and the last groups of meal duration (meal time 0-11 secs. p = 0.00002 Fishers exact test; meal times 11-21 secs. Chi^2 = 11.88 $p < 0.001$ d.f.= 1; meal times >50 secs. Chi^2 = 14.11 $p < 0.001$ d.f.= 1). During meals of 21-50 secs. duration the chicks took large and small prey in proportions not significantly different from random (Chi^2 = 0.69 $p > 0.05$ d.f.= 1).

These results are very similar to those obtained when the chicks were feeding alone and show that, regardless of the initial presentation frequency of the two types of prey, the chicks were tending to make a selection for the most profitable prey type.

However, comparing between the shortest and longest meal durations, at all initial presentation frequencies, shows that there was no significant reduction in selectivity for the Large prey (3L,3S, Chi^2 = 3.68 $p > 0.05$ d.f.= 1; 3L,6S Chi^2 = 1.11 $p > 0.05$ d.f.= 1; 6L,3S p = 0.055 fishers exact test). This suggests that, when feeding together, chicks remain selective for the most profitable prey type even when they are approaching satiation.

Comparing the degree of selection for large prey at different initial presentation frequencies of the two prey types (3L,6S and 6L,3S) shows similar trends to those shown by chicks feeding alone. However, this trend was significant for only three of the four groups of meal duration (meal time 0-10 secs. $p = 0.00002$ Fishers Exact test; meal times 11-20 secs. $Chi^2 = 14.26$ $p< 0.001$ d.f.= 1; meal times >50 secs. $Chi^2 = 17.27$ $p< 0.001$ d.f.= 1). The non significant result was associated with a small sample size (meal times 21-50 secs. $Chi^2 = 0.059$ $p> 0.05$ d.f.= 1).

Again these results contradict the predictions of the model and show that when feeding with a competitor, the degree of selection for the most profitable prey type was, to some extent, influenced by the relative abundance of the two prey types.

5.3.1.iii Summary of the results; broods 1, 2 & 3.

The chicks showed significant selection for the most profitable prey type both when feeding alone and when feeding with a competitor. The degree of selection, however, was affected by the state of satiation of the chicks and by the initial presentation frequencies of the prey even when the chicks were hungry.

5.3.2 EXPERIMENTS ON BROODS 4 AND 5.

The results presented in the previous section do not constitute a complete test of the model, because the strong preference for the large (most profitable) prey type could be interpreted as showing that the chicks have a preference for larger prey regardless of the relative profitability of the prey types. To investigate this hypothesis the experiment was repeated with broods 4 and 5. The selectivity of the birds was tested with a fixed profitability for the small prey and two different profitabilities for the large prey. The large prey were the most profitable in the first part of the experiment and the small prey were the most profitable in the second.

The handling times of the two prey types before and after the changes in profitability, are shown in Table 5.4. This shows that, before the handling time of the large prey was changed, large prey were over three and a half times more profitable than small prey and according to the Waddington and Holden model the chicks would be expected to eat the large prey before the small prey,. After the handling time of the large prey had been extended the small prey were over two and a half times more profitable than the large prey and according to the model the chicks would be expected to eat the small prey before the large prey.

TABLE 5.4 Mean handling times (in secs. ± S.D.) of the two prey types presented to broods 4 and 5.

Prey Type	Handling Time Normal	Handling Time Extended
Large	1.12 ± 0.2 n = 79	9.92 ± 7.3 n = 52
Small	0.95 ± 0.2 n = 60	unchanged

Note: Large prey weighed 5.09 ± 0.44 (S.D.) g. and small prey weighed 1.18 ± 0.32 (S.D.) g. The relative profitabilities (prof. Large / prof. small) of the two prey types were 3.66 before and 0.4 after the change in handling time of the large prey.

The degree of selection for the two prey types before and after the changes in relative profitability of the prey were made, are shown for different chicks in table 5.5. Because of the way that the handling time of the large prey was extended, there was considerable inter and intra chick variation in the handling time of these prey. This resulted in large variations in the time taken to eat a meal which, in turn made it impossible to examine changes in selection with satiation. For this reason the results from each chick were analysed separately.

Table 5.5 shows that all chicks took significantly more large prey than expected from a random choice, but only when these prey were the most profitable (chick 1: $Chi^2 = 142.9$ $p<0.001$ d.f.= 1. Chick 2: $Chi^2 = 61.5$ $p<0.001$ d.f.= 1. Chick 3: $Chi^2 = 231.4$ $p<0.001$ d.f.= 1. Chick 4: $Chi^2 = 117.97$ $p<0.001$ d.f.= 1). When the relative profitabilities of the two prey types were reversed so that the small prey became relatively more profitable, three of the chicks (1,3 and 4) took significantly more small prey than expected from a random choice ((chick 1: $Chi^2 = 73.98$ $p<0.001$ d.f.= 1. Chick 3: $Chi^2 = 100.1$ $p<0.001$ d.f.= 1. Chick 4: $Chi^2 = 107.6$ $p<0.001$ d.f.= 1). The other chick (2), however, continued to show significant selectivity for the large prey (chick 2: $Chi^2 = 12.66$ $p<0.001$ d.f.= 1), although it took significantly more small prey in the second part of the

TABLE 5.5 **The number of Large and Small prey eaten by the chicks when both prey types were still available in the regurgitate, before and after changes in the relative profitability of the prey.**

Large Prey Most Profitable

		chick 1	chick 2	chick 3	chick 4
Relative Profitability		6.66	6.54	6.56	5.10
Prey Type	L	129***	83***	147***	137***
	S	38	41	17	58

Small Prey Most Profitable

		chick 1	chick 2	chick 3	chick 4
Relative Profitability		0.60	0.83	0.23	0.16
Prey Type	L	55***	161***	12***	11***
	S	359	222	258	269

Note: Relative profitability is given as E/ht(Large) / E/ht(Small). Prey availability was 3L,6S in all experiments. All meal durations combined except unfinished meals. *** = $p < 0.001$ chi 2 test observed number of L and S prey against random predicted choice. d.f.= 1 in all cases.

experiment than in the first part ($Chi^2 = 22.26$ $p<0.001$ d.f.= 1).

An examination of the exact value of the relative profitability of the two prey types when the small prey were more profitable shows that, for chick 2, the small prey were only slightly more profitable than the large prey in this part of the experiment. If the degree of selection is dependant on the benefit to be derived from selection, as suggested by the results of Werner and Hall (1974), we would expect this chick to show the lowest degree of selection for S prey in the latter part of the experiment. This is in fact the case. However, chick 2 showed significant selection for the less profitable prey instead of the more profitable prey in the second part of the experiment. Therefore although the changes in selection were in the predicted direction chick 2 did not behave as predicted by the model.

5.3.3.i Further experiments on broods 4 and 5.

The mean time that the chicks spent in attempting to eat the large fish while there was still other food on the nest, is shown for the first and subsequent experimental repetitions during 5 different meals in table 5.6.

TABLE 5.6 Mean time spent by the chicks handling prey too large to eat, whilst there was still edible food available on the nest).

	First Presentation.	Other Presentations.
Meal 1.	43.17 ± 12.67 (n=6)	1.20 ± 0.95 (n=20)
Meal 2.	8.67 ± 5.07 (n=6)	0.64 ± 0.34 (n=11)
Meal 3.	13.17 ± 6.71 (n=6)	0.92 ± 0.63 (n=25)
Meal 4.	8.33 ± 3.31 (n=6)	0.27 ± 0.19 (n=11)
Meal 5.	0.20 ± 0.20 (n=5)	0.13 ± 0.13 (n=8)

Note: Mean times are given in seconds ± S.E. The data within the table are untransformed.

A comparison between the first presentations of each meal shows that the chicks spent a significantly longer time attempting to eat the large fish during the first meal than during the second meal ($t=3.194$ d.f=10 $p<0.01$). A similar significant difference occurred between meals 4 and 5 ($t=5.354$ d.f.=9 $p<0.01$) but there were no significant differences between meals 2 & 3 or 3 & 4.

During the first encounter with the large prey (meal 1 presentation 1) the chicks spent significantly longer on the large prey than in any subsequent presentation during the same meal ($t=9.299$ d.f.=24 $p<0.01$). A similarly significant trend occurred within the three subsequent meals ($t=2.523$ d.f.=6 $p<0.05$, $t=3.329$ d.f.=6 $p<0.02$ and $t=5.846$ d.f.=7 $p<0.01$, respectively).

By the last meal the chicks had learnt that the large prey could not be handled and almost completely ignored it in favour of eating the small prey, during all presentations. This behaviour appears to be well adapted to maximising prey intake rate, because a large fish (if it could be eaten) will usually represent the majority of food in the regurgitate. On the first encounter with such a prey the chicks have no evidence that it cannot be eaten and a chick ignoring this prey could make a costly mistake (in terms of losing food to other chicks in the brood) by not attempting to eat it. After previous experience of such prey, however, chicks would do well to ignore them, since by attempting to eat too large a fish they would be wasting valuable foraging time, during which their sibling competitors could eat the rest of the regurgitate.

The results from this experiment show that chicks rapidly learnt the handling time characteristics of the prey with which they were confronted and that they altered their behaviour in such a way that they ate their food in a more efficient manner.

5.4 DISCUSSION

The results presented in this chapter give qualitative support to the "optimal diet" model outlined in the introduction. This shows that it is not only adult birds which tend to follow foraging strategies that may improve their efficiency whilst feeding (see chapter 2). The most likely explanation for such a behaviour, by chicks, is that it has evolved to maximise individual prey intake rate, probably as a result of the selection pressures induced by inter-sibling competition. This is the first time that a prey selection strategy of this type has been shown in chicks, although other studies have shown the role of alternative strategies, such as direct aggression, in the apportionment of the parental regurgitate between sibling nestlings (Mock 1984, Moser 1984, Fujioka 1985).

However, the chicks did not select prey as efficiently as the model predicts. The main departure from the model is that the chicks showed only partial preferences for the most profitable prey type (see Tables 5.2, 5.3 & 5.5). In addition one chick, in the experiment where the relative profitability of the two prey types was reversed, remained selective for the large prey even though their profitability had been changed such that they were less profitable than the small prey (see Table 5.5). Partial preferences which are sometimes predicted by the simultaneous presentation model should not occur with these experiments because, as outlined earlier, the travel time differences between prey were very small. There are, however, several reasons why the birds may have shown only partial preferences for the most profitable prey type. These are outlined below.

The efficiency of selection appeared to be influenced by the internal state of the birds, since partially satiated birds were less selective for optimal prey than hungry birds (see Tables 5.2 & 5.3). A similar decline in prey intake rate for animals approaching satiation was found by Sibly and McFarland 1976 and McCleery 1977. As outlined in the results the decline in prey intake as the chicks were approaching satiation (see Figure 5.1) resulted because the chicks begin to pause between prey items and their prey intake rate was being affected by factors other than the handling time of the prey. Since this contradicts the basic assumptions of the Waddington and Holden model (that prey intake rate is controlled only by the handling time and the travel time to prey), partly satiated chicks would not necessarily be expected to select only the most profitable prey type.

This, however, does not explain the observation that hungry chicks (those which eat the meal in the shortest time) showed partial preference for prey at all presentation frequencies (except 6L,3S, chicks feeding together see table 5.3). It was not possible to starve the chicks for periods longer than 12 hours because extended periods of starvation induced intersibling aggression, which on two occasions resulted in the near death of smaller chicks. It is possible that with longer periods of starvation the degree of selection shown for the more profitable prey type, during the shortest meal times, may increase.

Discrimination errors may also account for partial preferences and such errors may account for the unexpected result that the degree of selection was influenced by prey availability. If the birds were making discrimination errors between prey one would expect that as the availability of one prey type increases the birds would take that prey at greater frequencies than when its availability was lower. The increase in the number of less profitable prey taken as their availability was increased (see tables 5.2 & 5.3) supports this hypothesis. Rechten et al. 1983 have shown that discrimination errors were at least partly responsible for the partial preferences made by the Great tits (Parus major) in the optimal foraging experiments of Krebs et al. 1977.

In addition to discrimination errors partial preferences may also occur for a variety of other reasons. Snyderman (1983) found that experience was an important factor which influenced the degree of selectivity shown by pigeons. The results from the additional experiments on broods 4 & 5 suggest that the birds require a certain time period to learn the handling time characteristics of the prey. This may explain some of the partial preferences shown in the earlier experiments, since results from relatively naive and experienced birds were combined within experiments to give sufficient data for analysis.

Other factors such as some reluctance of the birds to accept that smaller prey are of the same nutrient quality as larger prey (Pyke 1984) may also account for partial preferences. A final consideration in the explanation of the partial preferences shown by the birds is their age. The chicks were only between 10 and 30 days old and although no attempt was made to explore the development of prey selection behaviour with age it is very likely that younger birds are less efficient in prey selection than older ones. This is because motor and perception skills can change rapidly in young birds (O'Connor 1984).

As outlined earlier, the reduction in prey intake rate with satiation (see FIgure 5.1) shows that handling time constraints are not the only factor which governs the prey intake rate of the chicks. It is possible that a digestive bottleneck similar to those found in humming birds (Diamond _et_ _al_. 1986) was responsible for the chicks pausing between prey as they became satiated. Alternatively the motivational state of chicks approaching satiation may change, for example they might divert time and energy normally spent on feeding, into other activities (Sibly and McFarland 1976). The greater degree of selection for the more profitable prey type shown by birds feeding with a competitor (compared with birds feeding alone) supports the hypothesis that motivational state affects feeding behaviour.

Grey Heron chicks are involved in very few activities on the nest at this age and most of their time is spent either feeding or resting (pers obs). However predator avoidance may be an important factor which competes with feeding efficiency in determining feeding behaviour. It is possible that as they approach satiation, chicks switch from concentrating on prey type to more vigilant behaviour to detect potential predators. Marsh Harriers (_Circus aeruginosus_) the most common predator of Heron chicks in the Camargue, never attack whilst an adult Heron is present, but during some feeding bouts parents leave the nest immediately after regurgitation even during the chick guarding period. Although most young Heron chicks are unable to leave the nest, they often attempt to avoid detection by crouching low or deter predators with displays of aggression. This may result in differential survival of hungry and satiated chicks during a predator attack and may explain the changes in chick behaviour with satiation. It should be possible to test this hypothesis by examining the reactions of hungry and satiated chicks to a model predator whilst they are feeding.

The current study concentrated on the ability of chicks to select between types of different profitability in terms of energy intake rate. However, it is possible that, in the wild, chicks may also select prey on criteria other than relative profitability. For example chicks could select prey on nutrient quality. Diet selection based on nutrient quality has been shown in Moose by Belovsky (1978). Similarly adult birds have been shown to change the diet of their nestlings in a response to the changing nutrient requirements of the chicks (Yom-Tov 1975).

Optimal diet selection by Heron chicks may, when it first appeared in the species, have been an important factor in determining individual survival of nestlings. However, once all members of the population behave in the same way the behaviour will confer no relative advantage to any chick although the behaviour must be maintained because of the disadvantages of not being selective when other nest members are. It is also possible that by selecting between prey types in the nest chicks learn "optimal foraging" behaviours that allow them to forage more successfully once they have fledged and start catching prey for themselves.

5.5 SUMMARY

1) Grey Heron chicks were tested on their ability to select between two prey types, large and small, which differed only in their relative profitabilities. In the first experiments the large prey were the more profitable. When they were hungry the rate of biomass intake of the chicks was controlled by the handling time of the prey. However, when the chicks were approaching satiation their biomass intake rate fell. Thus, factors other than the handling time of the prey, must have also been affecting the biomass intake rate of partly satiated chicks.

2) When feeding alone and at most initial presentation frequencies of the two prey types, the chicks showed a significant selection for the more profitable prey type.

3) As the chicks approached satiation they became less selective for the most profitable prey.

4) The degree of selection for the more profitable prey type was dependant on the initial presentation frequency of the two prey types. This contradicts the proposed optimal diet model which predicts selection for the more profitable prey regardless of the relative proportions of the prey types.

5) When feeding together with a competitor, the trends for prey selection were very similar to those shown by the chicks feeding alone. However, the chicks tended to remain selective for the more profitable prey even as they approached satiation.

6) In an experiment where the relative profitabilities of the two prey types was reversed, three of the four chicks tested, reversed their selection for the two prey types as predicted by the model. The other chick, however, did not reverse its selection and took the less profitable prey after their relative profitabilities had been reversed. This may have been because, for this chick, the change in relative profitabilities of the two prey types was relatively small.

7) When the chicks were presented with a prey type which was just too large for them to eat they soon learnt to ignore this prey in favour of consuming more profitable prey.

8) The results support the optimal diet model and show that Grey Heron chicks tend to consume prey that maximise their biomass intake rate when foraging. This behaviour may be a response to competition, from siblings, for food.

CHAPTER 6 GENERAL DISCUSSION

THE FORAGING ECOLOGY OF THE GREY HERON: IMPLICATIONS FOR THE SUCCESS AND CONSERVATION OF THE SPECIES.

6.1 INTRODUCTION

The first pair of Grey Herons were recorded breeding in the Camargue in 1965 by Blondel (1965). Since then its numbers have risen, more or less steadily and in 1989 the breeding population stood at 1122 pairs. The population is still being reinforced by the southern migration of northern european birds particularly from Germany and Switzerland. This suggests that the habitats within the Camargue have not reached their carrying capacity for this species and that its numbers may continue to rise over the next few years. There is no doubt that, in addition to other factors such as the abundance of suitable nesting habitat, the success of the Grey Heron in the Camargue is partly due to the abundance of suitable food and feeding sites both for over-wintering and breeding birds. Nevertheless, some of the wintering birds return to northern Europe to breed.

The material presented in earlier chapters addressed specific issues and hypotheses related to the foraging patterns, feeding behaviour and diet of Grey Herons in the Camargue. This discussion chapter focuses on some broader issues and in particular examines how food and foraging behaviour may influence the success and survival of herons at different stages of their life cycle. Such factors will ultimately control the ability of the species to successfully colonise new habitats such as the Camargue. I conclude the chapter by discussing the implications of some of these factors for the conservation of the species throughout its range.

Although the issues within this chapter are discussed in relation to the Grey Heron they may also be of relevance to other heron species and, to some extent, other large species of colonial waterbird.

6.2 The influence of food and foraging behaviour on the success and survival of Grey Herons

Lack (1950) suggested that the time of hatching in bird species was timed to coincide with the period when their food was most abundant. Owen (1955) confirmed this for the Grey Heron and showed that the breeding success of the species was related to the availability of food since, when food was short, it was common for some of the brood to die of starvation. He also showed that, through asynchronous hatching, the youngest and smaller chicks, rather than the whole of the brood, died at times of food shortage (Owen 1960). However, in addition to the amount of food available to the birds other factors, such as the size and even species of prey, may also affect the success and survival of individuals at all stages of their life cycle.

In chapter 4, I discussed prey size constraints and showed that parents sometimes caught prey that were too large for their chicks to eat. This was also shown by Moser (1984). I also showed that parents sometimes avoided the problems of catching prey too large for their chicks, by pre-digesting large prey and feeding them to their chicks in small pieces. However, there is a time penalty incurred in pre-digesting prey which, if all the prey brought back to the nest had to be pre-digested, could create a "bottle neck" in the normal time budgets such that parents were spending time pre-digesting large prey rather than catching additional smaller food items for their brood. In these circumstances the delivery rate of food to the brood would be reduced and some of the brood could die, either directly through starvation or indirectly from inter-sibling aggression.

In the Camargue such a problem would be unlikely to occur because of the wide range of prey size classes brought back to the nest. However, in other areas this may not be the case. The breeding success of Arctic terns (<u>Sterna paradisea</u>) and indeed many other sea birds, in the north of Scotland, has fallen dramatically in recent years, primarily because of changes in food availability associated with commercial fishing of the Sand-eels (Ammodytes spp.) their principle prey (Avery & Green 1989). The reduction in the availability of prey seems to have resulted from the disappearance of the 0-group fish (first year fish), which ultimately caused a crash in the whole sand eel population. In some areas Arctic tern chicks were observed dying of starvation because their parents could catch only 1-group fish (fish in the second year after hatching) which were too large for the chicks to eat (Utley pers. com.).

Although terns are unable to predigest prey for their chicks (they carry food in their bills not in the oesophagus or stomach), the case of the Arctic Tern shows how important it is for some species to catch prey of certain size classes for their young. It is possible that, if small sized prey were completely absent from the herons diet, Grey Heron parents might not be able to pre-digest large prey at a rate sufficient to satisfy the food demands of their brood and chick deaths could result.

Another way in which prey size can affect the survival of chicks is through inter-sibling competition. Mock (1984) proposed that siblicidal aggression is facultative, with prey size (specifically, its "monopolisability") serving as a key proximate cause. In an experiment involving cross-fostering between two different species of Heron, Mock provided some evidence to support his hypothesis. If prey size and monopolisability elicit sibling aggression, when small defendable prey are fed to chicks, aggression may result in the death of smaller brood members. When large, non-defendable prey are fed to chicks siblicidal aggression may not occur.

In chapters 3 and 4, I suggested that factors such as the nutrient quality of prey may also affect the survival of the birds. Kluyver (1933) found that starling (Sturnus vulgaris) chicks fed only on larval leatherjackets (Tipula paludosa) produced watery faecal sacs which burst before the parents could remove them. The chicks became fouled and wet and could not thermoregulate properly. Kluyver concluded that chicks fed on Leatherjackets suffered higher mortality than chicks fed on other prey. Herons do not normally eat Leatherjackets, however, an important species within their diet is Carp, which is known to contain an enzyme which can cause vitamin deficiencies in piscivorous animals (see chapter 4). It therefore possible that, in some areas, where the diversity of prey is low, the species of prey caught by Herons may affect their own chances of survival or, more likely, in the breeding season that of their chicks.

There is therefore evidence to suggest that, in addition to the availability of prey, factors such as prey type (specifically prey species and prey size classes) could affect the survival of both adults and chicks. Thus the breeding success of herons in different areas could, to some extent, be dependant on prey type rather than the quantity of food that the birds can catch.

The ability of herons to locate and exploit food resources can also affect their success and survival. In chapter three Some of the evidence that I presented suggests that both fledglings and adults use the breeding colony as an information centre for the location of unpredictable food resources. The evidence also suggests that the information centre function of the colony may vary with the rate of departures to the feeding grounds. This supports the Scott Forbes hypothesis which suggests that when the numbers of departures from the colony are low, the time penalties incurred by potential followers may be sufficient for them to stop using the colony as an information centre. Scott Forbes suggested that because of this, small colonies could not function as information centres.

In areas where breeding colonies are small, for example where nesting sites are limited, or where colonisation of the area has just begun, the ability of both adults and fledglings to use the colony as an information centre will be reduced. This could severely effect the ability of birds to locate food within unpredictable environments and could result in reduced survival and breeding success. I have insufficient information to test whether breeding success in Camargue Grey Heron colonies varied with colony size or age. However, in an area where there are few other colony members, competition between individuals for food, once the feeding area has been located, is likely to be low. Thus individuals may achieve a higher foraging success which, in some cases, could compensate for the reduced ability to locate food patches.

The size of the local heron population may also affect the success of fledglings in a different way. Fledglings are less efficient than adults in their foraging skills (Recher & Recher 1968) and there is evidence that birds learn such skills, and sometimes the location of foraging sites, by social observation on the foraging grounds (Kushlan 1981). In areas where the local populations of herons are small, fledglings may be severely disadvantaged and may take longer to acquire both foraging skills and information about their foraging environment. This would reduce their rate of food intake and could reduce their post fledgling survival.

Another way that the size of the local heron population could affect the survival of herons is through competition on the feeding grounds. In Chapter 1, I provided some evidence that suggested that in the Camargue Grey Herons show a range of social foraging strategies from permanent territoriality to flock foraging. However, regardless of the type of social foraging strategy shown by the birds, the interactions between individuals may reduce their foraging success and possibly their survival. Where individual birds hold exclusive feeding territories the foraging success of competitors may be reduced since they cannot gain access to the food patches defended by the territory owner. In areas where birds feed in flocks interference between individuals may depress the foraging success of flock members. When the population is well below the carrying capacity (in terms of feeding habitat) for that species, the effects of competition between territory holders and flock members, on the foraging success of individuals is likely to be small and most individuals would be expected to forage successfully and to raise chicks. However, if the population was close to the carrying capacity of the habitat for that species the effects of competition between individuals would be expected to be much greater. At this stage the individual competitive abilities of the birds would be expected to determine which individuals had access to the best territories or which could dominate within the flock and only the competitively superior individuals would be expected to forage successfully and raise chicks. Competitively inferior birds might be unable to breed or may have to leave the area to breed elsewhere.

Outside the breeding season factors such as the local population size may be expected to affect the foraging success of individuals in much the same way as it does during the breeding season. However, when they are not breeding, herons do not have to focus their attention within easy foraging range of the breeding colony. They are therefore free to move to areas where their foraging success may be higher. There are considerable differences in the patterns of movement amongst camargue Grey Herons in winter. One bird from the Carrelet colony in 1984 occupied the same feeding territory that it had used throughout the breeding season, during the following winter and again at the start of the next breeding season. In contrast another bird from a nearby colony was found in Senegal West Africa the winter after it had been ringed in the Camargue. Such differences in the extent of movement between summer and winter feeding areas are observed in Grey Heron populations throughout Europe (Hancock and Kushlan 1984). The choice of over-wintering strategy by an individual may be dependant on factors such as body condition, competitive ability, severity of the climate and local food availability. There may also be a genetic component in such behaviours.

The advantages of staying near the breeding colony throughout the winter may be considerable. For instance individuals may obtain familiarity with feeding sites such that they can exploit patches more efficiently and have a greater breeding success the following breeding season. Over-wintering near the colony may also allow individuals to start breeding earlier than migratory birds and may also give them the first choice of nest sites and of mates. Conversely migrating before the winter may help individuals avoid competition on the feeding grounds and to avoid harsh weather conditions. It is possible that, in areas where winters are mild, food is abundant and where there is little competition between birds, that most of the population overwinters in the vicinity of the breeding colony. Whereas in areas where winters are severe, prey populations are low and where competition between individuals is high, many individuals may migrate.

6.3 The feeding ecology of the Grey Heron; Implications for the conservation of the species.

Over much of its range the Grey heron is not endangered, but severe winters and to some extent persecution by fish farmers have reduced the population in some areas (Hancock and Kushlan 1984). Hancock and Kushlan consider that, in Britain, breeding stocks of the species are under pressure and could be threatened if pollution, climatic factors and persecution by fish farmers combine to reduce the population further. Many of the factors discussed in this thesis have important implications for the conservation of the species.

The relationship between the abundance of appropriate food and the size of Grey Heron populations is well known and it is obviously important that, if the species is to be conserved, the prey populations are managed. The management of prey populations should ensure that there is an abundance of prey, particularly species such as Carp, Eels, Sunperch and aquatic insects, in areas suitable for the birds to feed in, at all times of year and especially during the breeding season. This could be achieved through habitat manipulation, the artificial introduction of suitable prey or the removal or control of potential predators of important prey species.

However, it may not always be sufficient to ensure that there is an abundance of prey for the birds to feed on. As outlined in this discussion both the size and species of prey within the feeding grounds may have important implications for the survival of the birds. At present we do not know for certain if a diet consisting entirely of Carp, or indeed any other single prey species, could adversely affect the success or survival of individuals. Nor do we know if parents can feed their small chicks exclusively on a diet of pre-digested large prey. However, these may be important factors controlling the survival of populations in some areas. If such factors are important, then it will be necessary to manage the prey populations within potential conservation areas to ensure that there is a diversity of prey in terms of both species and prey size. Such management could include the monitoring of prey populations, the management of habitats to ensure that a diversity of prey species can thrive and possibly even the controlled introduction of new prey species.

A programme of further research is necessary to determine just how important such factors are. This could include the captive rearing of chicks to determine how diets composed of different prey types affect chick survival and growth rates. Further observations on colonies or even on captive families (including parents) will also be necessary to determine whether parents can successfully feed their chicks on pre-digested large prey without suffering time budget problems. If these factors are identified as potential problems, then additional research will be required on the prey populations to see how they can be successfully managed to increase their abundance and diversity.

Additional research should be carried out on the diet and feeding behaviour of newly fledged chicks. It is probably just after fledging that many individuals begin to experience problems through being unable to find enough food. If the diet of fledglings can be identified then it may be possible to determine which prey species are easiest for them to catch. Such species could then be encouraged in habitats near to the breeding colonies to give fledglings a better food supply thus improving their foraging success and their post fledging survival.

In unpredictable feeding areas it is likely that, where the populations of birds are small, birds may have difficulty in locating good patches to feed in. To overcome this problem efforts could be made to attract birds to good feeding areas with the use of lures or models. Herons are known to be attracted to such lures and attracting them to good feeding areas may increase their foraging success sufficiently to ensure their survival or improve their breeding success.

Alternatively, measures could be undertaken to improve the stability and predictability of food patches. This could include management of habitats to increase or stabilise prey populations.

Once a Heron population has expanded individuals could use the breeding colony as an information centre or they might locate good feeding areas through social facilitation. At such a time measures, to stabilise the predictability of the habitat or to attract birds to good feeding areas, may not be necessary.

In the Camargue, many feeding areas are temporary and although these appear to provide good feeding conditions the management of such habitats is important if a diversity of prey is to be encouraged. In particular, many temporary marshes dry out completely during the summer and unless they are re-connected to permanent water bodies containing stocks of fish, the populations of permanently aquatic prey could be lost completely. Management of such habitats could include the creation of permanent water reservoirs within the temporary marsh, to provide a refuge for fish and other permanently aquatic prey when the rest of the marsh dries out. Alternatively the connecting together of permanent and temporary water bodies would ensure that, once the temporary marsh has re-filled with water, the prey populations could move back in.

In conclusion, to ensure the conservation of the Grey Heron, throughout its range, further detailed research is needed on specific aspects of its feeding ecology. This includes further research on the dietary requirements of the species especially of chicks and fledglings and further research into the management and manipulation of prey populations. Unless this is carried out the conservation of Grey Heron populations in some areas may be difficult or impossible to achieve.

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Appendix 1 Latin names of prey items in the diet of Grey Herons in the Camargue.

Fish.

- Carp (*cyprinus carpio*)
- Eel (*Anguilla anguilla*)
- Sun Perch (*Lepomis gibbosus*)
- Tench (*Tinca tinca*)
- Bream (*Blicca bjoerkna*)
- Rudd (*Scardinius erythropthalmus*)
- Roach (*Rutilus rutilus*)
- Mullet (*Mugil sp.*)
- Atherine (*Atherina* sp.)
- Gambuzia (*Gambusia affinis*)
- Stickleback (*Gasterosteus aculeatus*)
- Catfish (*Ictalurus nebulosus*)
- Pike (*Esox lucius*)
- Flounder (*Flesus flesus*)
- Pipe fish (*Sygnathus abaster*).

Insects.

- Aquatic insect larvae (Coleoptera and Odonata)
- Adult Insects (Odonata + Mole cricket)

Amphibians.

- Frog (*Rana* sp.)
- Amphibian larvae (*Rana* sp.)

Crustaceans.

- Crab (*carcinus* sp.)
- Crayfish (*Cambaris affinis*)
- Shrimp (*Crangon* & *Palaeomon*)

Reptiles.

- Snake (*Natrix* sp.)

Mammals.

- Shrew (*Sorex* sp.)
- Brown Rat (*Rattus rattus*)