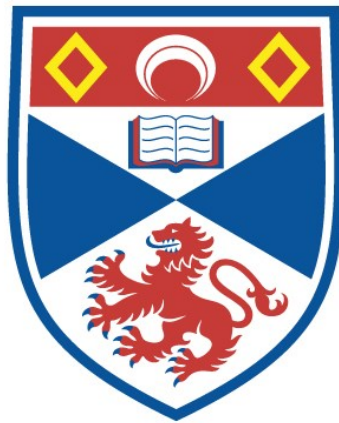


REPRODUCTIVE BEHAVIOUR IN A SMALL INLAND  
COLONY OF BLACK-HEADED GULLS (LARUS  
RIDIBUNDUS)

Fiona M. McCulloch

A Thesis Submitted for the Degree of PhD  
at the  
University of St Andrews



1990

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Reproductive behaviour in a small inland colony  
of black-headed gulls (*Larus ridibundus*).

by

Fiona M McCulloch

Department of Psychology

University of St Andrews

A thesis submitted for the degree of Doctor of Philosophy

1988.





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Dr A Whiten

Dept. of Psychology.

### Declaration

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## ABSTRACT

This study was carried out over three breeding seasons at a small marsh-nesting black-headed gull (*Larus ridibundus*) colony. Two of the years proved to be atypically hot and dry, resulting in the drying out of parts of the colony. This facilitated predation by foxes and resulted in almost complete breeding failure in these two years. Synchronisation of breeding was evident but the average clutch size was smaller than generally recorded for black-headed gulls. There was a tendency for third laid eggs and third hatched chicks to have the highest mortality rate, and third hatched chicks put on less weight during their first three days of life than all other chicks. Pairs of gulls that did not successfully retain their territories and lay eggs spent less time on the territory than those that were successful. The unsuccessful males were also more restless and more aggressive than successful males. In general, the gulls spent most time on the territory during the incubation stage, although partners spent the most time together on the territory during the pre-egg stage. The territory was never left unattended during the incubation stage, but it was occasionally deserted during the pre-egg stage, and increasingly deserted as the chick stage proceeded. In one year, but not another, males spent most time on the territory and incubating during the egg stage, while females spent most time on the territory and brooding during the chick stage. The gulls were most aggressive during the pre-egg stage and least aggressive during the incubation stage, and the males played the greater role in defence during the pre-egg and egg stages. The sexes shared equally the feeding of the chicks and became less eager to feed the chicks as they grew. The number of feeds given per hour per chick decreased with increasing brood size.

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## CHAPTER 1 - INTRODUCTION

The original aim of this project was to make a study of a colony of approximately 250 breeding pairs of black-headed gulls, obtaining measures of breeding success over three years and examining how differences in some of the behavioural patterns of breeding gulls effected their subsequent breeding success. As with many field oriented projects, however, Mother Nature had other ideas, and in two of the three years of the study, atypical weather conditions resulted indirectly in almost total breeding failure of the colony. Therefore, in these two years it was impossible to try to relate differences in the behaviour of the gulls to their breeding success, and there were not sufficient data available from the only successful year to do so either. However, the unusually dry weather produced marked changes in the vegetation of the myre on which the colony was situated, and on the levels of predation of eggs and chicks, and so provided insight into the effects of these on the breeding behaviour of the gulls.

Kruuk (1964) conducted a very thorough investigation into the behaviour of many different predators on a black-headed gull colony, and into the effectiveness of the gulls' antipredator behaviour against them. So, although all the instances of predation observed in the colony were recorded, no attempt was made to examine the predator and anti-predator behaviour in very great detail. However, the dry weather mediated a marked increase in predation in the colony, and the effects of this on the breeding success, and on the gulls' behaviour, were studied closely.

Several studies have examined the breeding biology of black-headed gulls and given a general account of some of their behavioural patterns during the breeding season (Kirkman 1937; Goodbody 1955; Moynihan 1955; Ytreberg 1956). A considerable amount of work has been done to examine egg-shell recognition and the removal of egg shells from the nest after the chicks have hatched (Kruuk et al 1962; Tinbergen et al 1962a; Tinbergen et al 1962b). A lot of information is also available on the egg-laying, nest-building and aspects of the incubation behaviour of black-headed gulls (Moynihan 1953; Weidman 1956; Ytreberg 1956; Beer 1961, 1962, 1963a, 1963b, 1966; Patterson 1965; Burger 1976; Pourtois 1977). However, little work has been done to investigate several other aspects of the breeding behaviour of

black-headed gulls, namely; how much time they spend on the territory at different times of the season; how they chase off intruders on their territories and how this changes with the reproductive stage; and how they interact with their offspring at feeding times. Therefore, I set out to conduct a descriptive analysis of these behavioural patterns, paying particular attention to the division of labour between the sexes, to changes in the behaviour between different stages of reproduction, and to differences in the behaviour of parents with different sized broods and different aged chicks where appropriate.

Synchronisation in the timing of breeding has been reported in many colonial nesting gulls (Darling 1938; Paynter 1949; Ytreberg 1956; Patterson 1965; Parsons 1971, 1975, 1976; Burger 1974; Fetterolf 1984). Regular visits were made to a study area containing up to 100 nests, to record the laying and hatching dates of all the eggs, in order to measure the breeding success of the gulls. A record was also kept throughout the breeding season of the numbers of gulls, and their activities, in various parts of the colony to give a general picture of the ways in which the gulls were spending their time in the colony at different times of the breeding season. These records were also used to check on the levels of synchronisation of breeding in the colony for reference to the results found throughout the study.

Several studies on herring gulls (*Larus argentatus*) have reported a lower hatching success for 2-egg clutches than 3-egg clutches (Paynter 1949; Brown 1967; Kadlec et al 1969). The hatching success of all the breeding pairs on the study area was one of the measures taken to show the breeding success of the gulls and as all instances of egg and chick mortality, and the reasons for them (where known) were recorded it was hoped that this information might reveal the reason for such a reduced hatching success.

The third laid egg in many gull species is smaller than the first two and produces a lighter weight chick (Coulson 1963; Parsons 1970, 1972, 1975; Graves et al 1984). Many studies have reported that chicks hatching from these smaller third laid eggs have a higher mortality rate than those hatching from first or second laid eggs (Parsons 1970, 1971, 1975; Nisbet 1973; Graves et al 1984) and although several theories have been produced to account for the presence of a third egg, it is commonly assumed that it

is there to take advantage of a fluctuating food supply when it is plentiful, and when it is not the smaller third chick is simply starved (Lack 1954, 1968; Ricklefs 1965; Howe 1976, 1978; O'Connor 1978; Mock & Parker 1986). To investigate whether or not this third-chick mortality could be due to starvation the hatching and fledging success, not only of each clutch, but of each individual egg on the study area and the reasons for any mortality were recorded. Most of the third-chick mortality has been reported to occur during the first few days of life (Parsons 1971; Langham 1972; Graves et al 1984; Fujioka 1985) so all the chicks on the study area were weighed during their first week of life, where possible, so that the growth rates of the different hatch-position chicks could be compared.

The time that breeding gulls spend on the territory, incubating and brooding, how they react towards intruders on their territories, and how they interact with their offspring while feeding them have not been investigated in very great detail in black-headed gulls. In this study a further aim was thus to describe these behavioural patterns and any changes occurring in them throughout the gulls' breeding season.

Manley (1960) made a study of the swoop-and-soar defensive behaviour of black-headed gulls, and Huxley & Fisher (1940) and Hutson (1977) investigated some aspects of their agonistic display. Here, however, an attempt was made to describe in detail how the aggressive behaviour of breeding black-headed gulls varied with the stage of reproduction, and the type of intruder on their territory, paying particular attention to any differences between the sexes. There are several factors which could effect the reaction of a territory holder towards an intruder and it is expected that such aggression will vary depending on the threat that the individual intruder poses at that time.

Many studies have been done on the pecking behaviour of black-headed gull chicks at their parents bills to induce them to regurgitate (Weidmann & Weidmann 1958; Weidmann 1961; Dawkins & Impekoven 1969; Impekoven 1969). However, little material is available about the actual feeding of the chicks. Therefore, the aim here was to describe the behaviour of the parents after the chicks began begging, looking for any differences between the sexes and between parents with different brood sizes

and different aged chicks, as well as to examine the level of begging required from different brood sizes and different aged chicks to induce the parents to feed them. It had been hoped that it would be possible to show whether or not the third chicks were given less food than their older siblings to investigate the theory that starvation of third chicks results in their decreased survival compared to first and second hatched chicks. However, there were insufficient data available from 3-chick broods to do this and an examination was only possible of the total number of feeds given to different sized broods. As the chicks grew a conflict was predicted between the amount of care the chicks 'wanted' from the adults and the amount of care the adults were prepared to give the chicks (Trivers 1974), and any evidence for this was examined in the analysis of the data for different age groups of chicks.

Colonial seabirds make excellent study subjects because of their tendency to breed in large numbers at traditional sites where the number of environmental variables is small. The majority of studies on such colonies have been concerned with the larger gulls and so it is hoped that this study will provide an insight into some aspects of the breeding behaviour of one of the smallest European breeding gulls, the black-headed gull.

## CHAPTER 2 - THE BLACK-HEADED GULL

The black-headed gull is the smallest common breeding gull of Europe (Plate 1) with an average length of 35-38cm. In summer plumage it sports a chocolate-brown hood and can also be identified by the broad white leading edge of the wing, a slender red bill and red legs. In winter plumage the head is white with a dark patch in the ear coverts.

The black-headed gull has made a spectacular increase in numbers in Europe, during the twentieth century (Hayman & Burton 1978; Harris 1970) due mainly to a rapid adaptation to the changes brought about by Man. The black-headed gull is well known for its behaviour of following the ploughs but it also benefits from rubbish dumps, park lakes, playing fields and suburban gardens, picking up rubbish and foraging for soil invertebrates.

Black-headed gulls nest in colonies, sometimes of several thousand pairs. Breeding sites include marshes, dunes, shingle, islands in lakes, sewage farms and gravel pits. They frequently nest near the sea but often colonies are far inland. Nests are roughly built of any available vegetable matter and on marshy sites some nests are built on floating structures among vegetation.

Reproduction occurs from mid-April. Normally three eggs are laid, although frequently only two. Eggs range from light buff to deep umber brown (and occasionally turquoise), spotted and blotched with dark blackish-brown and purple marks. Both sexes incubate the eggs for 22-28 days and both sexes care for the young, which fledge at five to six weeks of age.

PLATE 1

Black-headed gull (*Larus ridibundus*).

PLATE 1





## CHAPTER 3 - STUDY SITE AND GENERAL METHODS

### 3.1 Study Site - Red Myre

The colony used for this study is situated 3km north east of Auchtermuchty in Fife and is called Red Myre (Plate 2). The gulls nest on islands of vegetation in a marshy pond, about one hectare in size, which is surrounded by a plantation of Norway Spruce (*Picea abies*) owned by the Forestry Commission.

The majority of the gulls nest on or beside clumps of bladder sedge (*Carex vesicaria*) and common rush (*Juncus subuliflorus*) which grows on islands in the central area of the myre. Around the edges of these islands and of the myre, bogbean (*Menyanthes trifoliata*) is fairly abundant and some gulls nest on the mat it creates.

### 3.2 The Hide

To obtain a good view of the nests on the study area a hide was built in the trees on the edge of the colony (Plate 2). Four trees situated in a rectangle were used as corner posts to build a platform, using dead Norway Spruce tree trunks, about 3.5m above the ground. Branches were then used to make a framework for the hide on top of this, to which sheets of plywood were attached to construct the hide itself. The top 0.5m of the front of the hide was left open and a piece of hessian was pinned over this leaving a gap of approximately 10cm along the bottom. It was hoped that this would give the observer a good view of the colony while avoiding disturbance of the gulls.

At the beginning of the breeding season black-headed gulls are very nervous and flighty and are easily disturbed. Thus, I unavoidably disturbed the gulls when I entered the hide. In 1982, the first year of

PLATE 2

The black-headed gull colony at Red Myre, Fife. The hide used during this study is situated in the trees at the edge of the myre.

PLATE 2



the study, this usually resulted in the gulls leaving the colony and not returning while I was there. After a week of this I gained the impression that the gulls could see my presence in the hide and were not returning for that reason. So, the front of the hide was completely covered with hessian and a 15cm<sup>2</sup> section cut out at the bottom. This made no difference to the gulls behaviour and neither did the "two into the hide, one out of it" trick which was also tried. Finally I had to spend one night in the hide so that I was there when the gulls arrived at first light. (Black-headed gulls only spend daylight hours in the colony at the start of the season, going away to roost else where at night. This usually continues until several gulls have laid eggs (Kirkman 1937).) After this success I discovered that if all the openings in the front of the hide were covered up when I entered it and were not uncovered until the gulls had settled down again, there were no problems with them leaving the colony.

### 3.3 Access to Study Site

It is possible to walk on the bottom of the myre in certain areas but there is a belt of very deep mud around the edge making it impossible to wade out to the study area. To overcome this a 2-man inflatable boat was punted to and from the study area when necessary. The boat was partially deflated each day and kept in the hide when not in use.

### 3.4 Nest Markers

At the start of each season, as gulls began to set up territories and build nests, numbered markers were put beside all the nests in the study area. These markers were constructed using long twigs to which a stiff square of plastic was attached with drawing pins. On the plastic (8cm x 8cm) a number was printed using a thick permanent felt-tip marker so as to be legible to an observer using binoculars in the hide.

### 3.5 Egg Counting and Marking

When the first egg was due to be laid all the nests on the study area were examined every day, when possible, for the presence of eggs. This was carried out in both 1983 and 1984 but in 1982, the first year of the study, regular checks were not made on the eggs in the nests and the data collected were from only five visits before the chicks started to hatch. In 1983 and 1984 the study area was not visited if it was raining for fear of eggs getting chilled while the gulls were off the nests, and then failing to hatch.

Notes were kept on the date each egg was laid and the number of the nest it was laid in. The eggs were also numbered to indicate whether they were the first, second or third egg laid in the nest. A permanent felt-tip marker was used to write the number on opposite sides of the egg. This also ensured that a single egg in a nest was not recorded as the same one seen the day before when in fact it was a new egg laid after the first egg had been lost. The date and place of any broken eggs or eggs found lying outside the nests were also recorded.

### 3.6 Chick Counting and Ringing

When the chicks started to hatch, as well as continuing to keep records of egg laying, records of the hatching dates and nest number of all the newly hatched chicks were kept. To be able to identify all the chicks individually, coloured rings were put onto the chicks' legs. These were made from ¼ inch thick Dymo tape which was stapled around the chicks' legs in such a way that there was room for their legs to grow to the size of a fully-grown adult's before the staple would rust to allow the ring to fall off (Figure 3.1). Two rings were put on each leg of each chick and a colour code used that enabled identification of the nest each chick had come from and whether it was the first, second or third chick hatched on that nest. Any dead chicks found were examined for clues as to the cause of death and the identity and position of the chick relative to its own nest was noted. Towards the end of the breeding season when chicks started to fledge, notes were kept of the identities of all the fledged chicks seen. A chick was considered to have fledged when it was seen at the age of six weeks or older.

FIGURE 3.1

Dymo tape folded double and stapled around the chicks' legs for identification purposes.

FIGURE 3.2

Remote controlled trap used to catch gulls on nests for ringing.

FIGURE 3.3

Three of the wing patterns observed on gulls in the colony.

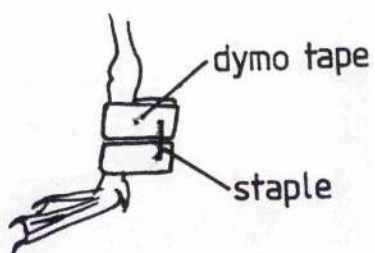


FIG 3.1



FIG 3.2

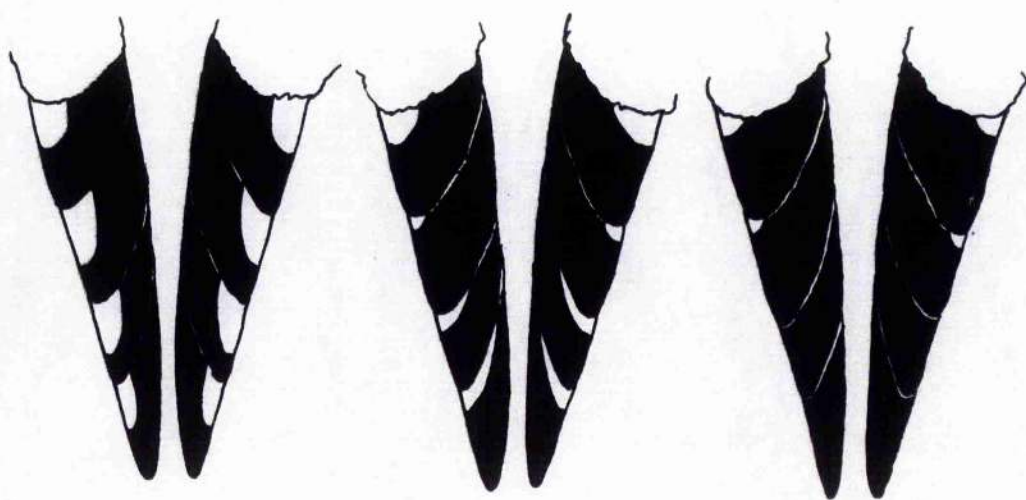


FIG 3.3

### 3.7 Chick Weighing

When the newly hatched chicks were ringed they were also weighed using a spring balance with a small hessian bag attached. The weight was measured to the nearest gram. An attempt was made to weigh all the chicks on the study area, on each day of their first week of life. This proved difficult because black-headed gull chicks become mobile by their second day of life and thereafter seek shelter in the surrounding vegetation when the colony is disturbed. Thus, when trips were made to the study area many of the chicks were so well hidden that they could not be found to be weighed.

### 3.8 Adult Identification

When adult gulls have their wings folded by their sides a black and white pattern is visible in the wing tips formed by the overlapping of feathers (see Plate 1 and Figure 3.3). The pattern on both wing tips is the same and is usually unique to the bird. This provides a method of distinguishing between adult gulls. Unfortunately, there is not a lot of scope for variability and many of the patterns were too similar to be told apart with certainty. However, in most cases two birds of a pair could be told apart using this method. (Figure 3.3 shows some of the more variable patterns observed.) Where the two birds of a pair had similar patterns so that confusion was likely, one of the gulls was caught, if possible, and ringed.

In the first year of the study male and female gulls of a pair were identified purely by observing mating. Two or three instances were required to be seen before the sex of each bird was decided on because a few instances of female gulls mounting males were observed. In the second and third years of the study, experience allowed males and females to be distinguished by size. When the two gulls are together the size difference is very obvious. The female's head also tends to be narrower and more pointed on top and the bill of the female may be shorter. Moynihan (1955) also noted this size difference and used it to sex the gulls. In many cases the sexes were double checked with mating



observations and in all cases the sexing by the size difference proved to be correct. There were a few pairs of gulls in which the males and females were of a similar size and these were only sexed if two or three matings were observed.

### 3.9 Adult Ringing

Because of the nesting habitat at Red Myre it was impossible to catch gulls by netting for fear of drowning them. Thus, those gulls required to be ringed for identification purposes had to be caught individually. This was done using remote controlled traps. The traps were constructed of wire mesh made into an igloo shape with a square down-falling door. A mousetrap fixed to the trap held the door open when it was set and the remote control device, when activated, set off the mouse-trap so closing the door. These traps were placed over the nest belonging to the pair of gulls concerned (Figure 3.2).

The gulls varied in their reaction to the traps. Some walked in to sit on their nests almost immediately they returned to their territory. Others spent a long time walking around the trap before having the courage to enter. Although two of these traps were set up at a time, it was rare to have a gull in both traps at the same time.

Traps could only be used to catch gulls when they had eggs on their nest because the 'desire' to sit on their eggs usually conquered their fear of the trap. If there were chicks in the nest the gulls simply called to the chicks which could leave the nest and go to their parents.

When a gull was caught it was taken out of the trap and ringed on one leg with a BTO numbered ring and a pink coloured study ring, and on the other leg with two coloured rings which identified the gull individually.

### 3.10 Detailed Observations

Up to 100 nests on the study area were used to obtain measures of breeding success, but only a small number of nests were used for detailed behavioural observations. At the beginning of each season three groups of five nests, which were clearly visible from the hide, were chosen. (Five nests proved to be the maximum number that could be kept under observation at one time.) The five nests in each group were chosen so that they were close together, enabling a watch to be kept on all five at one time, and normally two of these groups were watched for 2-3 hours each per day. Unfortunately, during the first two years of the project, restrictions were made on the times it was possible to observe the colony. Use of public transport in 1982 and employment commitments in both 1982 and 1983 (the study was conducted part-time during these two years) resulted in most of the observations being made between mid-morning and late afternoon/early evening. In 1984 these times were kept to in order to maximise the numbers of observations available for comparative analysis.

The nests in each group had often to be changed throughout the season as some gulls failed to breed, lost eggs or chicks, or moved to another site not visible from the hide. When this happened, nests nearby those already being observed were included in the group.

The information collected during the detailed observations included the arrival and departure times of all the territory holders, any instances of aggression, and in 1984 the onset and offset of incubation and brooding was also recorded. When the chicks started to hatch, all instances of feeding of the chicks were recorded.

Specific details of observational methods are described as appropriate in later chapters.

### 3.11 Statistics

After analysis of variance tests where a significant variance ratio was obtained, post-hoc tests were carried out to examine individual differences between means. Where the number of comparisons to be made was small, Tukey's HSD test was used and when there were more than 5 comparisons to be made the Newman-Keuls test was used. Significance levels of  $p = 0.05$  used in these tests (Parker 1980).

When a significant value was found in a chi-square test and it was necessary to identify which of the frequencies in the table significantly contributed to the result, the observed frequencies in individual cells with a  $\chi^2$  value of 3.84 (the value for  $\chi^2$  at which  $p = 0.05$  for 1d.f.) or greater were taken as being significantly different from the expected frequencies.

## CHAPTER 4 - CHANGES IN THE STRUCTURE OF THE THE MYRE AND LOCATIONS OF

### NEST SITES

During the three years of this study the vegetation in the myre changed considerably. In 1982 (the first year of the study) there was a small area of islands, suitable for nesting on, in the centre of the myre, and a lot of bogbean around the edges (Plate 3). Approximately 250 pairs of gulls nested in 1982 and the nests were very close together in places. In the study area of approximately 100m<sup>2</sup>, 100 pairs of gulls built nests during the breeding season.

The majority of gulls nested on areas of sedge and/or rushes. Only a few gulls nested on the bogbean. The brown nests were quite visible against the green bogbean and so gulls nesting there are more likely to suffer losses through predation. Thus, natural selection has probably reduced the frequency of breeding on these areas. Fewer gulls nested on the suitable areas to the south-east of the myre than in the centre, probably because this was close to the track which was used by forestry commission vehicles and by people out for walks (see Figure 4.1).

The structure of the pond showed marked annual fluctuations caused by local weather conditions. Information was obtained from the meteorological office giving figures for the amount of rainfall and bright sunshine per month at the weather station in Cupar, approximately 12km east of Red Myre. The figures for the duration of the project are shown in Appendix 1 and Figure 4.2.

From the graphs it can be seen that there was little rain in 1982 from February to August and a lot of bright sunshine from March to August. In this year the water level at Red Myre went down so much that almost 70% of the myre dried out. In 1983, presumably as a result of the drying out the previous year, the islands of vegetation had increased considerably in area, while the bogbean around the edges had been choked by the mud and was greatly reduced (Plate 4). The number of nests built in the study area decreased from 100 in 1982 to 25 in 1983, while the number of gulls nesting in the whole colony

PLATE 3

Part of the colony showing the large areas of bog bean around the edges of the myre and the nesting areas in 1982.

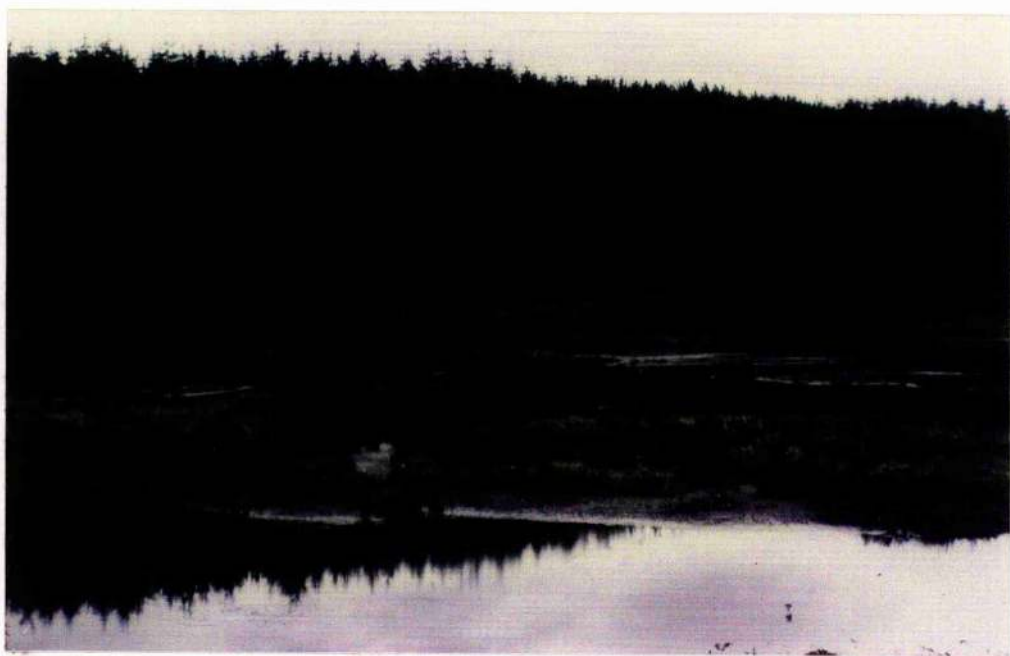
PLATE 4

Part of the colony showing the decrease in the amount of bog bean in the myre and the increase in size of the nesting areas in 1983.

PLATE 3



PLATE 4



**FIGURE 4.1**

Maps showing the changes that occurred in the structure of the myre during the three years of the study.








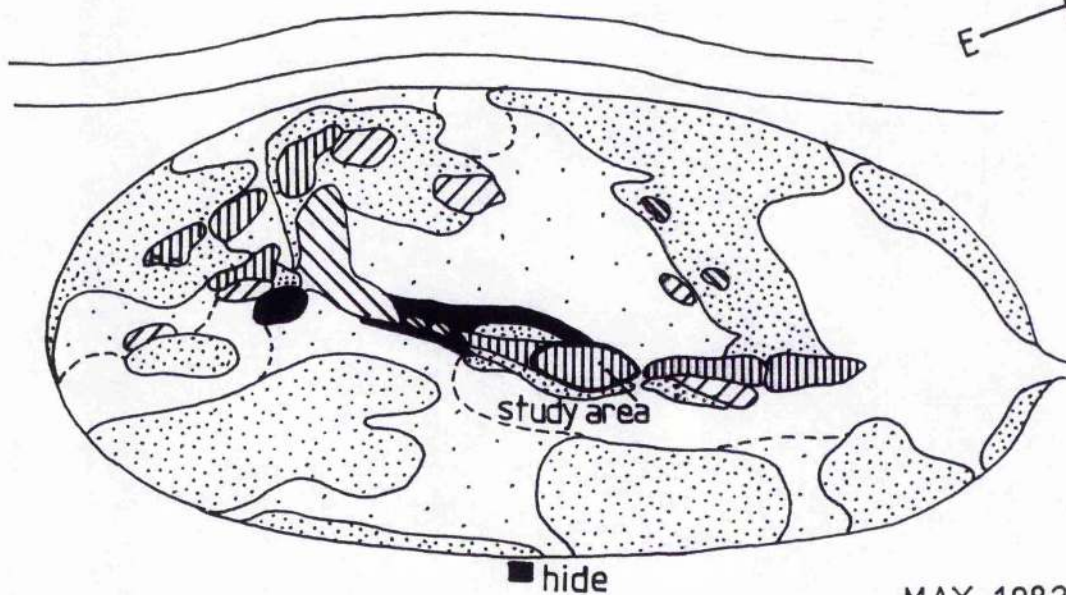
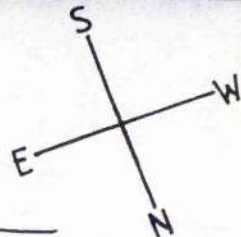
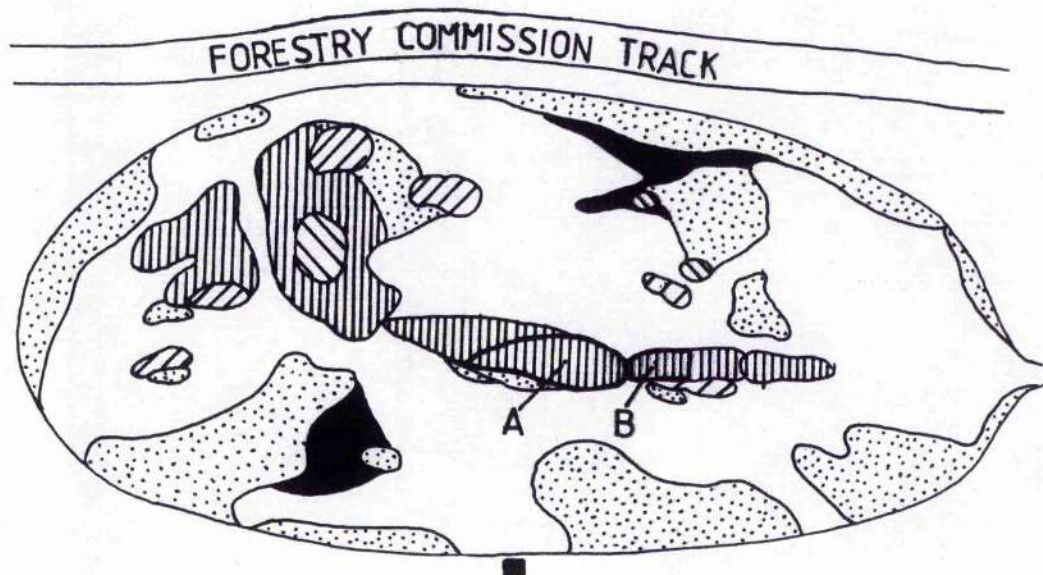
	Areas of sedge
	Areas of rushes
	Areas of sedge and rushes mixed
	Areas of bogbean
	Areas of dried mud
	Areas of water
	Areas of water that dried out later in the season
A	Study area A
B	Study area B



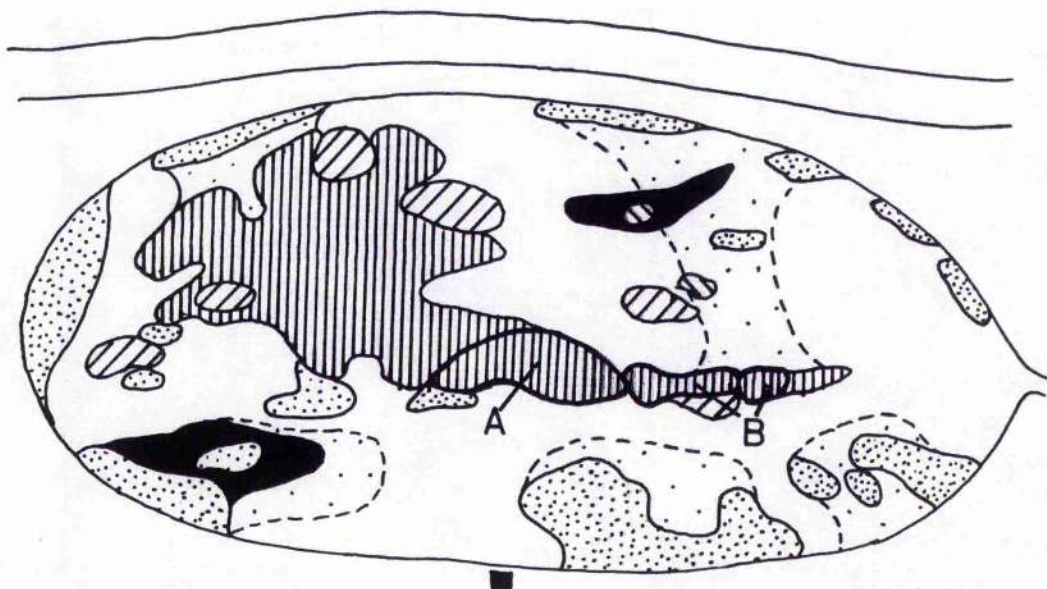
FIG 4.1



MAY 1982



MAY 1983



MAY 1984



**FIGURE 4.2**

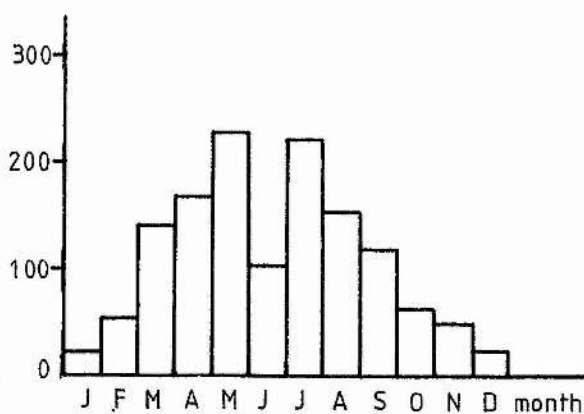
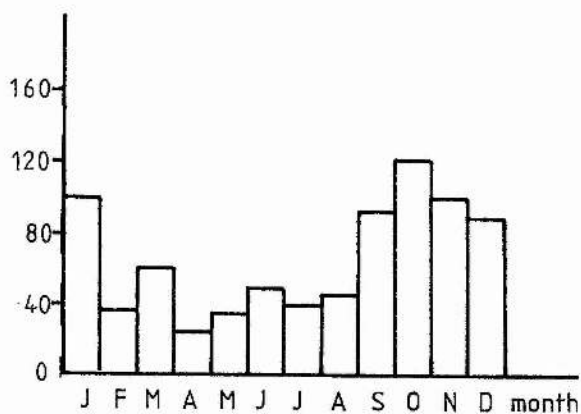
Total rainfall and hours of bright sunshine during each month of the three years of the study. (Data in Appendix 1)

FIG 4.2

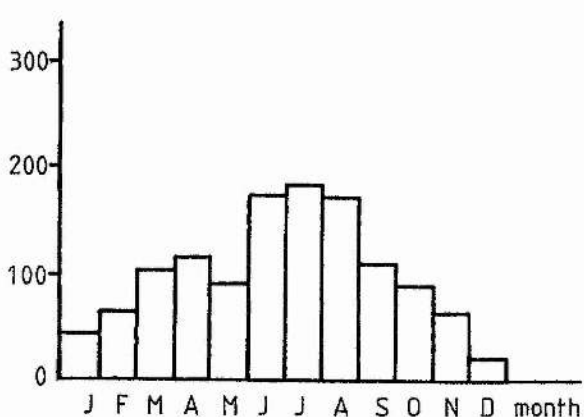
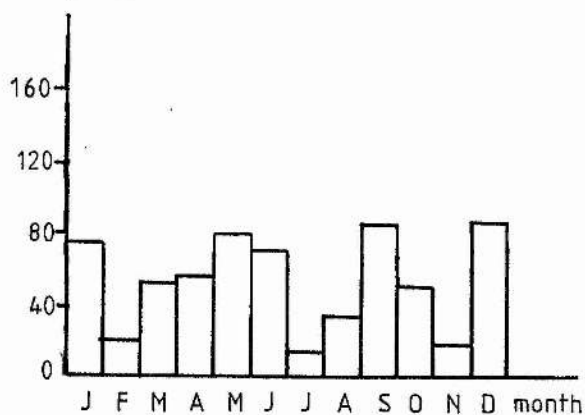
RAINFALL (mm)

BRIGHT SUNSHINE (hrs)

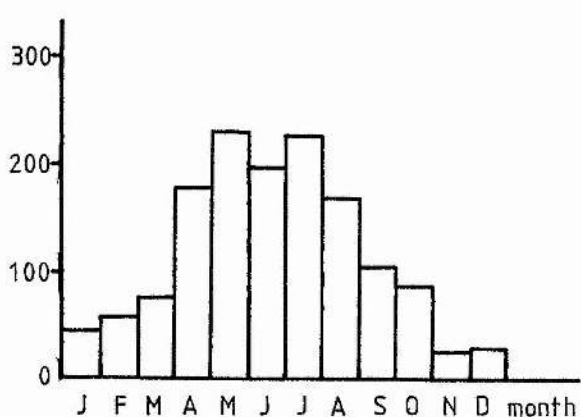
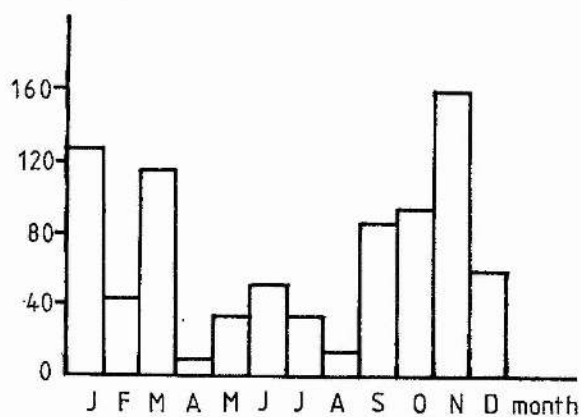
1982



1983



1984



decreased by only 20%, and it is thought that this was due to the increase in available island nesting ground in the colony. In 1983 there was more rain from April to July, than there was during the other two years, and less sunshine throughout most of the year. Very little drying out occurred at all in 1983 and some of the areas in the colony that were nested on in 1982 and 1984 were underwater during part of the season. This included some parts of the study area and so may have contributed to the reduction in the number of gulls nesting on the study area in 1983. To compensate for this decrease in numbers another area of 50m<sup>2</sup> was marked out nearby, and the original study area increased to approximately 120m<sup>2</sup> so that around 60 nests were under study altogether. By 1984 the islands had further increased in area (Plate 5) and both the study areas were increased to approximately 160m<sup>2</sup> and 90m<sup>2</sup> to include a total of 100 nests. In 1984 there was little rain from April to August and a lot of sunshine during the same period. The myre did not dry up so much in 1984 as it did in 1982. The main reason for this is probably the large amount of rain that fell in January and March in 1984 resulting in a higher water level in the myre at the beginning of the season.

Rainfall and sunshine information was obtained for 13 years from 1973 to 1985 so that a comparison could be made to see whether or not the weather during the 3 years of the study was typical. The main drying out periods were from February to May in 1982 and April to July in 1984, so total rainfall and sunshine figures were calculated for these two periods for all 13 years. [Data for early 1973 were incomplete and so could not be included in the February to May period.] The figures are shown in Appendix 2 and Figure 4.3.

During the period from February to May the level of bright sunshine was highest in 1982 and high in 1984 and 1975. The amount of rain that fell during this period was lowest in 1975 and 1982 while 1984 had just below average rainfall. 1983 had the lowest level of sunshine recorded and 1976 was also low. However, the rainfall figures for both these years were close to the mean for the 12 years. 1977 and 1978 had very high amounts of rainfall during this period but the levels of sunshine for these two years were close to the average.

PLATE 5

Part of the colony showing how little bog bean there is left and how the nesting areas have increased further in size in 1984.

PLATE 6

Part of the colony which dried out in 1984 and enabled a fox to walk across to the nesting areas.

PLATE 5



PLATE 6

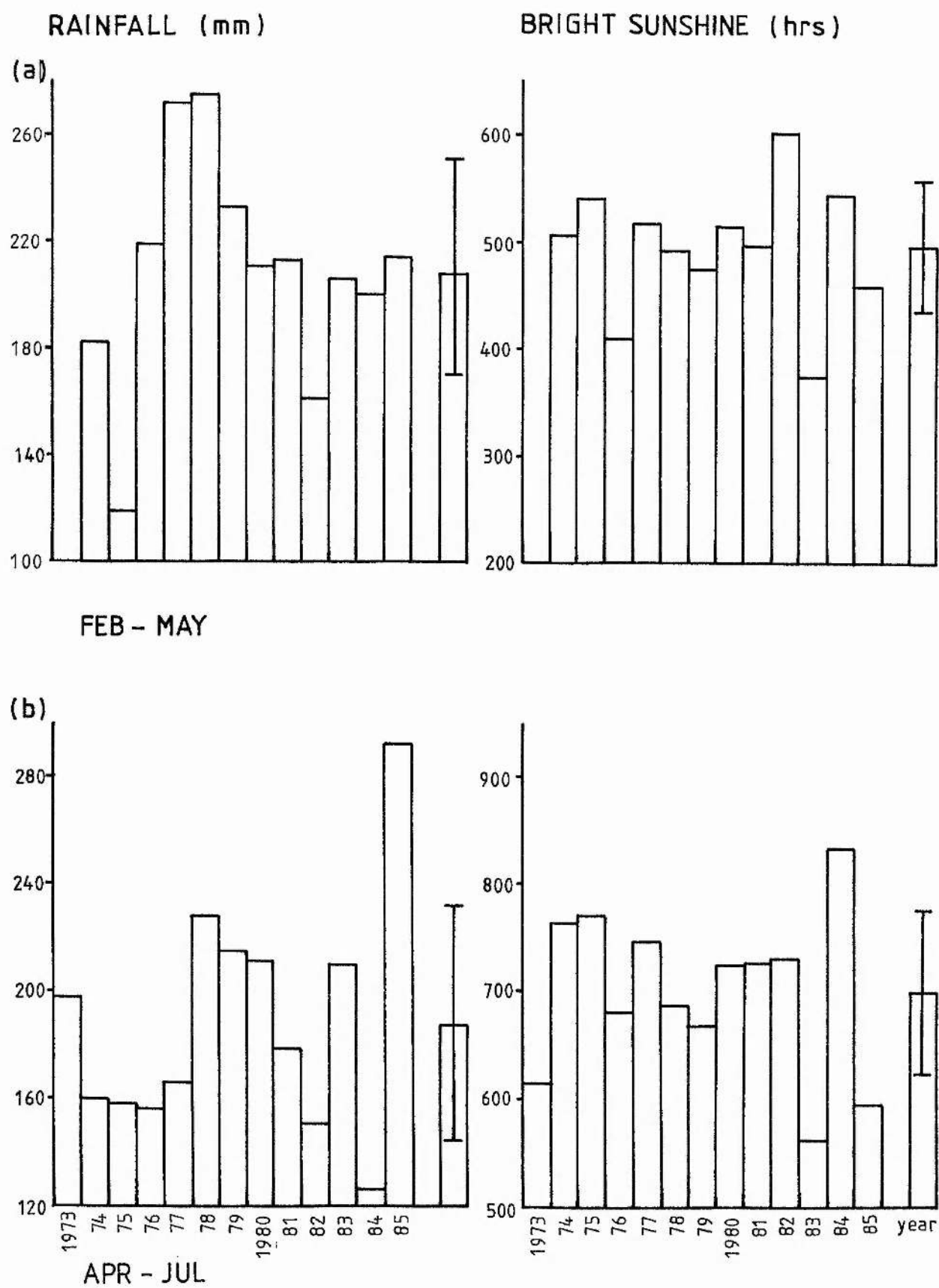


FIGURE 4.3

- (a) Total rainfall and hours of bright sunshine for the months of February to May from 1974 to 1985.
- (b) Total rainfall and hours of bright sunshine for the months of April to July from 1973 to 1985.

The last column in each graph shows the mean and standard deviation. (Data in Appendix 2)

FIG 4.3



Thus, during the period from February to May, 1975 and 1982 were unusually dry and sunny and it is likely that the weather in 1975 would have resulted in a similar drying up in the myre as was seen in 1982.

During the period from April to July the amount of sunshine was the highest in 1984. The amount of rainfall was the lowest recorded in 1984 and was also low in 1982. However, the level of sunshine in 1982 during this period was just above average. The level of sunshine was lowest in 1983 and 1985 and the amount of rainfall was highest for 1985 but only above average for 1983. Thus the period from April to July in 1984 was unusually sunny and dry and in 1985 was unusually wet and cloudy.

1983 had the lowest levels of sunshine recorded in 13 years in both the periods shown, although the figures for rainfall were close to average. So, it is likely that the myre was unusually wet in this year because of reduced evaporation of the water.

During the two study years in which the myre dried out the weather conditions were very unusual. This could explain why the vegetation in the myre changed so much during the project. As the weather dried out the myre, those plants that grew in the mud flourished while those plants that grew in the water were choked by the mud and died back. Thus, the island areas in the centre of the myre increased greatly in size while the edges almost disappeared in places.



## CHAPTER 5 - PREDATION ON GULLS, THEIR EGGS AND THEIR CHICKS.

### 5.1 Introduction

Nest predation is the major cause of nesting failure in birds (Ricklefs 1969) and accounts for a major portion of all egg and chick loss in the black-headed gull (Kruuk 1964; Patterson 1965; Tinbergen et al 1967).

There are two different forms of defence of birds against predators. They can minimise the chance of predation by their choice of habitat, degree of conspicuousness and density of nesting, and they can act directly towards a predator to influence the outcome of a meeting.

Some birds choose nesting habitats in which their nests and young will be well camouflaged and inconspicuous. Others choose sites that are inaccessible to predators, eg. many seabirds nest on tiny ledges on sheer cliffs where no ground predators can reach them. In those birds whose main defence is to avoid detection, predation seems to favour spacing out. Tinbergen et al (1967), Goransson et al (1975) and Anderson & Wilklund (1978) all showed experimentally that predation rates increased with the local prey density. Positive correlation between predation and nest density was also noted in great tits (*Parus major*) by Krebs (1971) and Dunn (1977) and in field sparrows (*Spizella pusilla*) by Fretwell (1972). Many predators tend to react to the discovery of a prey by concentrating for some time on that type of prey (Tinbergen 1952) and this 'area-concentrated search' (Smith 1974) seems to be the reason for the correlation between predation and prey density. Thus, protection derived from cryptic colouration should be more effective if nests and chicks are widely spaced.

Why then do birds nest in groups and colonies that are much more conspicuous and in which nests are often very close together?

Among colonial birds the most commonly observed form of group defence against predators is mobbing. The fact that avian mobs are at least sometimes successful in deterring predators has been repeatedly demonstrated (eg. Kruuk 1964; Horn 1968; Burger 1974; Goransson et al 1975). Kruuk (1964) showed that predation on the eggs in a colony of black-headed gulls was much less than the predation on a group of experimental nests placed away from the colony where no adult gulls were present.

If colonial breeding has an anti-predator function then those selecting nests in low density areas should be most prone to predation. Andersson & Wiklund (1978) and Gotmark & Andersson (1984) found that nest predation on experimental eggs was lower near fieldfare (*Turdus pilaris*) and common gull (*Larus canus*) colonies than near solitary nests. Gotmark & Andersson (1984) and Wiklund & Andersson (1980) also noted that colonial nesting common gull and fieldfare pairs had a higher nesting success than solitary pairs. In all cases communal anti-predator attacks were said to be the likely cause of the reduced predation.

Thus, the dispersion pattern optimal for avoiding predation should tend towards well-spaced, solitary pairs in vulnerable species, and towards clumped colonies in species with efficient communal defence.

Some of the largest gulls eg. glaucous gull (*Larus hyperboreus*, Cramp & Simmons 1983) and great black-backed gull (*Larus marinus*, Gotmark 1982) do nest solitarily or in colonies of low density. Within colonies of great black-backed gulls, pairs on areas of low density produce more chicks than pairs in crowded areas (Butler & Trivelpiece 1981). Solitary or low density nesting in these gulls may be related to large body size, and hence a low risk of nest predation by other birds, and also to intraspecific killing of chicks by neighbours, as cannibalism is quite common in the larger gulls (Emlen 1956; Kadlec et al 1969; Parsons 1971, 1976; Panov et al 1980; Fetterolf 1984).

Black-headed gulls use both choice of habitat and direct mobbing of predators as their main defence against predation. They nest in sites that are usually inaccessible to ground predators, eg. marshes,

islands in lakes, gravel pits etc., and they communally mob any avian predators that enter their colonies.

Kruuk (1964) carried out a comprehensive study on the predators of black-headed gulls. For each type of predator he observed the reaction of the gulls towards the predator and the effect this had on the predator ie. whether or not it prevented the predator from taking its prey of eggs, chicks, or adult gulls themselves.

The observations made in this study are similar to those reported by Kruuk and are detailed below. Instances of predation observed at Red Myre were too few to permit a quantitative study but systematic data was collected on all instances seen as follows

- 1) Identity of the predator
- 2) Nature of the attack
- 3) Response of gulls
- 4) Success or failure of the predator

## 5.2 Predators

### 5.2.1 Carrion Crow

By nesting on islands in water, the black-headed gulls at Red Myre are safe from most mammalian predators, but several species of bird prey on the eggs and small chicks. The main avian predator is the carrion crow (*Corvus corone corone*). Crows are usually deterred by the large numbers of gulls that chase them when they enter the colony but they do sometimes manage to take eggs and small chicks.

Most of the successful predation by crows was at nests on the outskirts of the colony. Thirteen such incidents were seen, in the three seasons study, when single eggs were taken from nests, or occasionally eaten on the nest, and four incidents when small chicks were taken. However, on five occasions individual crows were seen taking eggs or small chicks from the centre of the colony. In three of these incidents the crows returned again and again to the same spot to try for more.

During the occasions when eggs or chicks were taken from nests on the edge of the colony, the crows usually emerged from the trees around the colony, at a point close to the nest they raided. This suggests that the crow had spotted and singled out a nest from the cover of the trees, presumably because the nest was unprotected at the time. The crows flew straight to the chosen nest and took the prey in their bills and flew back into the trees. In only three cases were crows seen to remain in the nest to eat an egg before leaving with part of an egg in their bills.

On the occasions that crows were seen taking prey from the centre of the colony, the crows flew across the colony looking at the ground below and then suddenly dropped to the ground where an unattended nest must have been spotted. Again the crows either flew back to the wood with an egg or chick or more rarely spent some time eating at the nest before flying off with the remains of an egg. On three out of five such occasions the crows, encouraged by their previous success, returned to the same spot up to four more times, in one case, although few of these subsequent trips proved successful.

The reaction of the gulls towards crows in the colony varied depending on how suddenly the crow appeared, how close it flew to the nests and how much the gulls had been disturbed previously. (A lot of disturbance by predators or humans made the gulls nervous and more likely to react to any sudden movements.) For example, a crow appearing suddenly over the tops of the trees sometimes caused the whole colony to rise in silent flight after which 20-30 gulls chased the crow away if it flew into the colony, while the rest returned to their nests. At the other extreme, a crow flying along the edge of the colony or hopping about in the trees in sight of the colony sometimes only attracted the attention of a couple of gulls which chased after it or dived at it while the rest of the colony remained undisturbed.

When a crow landed on the outskirts of the colony to take an egg or chick from a nest, it was dived at by gulls from nearby territories and then chased away by them when it left. If the crow remained on the ground, other gulls from around the colony joined the diving group until 20-30 gulls were flying about the crow. They very rarely came into contact with the crow which ducked every time a gull flew near it. This behaviour by the gulls usually resulted in the crow flying back to the cover of the woods hotly pursued by the gulls.

Any crow flying across the colony was immediately chased by the gulls in its vicinity. This usually deterred crows from landing in the colony but on the occasions that they did they were chased out again by even more gulls. During the incidents seen when a crow returned to the same spot in the colony several times, the number of gulls chasing it increased each time it entered and left the colony until over 50 gulls were seen chasing one crow away. The gulls also became more aggressive and flew closer to the crows and grabbed at their feathers from behind in flight. This caused one crow to drop an egg on two successive flights out of the colony after its first success. It did not return after that.

### 5.2.2 Coot and Moorhen

Coots (*Fulica atra*) are also predators of gulls eggs. The black-headed gulls usually ignored coots unless they came close to the nest, when they reacted with bouts of tremulous calls and advanced towards the coot if it did not leave. One coot was seen raiding a gull's nest while the owners displayed nearby, too 'frightened' of the coot to defend their eggs. It is rare to see this happen while the territory holders are present, and the other three instances seen where coots took eggs were at unattended nests or were eggs that had rolled out of a nest.

A moorhen (*Gallinula chloropus*) was seen to eat the contents of an egg in an abandoned nest and to inspect nests that had just been raided by crows or coots, for left overs. However, moorhens have not been seen to take eggs while there were adult gulls around. Like coots, moorhens were usually ignored by gulls unless they went very close to the nest.

### 5.2.3 Sparrowhawk

The only other avian predation seen at Red Myre was that of a sparrowhawk (*Accipter nisus*) on an adult gull. The sparrowhawk flew out of the trees and landed in top of a gull on the outskirts of the colony. It struggled with it until it had pushed it under the mud and drowned it. Gulls started to dive at the hawk when the struggling began, and eventually it flew away, with 10-20 gulls chasing it, leaving its dead prey behind. During the study five other gulls were found lying dead in the water near the edges of the colony. Although not a certainty, it is possible that they may have suffered a similar fate. It is also quite possible that the sparrowhawk took chicks from the colony, although it was never seen to.

#### 5.2.4 Man

There are several mammals that will prey on black-headed gulls, their eggs or their chicks, given the chance. Usually the gulls nests are protected from mammals because they nest in places inaccessible to them. However, during this study circumstances occurred which resulted in big losses from mammalian predation at Red Myre.

The public have access to the forest around Red Myre and one of the tracks runs alongside one edge of the myre. Unfortunately, this resulted in a lot of disturbance of the colony as people passed by, especially at weekends and holiday periods. Unfortunately too, children discovered the presence of the colony and the temptation to take eggs was so great that they have had to be included on the list of predators.

In both 1982 and 1983 eggs were taken from the colony by children who managed to wade across to the islands after laying dead tree trunks down on the bogbean above the deepest area. In 1982 36 eggs were taken from obviously numbered nests in the study area, and in 1983 an unknown number of eggs were taken from another part of the colony and smashed against the hide 'for fun'.

There is little that the gulls can do to protect their nests from man. Their reaction to humans at the colony is to rise from their nests and fly around the colony mostly above the humans. Many gulls will dive at them, sometimes very close but this will only drive away people that are afraid of the gulls hitting them.

The gulls' reaction to my presence in the study area changed as the season progressed. At the beginning of the season they reacted as they would to any human near the colony, flying above me in a group with only a few diving towards me. As the season progressed only the gulls within approximately 15m of me, and sometime less, left their nests unattended. A small circle of ground was left clear while birds sat on their nests beyond. The gulls flying above me also became bolder and more aggressive and

regularly hit me on the back of the head and shoulders while I was busy numbering eggs and ringing chicks. Only when I stood and stared at the swooping gulls, or at the gulls in the nests, were they less aggressive.

#### 5.2.5 Fox

In 1982 and 1984 the water level in the myre went down drastically because of the very hot weather. The exposed mud dried out and formed a hard crust that enabled a fox (*Vulpes vulpes*) to get across to the nests (Plate 6).

In 1982 a fox first entered the colony on the night of 31<sup>st</sup> May, just eleven days after the first chick had hatched. The next day, many empty and deserted nests were found, and the remains of one adult gull on the edge of the colony. During the next two nights the fox returned and emptied all the nests in the colony (up to 200) of eggs and young chicks. The only chicks that survived were a small number that were large enough to swim out onto the water to safety during the disturbance. A fox was seen in the colony during several afternoons, after this incident, and it did manage to take away some more of the larger chicks - the ones that took cover in the vegetation rather than swimming out onto the water. About 200 chicks had been expected to fledge in 1982 but only 9 chicks did so.

In 1984, the first night that the fox got into the colony (21<sup>st</sup> May, seven days after the first chick hatched) it must have done so at night when it was dark and the gulls couldn't see it. The next day ten dead gulls were found in the study area, one left with a badly broken wing and several more dead gulls could be seen on other parts of the colony. Some eggs and chicks had been taken too. The study area was immediately fenced off so that the fox could not get into it. This protected the study area while the fox took most of the remaining eggs and chicks from the rest of the colony, leaving only those in nests still surrounded by water or soft mud. At this point there were still about 40 breeding pairs remaining, but still eggs and chicks disappeared from nests, including those in the study area. These new losses could not be attributed to a fox as the nests were inaccessible to one. During this period seven



instances were seen of crow predation (not reported in the crow section because of the unusual circumstances). Crow predation had clearly increased at this point as only 22 other instances of crow predation were recorded in the previous 2½ seasons of the study. Thus it seems probable that crows were responsible for the continuing loss of eggs and small chicks. Like 1982, about 200 chicks were expected to fledge, but only 25 survived to do so.

#### 5.2.6 Stoat

Another mammal known as a predator of black-headed gulls' eggs and chicks, is the stoat (*Mustella erminea*). A stoat was seen on several occasions on the edge of the colony, in 1982 and 1983. No predation by the stoat was seen but it is likely that stoats too could have taken advantage of the dry conditions and taken eggs or chicks from the colony.

On the occasions a stoat was seen at the colony it was usually noticed because of the behaviour of the gulls towards it. Several gulls started flying around in small circles above where the stoat was. Very little dive bombing of the stoat occurred but as more gulls collected up to 20 gulls were seen flying around above it.

### 5.3 Discussion

The choice of nesting habitat in Red Myre obviously affords a lot of protection against ground predators, as the nests are surrounded by water and soft mud that is too deep even for humans to wade through. There are few places, however, that man cannot go if he is determined to do so and about 5% of the total eggs in the colony were taken by children in two of the three study years.

In 1983 no other ground predator was able to enter the colony because of the habitat and only avian predators were successful. However, in the other two years of the study the weather was very warm and dry and the water in the colony dried up in places enabling foxes to get into the colony. The number of gulls eaten by foxes is very small compared with the total number killed by them. Killing seems independent of the state of hunger. On the whole adult gulls can adequately protect themselves against fox predation, but the brood seems almost entirely defenceless. On dark nights, however, the adults are just as vulnerable as the brood. Kruuk (1972) reported that on very dark rainy nights, black-headed gulls showed an almost complete lack of anti-predator response and could be picked up by humans without any difficulty. In one breeding season he estimated that about 200 gulls were killed per adult fox without being eaten. In 1982 less than 5% of the number of chicks otherwise capable of fledging actually did so and less than 10% in 1984. It must be remembered, however, that this would not have occurred if the weather had not been so unusually hot and dry in these two years. Similar weather conditions were recorded only in one other year, 1975, from 1973 to 1985 inclusive (Figure 4.3).

This shows just how much protection the habitat did give in 1983. In that year 150-200 chicks survived to fledge while in 1982 and 1984 only 9 and 25 chicks, respectively, were fledged.

Avian predation appeared usually to have very little effect on the nesting success at Red Myre. The numbers of eggs and chicks seen to be taken were relatively small, although more could have been taken outside the observation period, and in most cases these were taken from nests on the edge of the

colony. These nests were likely to belong to poorer quality breeders since they chose or were forced to nest in such bad positions (Coulson 1968).

It is obvious that black-headed gulls can have an influence on the outcome of some predators entering the colony or entering their territory. Coots and moorhens were easily chased out of a gull's territory by the advancement of a gull towards the intruder. On the one occasion when a coot was seen to take an egg from a nest while the adults were on the territory, it only succeeded because for some reason (perhaps because they were first time breeders), unlike most of the other gulls in the colony, this pair were too 'afraid' of the coot to defend their nest.

Crows are deterred from entering the colony by the mobbing action of the gulls and far more eggs would be taken but for that (Hoogland & Sherman 1976; Fuchs 1977; Veen 1977; Andersson & Wiklund 1978; Gotmark & Andersson 1984). Kruuk (1964) placed clutches of eggs away from the main black-headed gull colony, where no adult gulls were present, and reported the removal of 60 eggs by crows in four hours. Thus, the presence of the gulls in a colony must afford effective protection of the brood.

It has been said that one effect of breeding in colonies, is that territorial predators may become satiated in space and time, ie. a breeding colony may contain more prey than a territorial predator can eat in a short time (Patterson 1965; Nisbet 1975; Feare 1976; Birkhead 1977; Findlay & Cook 1982). However, given the chance, a pair of crows can probably eat or hoard a very large number of eggs during the nesting period (Kruuk 1964; Loman & Goransson 1978; Verbeek 1982) and so this theory does not hold for the black-headed gulls at Red Myre.

In 1984, although the study area was protected from the fox by a wire mesh fence, when all the other nests in the colony had been deserted crows gradually took most of the remaining eggs and some small chicks from the study area. This must have occurred because there were too few adult gulls left in the colony to deter the crows from entering it. The effectiveness of mobbing as a defence was seen to be

greater when more gulls adopted it against the crows. This was also observed by Holley (1971) in a study of several larus gulls. A greater number of defenders was observed to reduce predator success in colonial breeding gulls (Kruuk 1964; Andersson 1976), and Hoogland & Sherman (1976) observed that predators at larger bank swallow (*Riparia riparia*) colonies were detected more quickly and mobbed by a greater number of birds.

Crows that ventured into the centre of the colony were mobbed by more gulls than those at the outskirts and there were fewer instances of predation by crows seen at the centre. Kruuk (1964) showed that egg predation was lower within than outside a black-headed gull colony as did Hoogland & Sherman (1976), Veen (1977) and Andersson & Wiklund (1978) for several other species of colonial breeding birds. Breeding success was lowest for peripheral and highest for central pairs in a black-headed gull colony observed by Patterson (1965), and Kruuk (1964) observed that if predators are attacked by the owners of a nest over a greater distance from their nest than the average inter-nest distance, there will be more potential attackers within the centre of the colony than at the edge.

The numbers of gulls which chased the crows as they entered and left the colony on successive raid attempts increased with each flight. The gulls also became bolder with each exposure to the crow until they were coming into contact with it from behind. Repeated exposure to a potential predator without the nest being harmed, provides defending parents with substantial positive reinforcement of their defence behaviour (Knight & Temple 1986b). This was also observed in the increase in boldness and aggressiveness of the gulls to my presence in the study area throughout the season, and a decrease in avoidance behaviour by the gulls nesting on the study area was evident. The gulls probably received positive reinforcement when they were repeatedly successful in defending their nests against a particular human intruder, and lost their initial fear of my being at the nests because I did not harm the defending gulls.

Knight & Temple (1986a), working on redwinged blackbirds, noted that the posture or behaviour of a person or predator affected the response of the parent birds, and that the direct stare of a predator

inhibited aggressive responses by mobbing birds. This too was observed in the reactions of the gulls to my behaviour in the study area. Kruuk (1964) also observed that black-headed gulls were less aggressive in mobbing a human carrying a stick than one with nothing in their hands and he attributed this to the recognition of an increased risk in approaching an armed intruder.

Thus, during an average breeding season the choice of habitat and the defensive mobbing behaviour of black-headed gulls is sufficient to protect the majority of the eggs and chicks in the colony. Unfortunately in two of the three study years, unusual weather conditions thwarted these defence mechanisms by enabling access to the colony by predators that the gulls could not defend their offspring against and so reduced the breeding success almost to zero.

## CHAPTER 6 - ATTENDANCE AT THE COLONY

### 6.1 Introduction and Methods

To obtain an overall picture of how the gulls were spending their time in the colony throughout the breeding season, half-hour counts were conducted of the gulls on the study area and their activities.

The details recorded each half-hour were as follows:

- 1) The total number of gulls on the study area.
- 2) The number of gulls sitting on nests in the study area.
- 3) The number of other gulls on the study area.
- 4) The number of gulls fighting on the study area.
- 5) The number of gulls mating on the study area.

All these counts consisted of adult gulls only.

This information was collected to give an indication of whether, in general, both birds of a pair, or only one, were spending time on the territory at different times of the season.

In 1983 a second study area had to be marked out partway into the breeding season when it was realised that there were going to be fewer gulls nesting on the original study area than there were during the previous year. The counts for the two areas were kept separate. In 1984 both areas were extended and again the counts kept separate for the two areas.

In 1983 and 1984 the number of gulls on the water and non-nesting areas of land was also noted throughout the season. On some of the non-nesting areas of ground the gulls congregated to sleep or preen themselves. Moynihan (1955) also observed these communal areas which sprung up about the

time of incubation near the outskirts of the colony. The counts made of gulls on these areas will show to a certain extent whether birds not on their territories are spending time in the colony or away foraging, at different times of the season.

## 6.2 Results

The results shown in Appendices 3 to 9 and in Figures 6.1 to 6.8 give the average numbers of adult gulls counted during each day's observations. The standard deviations for each day, although included in the Appendices, have not been shown on the graphs because, in most cases, they are so small they would simply obscure the graph line. In other words, the numbers of gulls in attendance on the study area tended to be extremely stable over the observation period, and it was only in the data collected of the numbers of gulls on the water and on communal areas of ground that the standard deviations were occasionally high. The numbers of gulls recorded fighting and mating on the study area during the half-hour counts were very small. Most of the occurrences of gulls mating were recorded at the beginning of the season, as would be expected, and Chapter 8 on aggression gives a much better insight into the fighting activities of the gulls than the relatively few instances recorded here. Accordingly, these results have not been included in the present chapter.

In general, at least up to the time the fox invaded the colony, the results are very similar for the three years of the study. The total number of gulls in the study area (Figures 6.1 and 6.2) increased sharply to a peak during the first 3.5 weeks of the breeding season in 1982 and 1983, and during the first month in 1984. This peak occurred about the time of peak laying in all three years. After this the number gradually decreased and dropped to zero at the end of the season. In 1983 (Figures 6.1b and 6.2a) this occurred two months after peak laying but in 1982 (Figure 6.1a) and 1984 (Figures 6.1c and 6.2b) the number decreased sharply after the fox had been in the colony.

In 1982 (Figure 6.1a) the total number of gulls on the study area fell very sharply immediately after the fox gained entry into the colony because the fox took the contents of most of the nests in the area. In 1984 (Figures 6.1c and 6.2b) the drop in gull numbers after the fox entered the colony was not so sharp. However, there was a considerable decline in numbers at this point. The number of gulls on study area A (Figure 6.1c) dropped to zero in early June of 1984 while the number on study area B (Figure 6.2b) was between two and ten until the end of June. In 1983 (Figures 6.1b and 6.2a) the total number of



## KEY FOR GRAPHS IN CHAPTER 6

'YEAR' A - study area A

'YEAR' B - study area B

E date first egg laid

L date of peak laying

C date first chick hatched

H date of peak hatching

F date fox gained entry into colony

## FIGURES 6.1 AND 6.2

Total number of gulls seen on the study area on different dates throughout the breeding season for the three years of the study. (Data in Appendices 3 to 5 & 7 to 8)

FIG 6.1

TOTAL NUMBER OF GULLS ON STUDY AREA

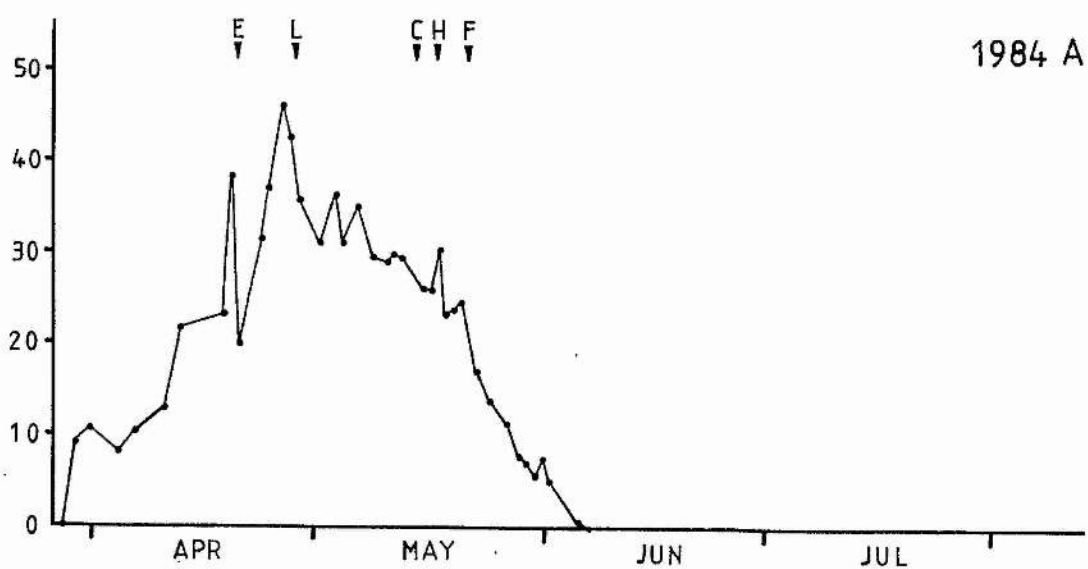
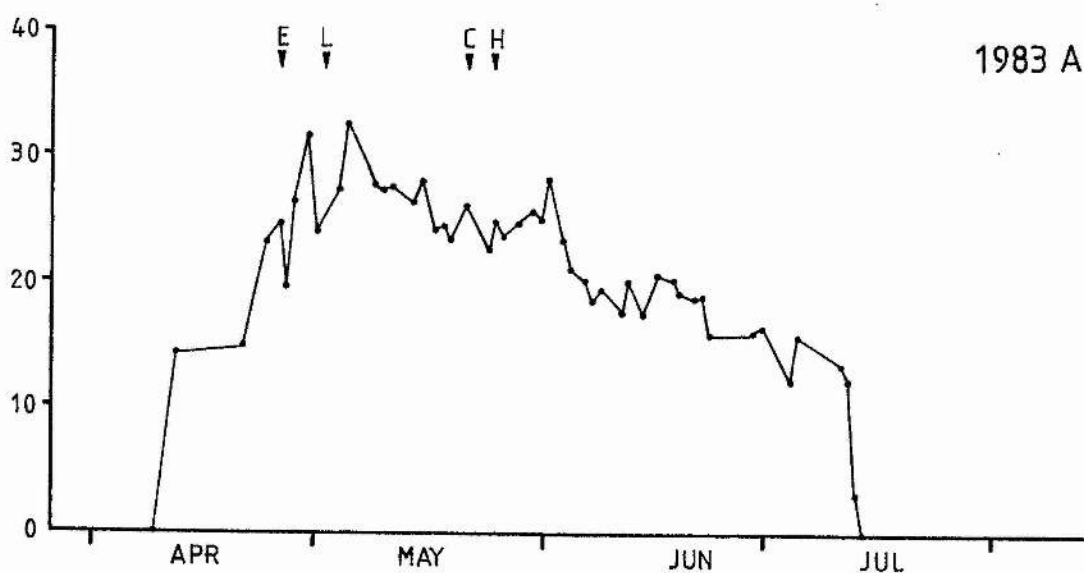
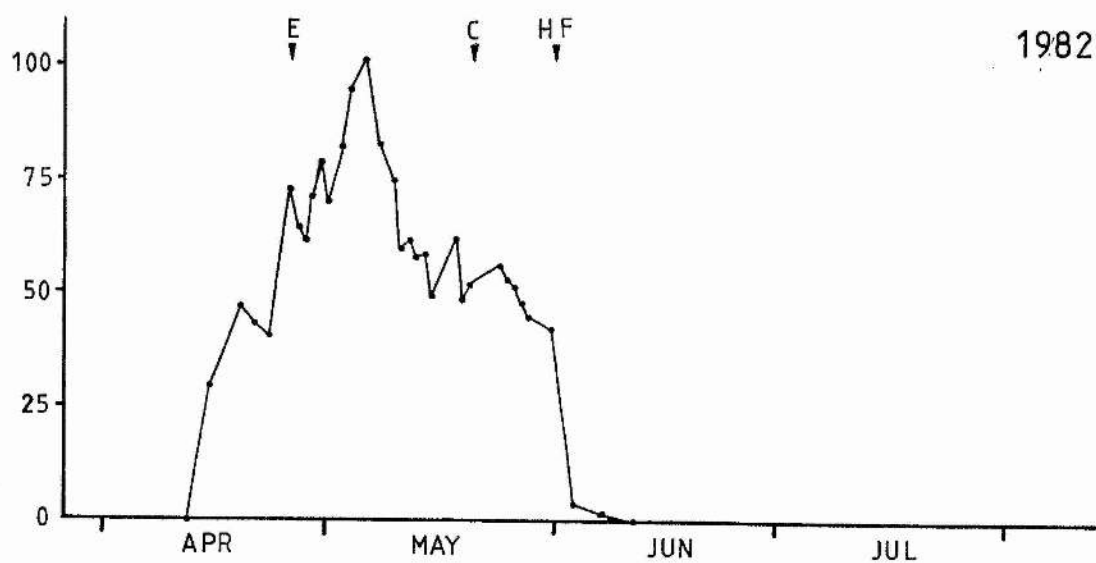
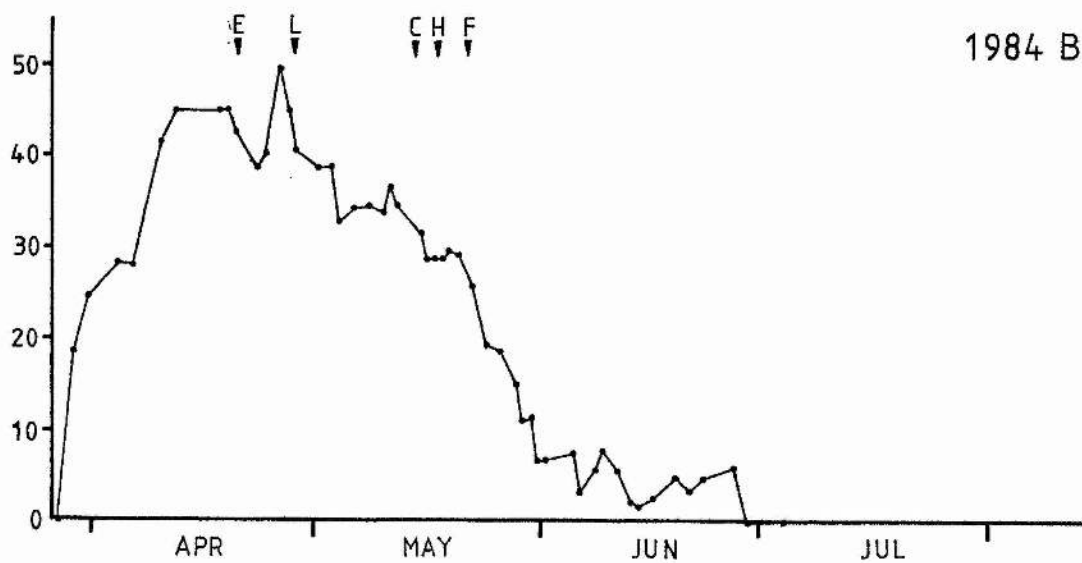
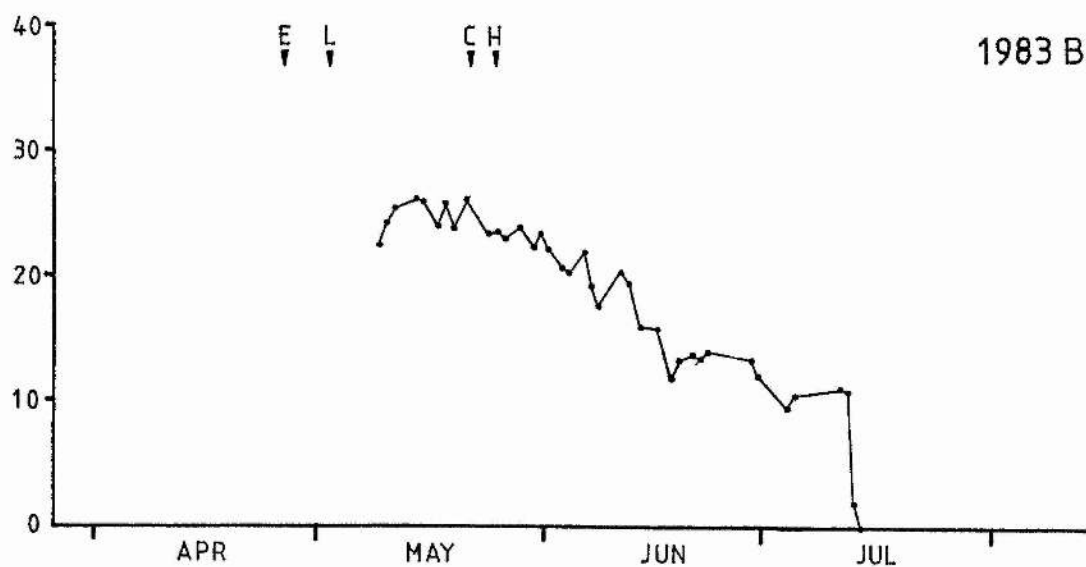


FIG 6.2

TOTAL NUMBER OF GULLS ON STUDY AREA



gulls on the study area decreased gradually from peak laying time until mid July when the number dropped very rapidly to zero.

The number of gulls sitting on nests on the study area (Figures 6.3 and 6.4) gradually increased to a plateau during the first 3 weeks of the breeding season in 1982, the first 4 weeks in 1983 and the first 5 weeks in 1984. The beginning of the plateau occurred about the time of peak laying. The number remained fairly constant for 3 weeks then sharply decreased to a very low level after peak hatching time. The number then remained low until the end of the season. In 1984 the number of gulls sitting on nests in study area A (Figure 6.3c) dropped to zero in early June while the number in study area B (Figure 6.4b) did not reach zero until the end of June. In 1983 (Figures 6.3b and 6.4a) the number of gulls sitting on nests fluctuated between zero and five from early June to mid July. A few of these would have been gulls incubating and brooding late clutches but most were simply gulls sitting on their empty nests during their time on the territory with their chicks.

The number of other gulls, not sitting on nests, on the study area (Figures 6.5 and 6.6) may have included some strange gulls (non-territory holders) but observations suggest this number was likely to be low. In the main it included mates of the gulls that are sitting on nests or pairs of gulls establishing territories, and towards the end of the season it included gulls on the territories with their chicks but not brooding them. The number of gulls not sitting on nests on the study area increased rapidly during the first 2.5 weeks in 1982 and 1983, and the first 3 weeks in 1984, to a peak at about the time the first egg was laid. The number remained high until soon after peak laying when it decreased rapidly to a low level. The number remained low until peak hatching time (1983) when it gradually increased during the next 2-3 weeks to another high. It then remained fairly constant until the end of the season when it decreased sharply as all the gulls left the colony.

The number of adult gulls on the water (Figure 6.7) was high at the start of the season and increased during the first 1.5 weeks in 1983 and first 2 weeks in 1984, to a peak just before the first egg was laid.

**FIGURES 6.3 & 6.4**

Total number of gulls seen sitting on nests in the study area on different dates throughout the breeding season for the three years of the study. (Data in Appendices 3 to 5 & 7 to 8)

FIG 6.3

NUMBER OF GULLS SITTING ON NESTS

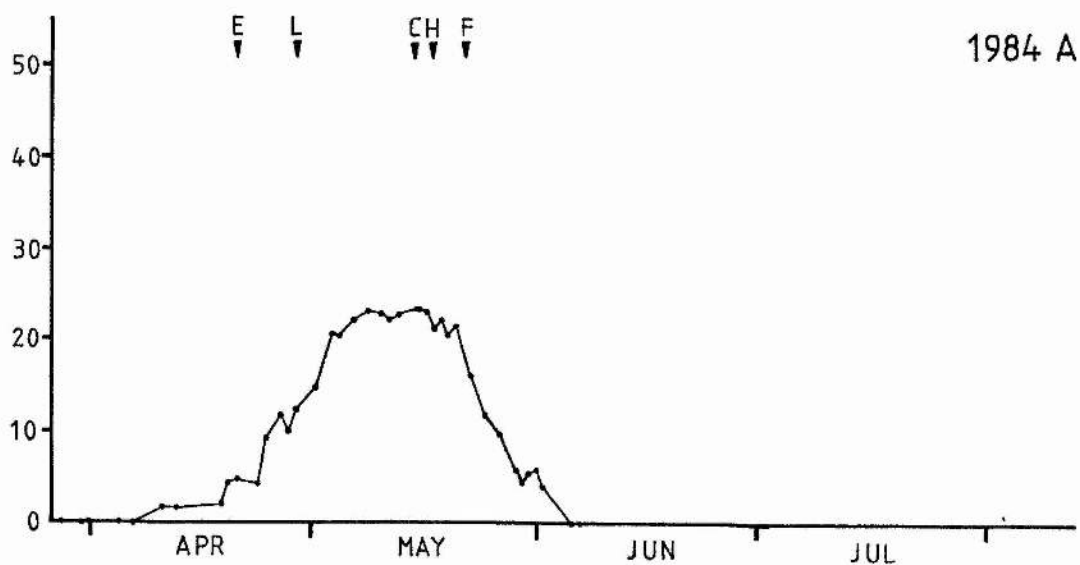
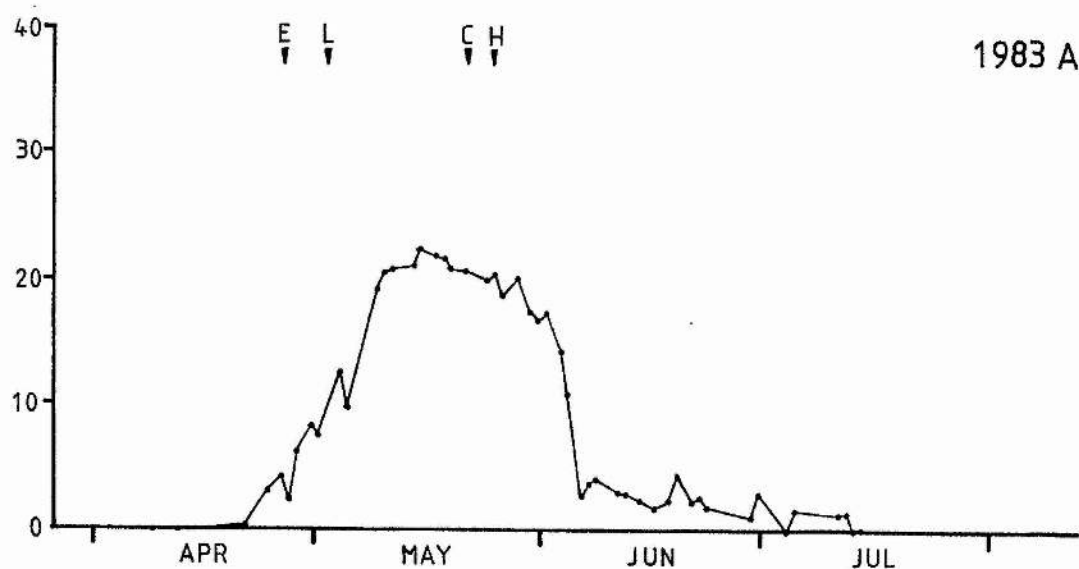
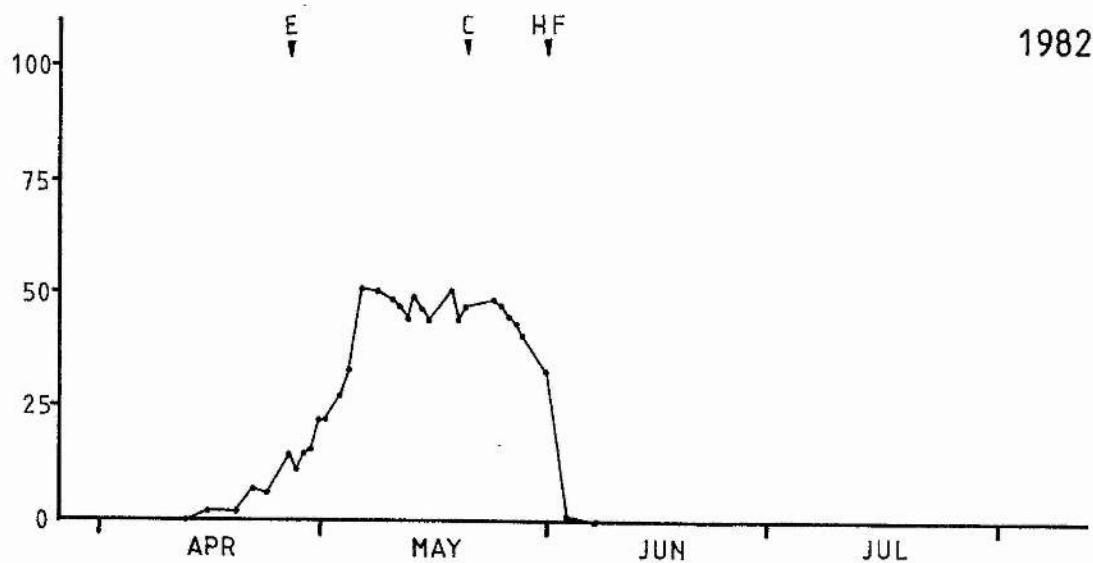
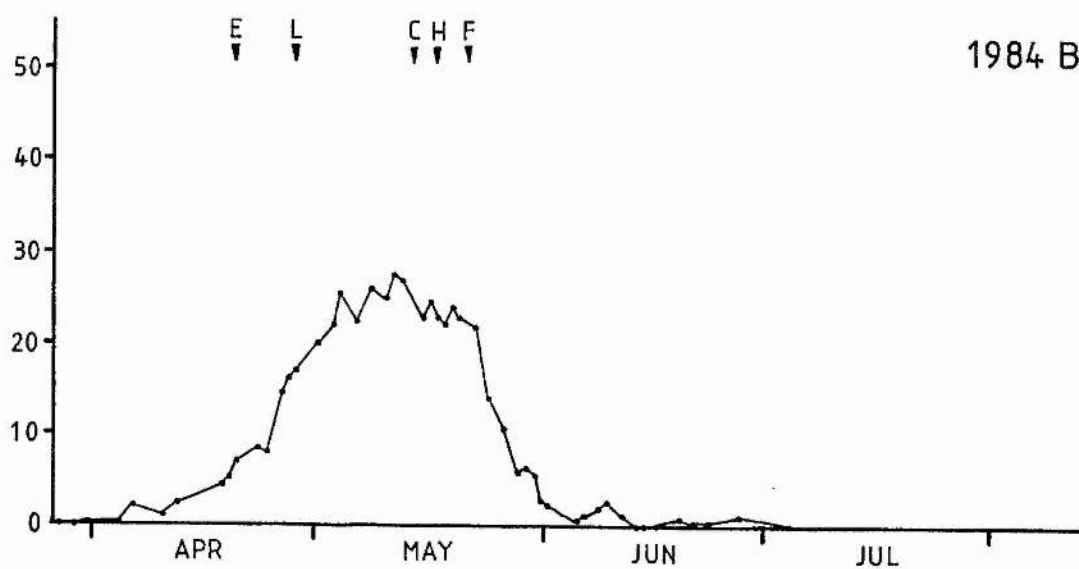
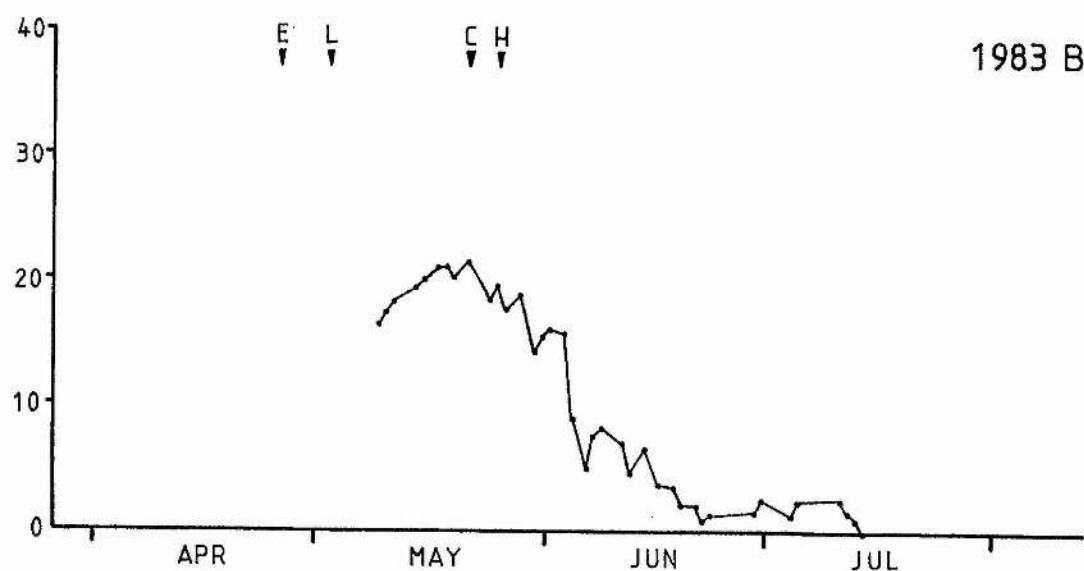


FIG 6.4

NUMBER OF GULLS SITTING ON NESTS



FIGURES 6.5 & 6.6

Number of other gulls seen not sitting on nests in the study area on different dates throughout the breeding season for the three years of the study. (Data in Appendices 3 to 5 & 7 to 8)



**FIG 6.5**

**NUMBER OF OTHER GULLS NOT SITTING ON NESTS**

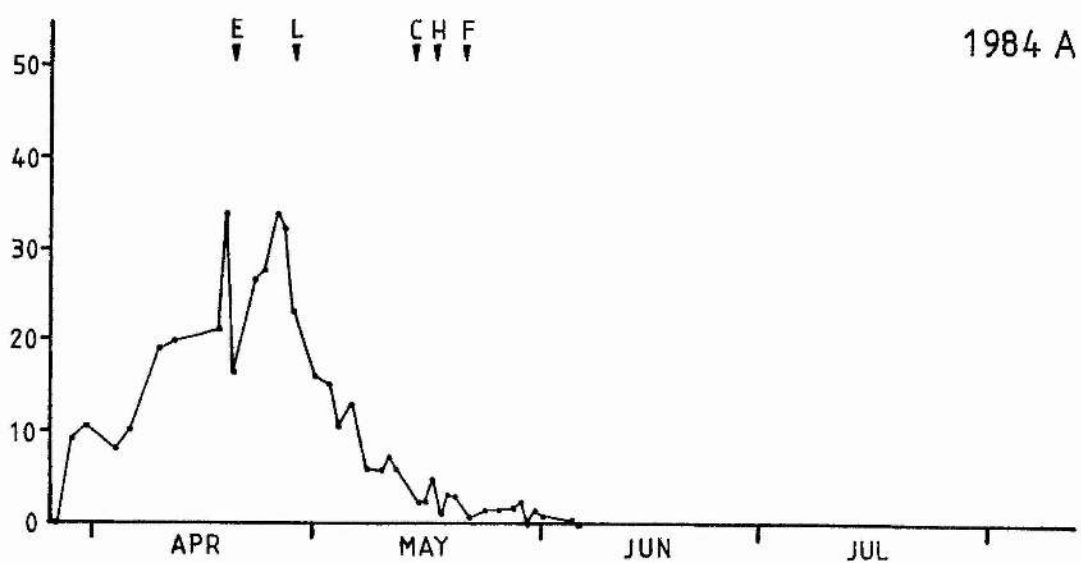
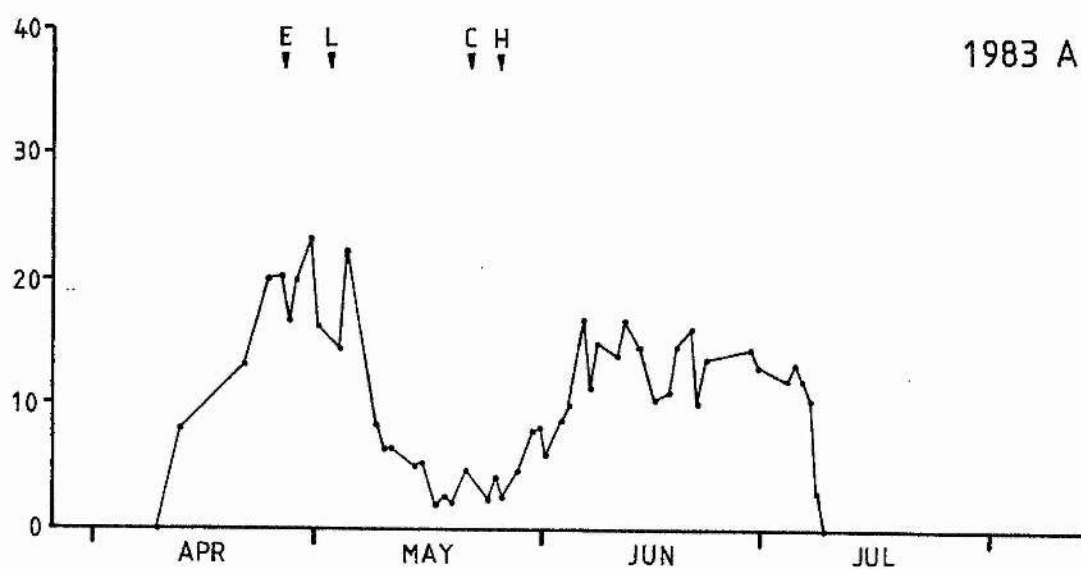
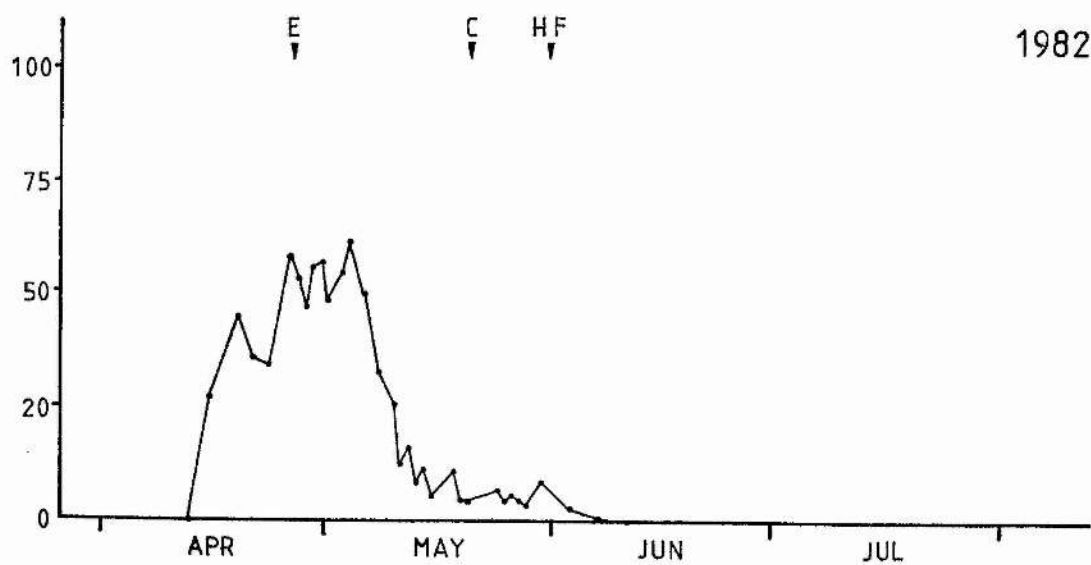
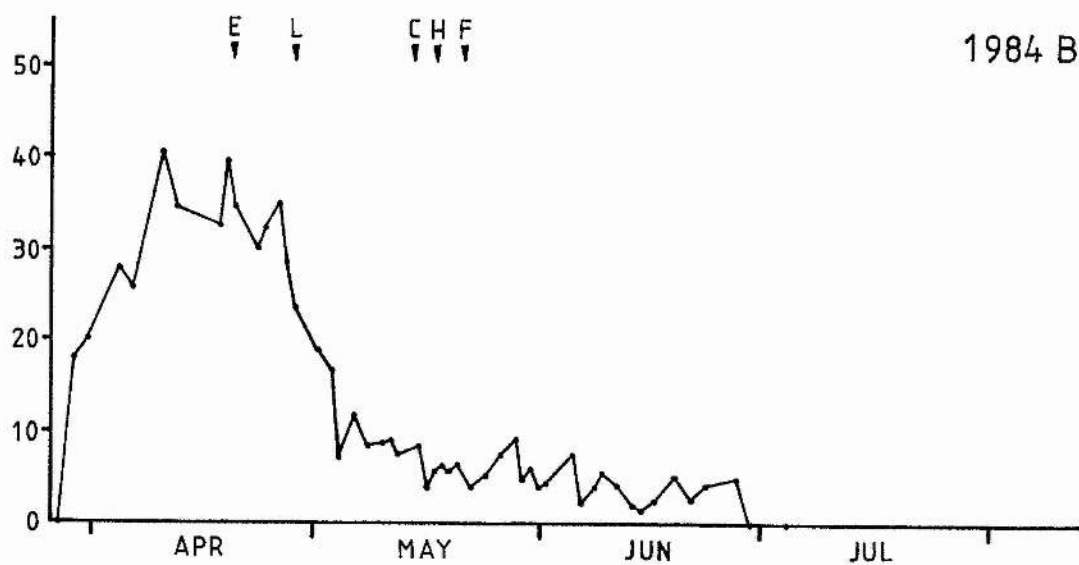
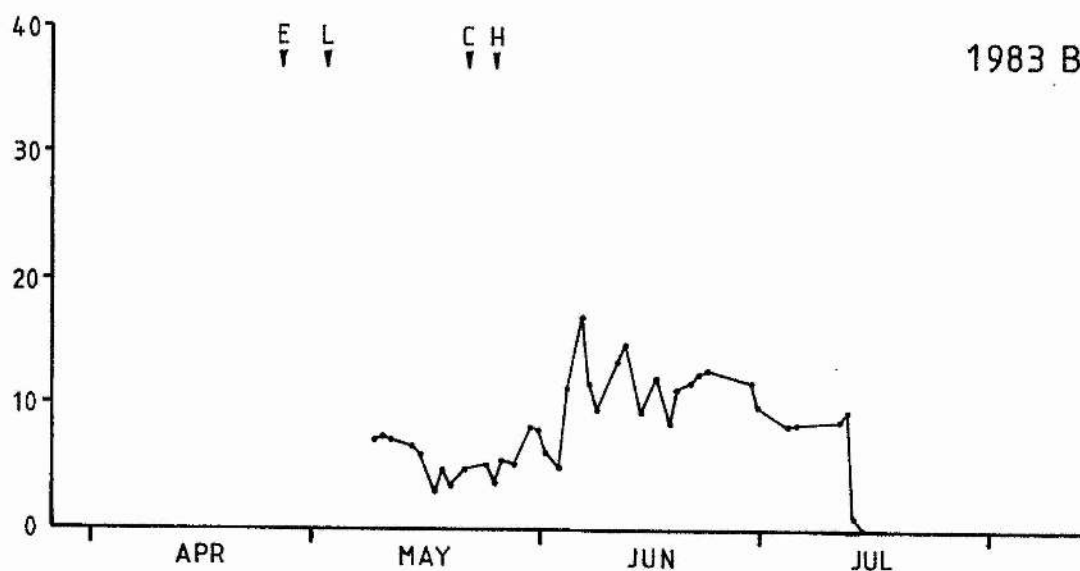


FIG 6.6

NUMBER OF OTHER GULLS NOT SITTING ON NESTS



The number decreased over the next 3.5 weeks reaching a low level after peak hatching time. The number then gradually increased to a smaller peak about 3 weeks after peak hatching.

The number of adult gulls on communal, non-nesting areas of ground (Figure 6.8) revealed a different picture from those on the water. Here the number began very low and started to increase around the time the first egg was laid. The number was very variable after this but generally decreasing and then peaking again towards the end of the season at the same time as the second peak of the number of adult gulls on the water. The number of gulls on the communal areas was similar in both 1983 and 1984 but the number of gulls on the water in these two years was very different. In 1983 the maximum number of gulls seen on the water was about 115, but in 1984 it was about 330. However, the peak of the number of gulls seen on the water 3 weeks after peak hatching was similar in both 1983 and 1984.

FIGURE 6.7

Number of gulls seen swimming on the water in the colony on different dates during the breeding season for 1983 and 1984. (Data in Appendices 6 & 9)

FIG 6.7

NUMBER OF GULLS ON WATER

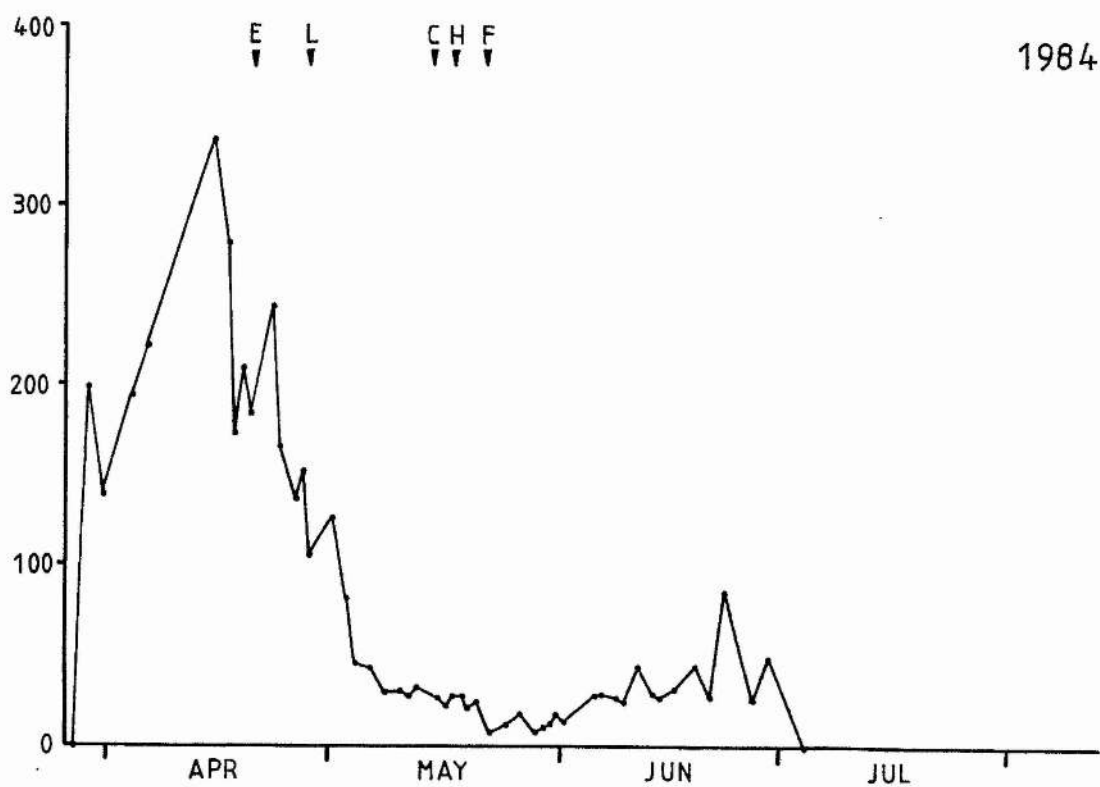
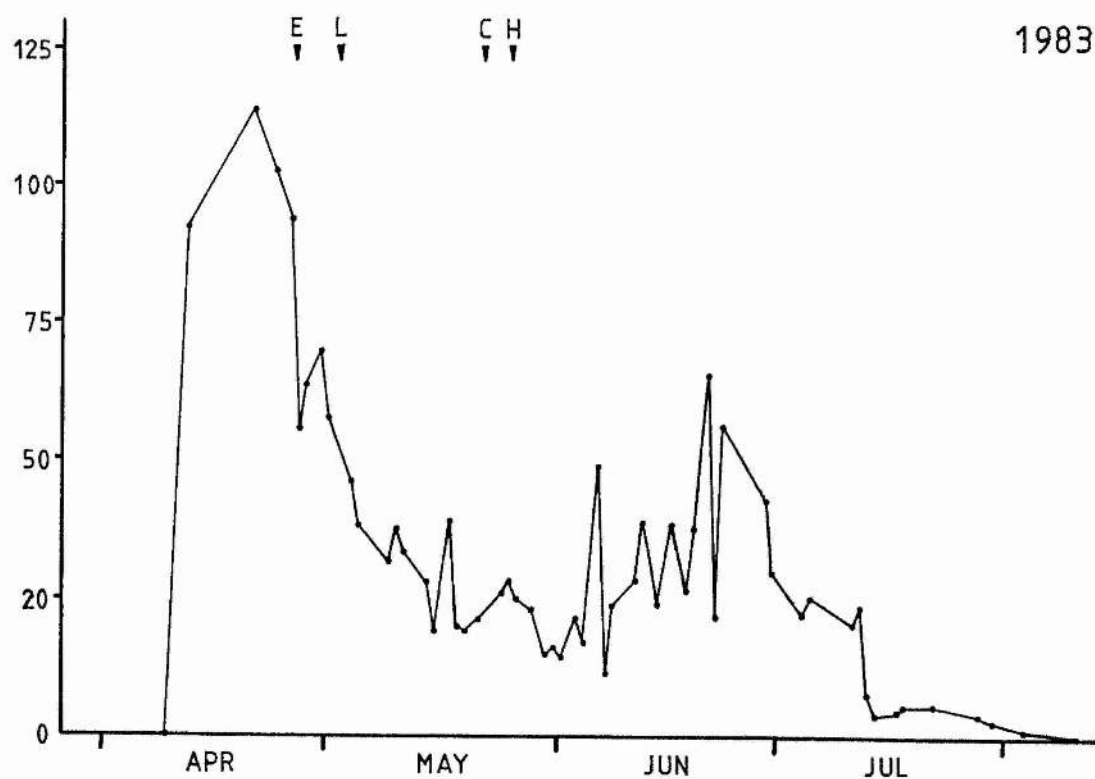


FIGURE 6.8

Number of gulls seen on communal, non-nesting areas of ground in the colony on different dates during the breeding season for 1983 and 1984. (Data in Appendices 6 & 9)

FIG 6.8

NUMBER OF GULLS ON NON-NESTING AREAS OF GROUND

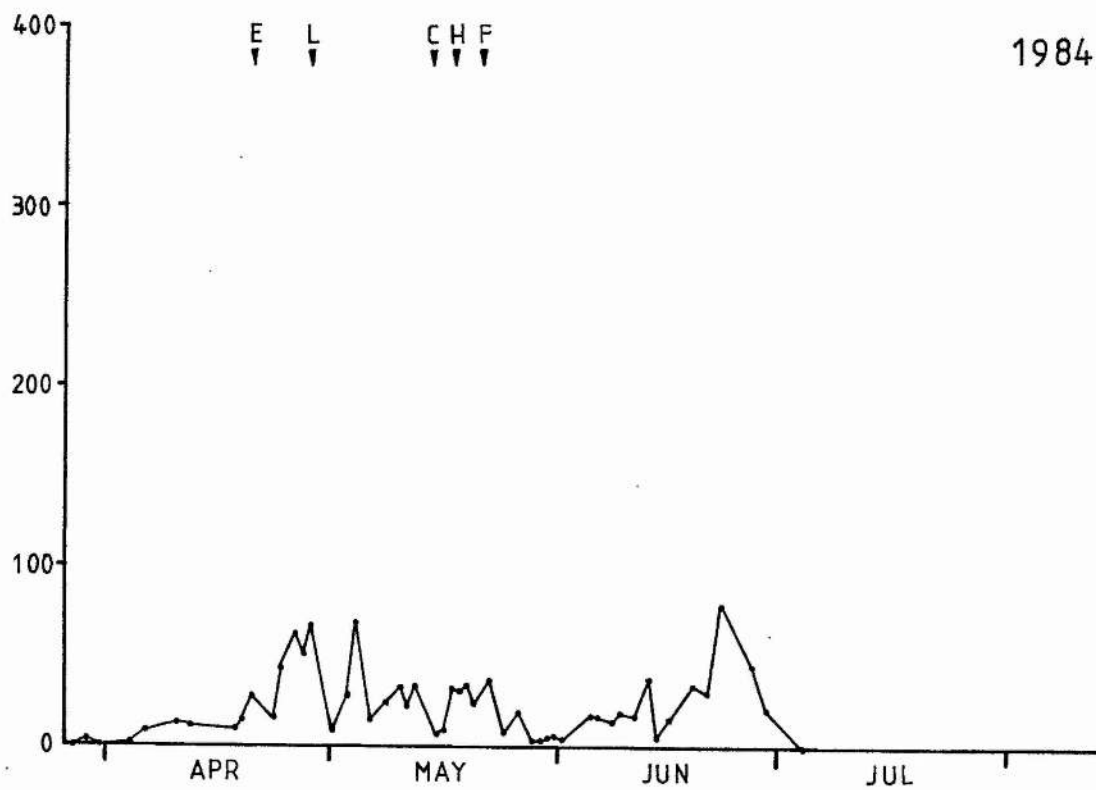
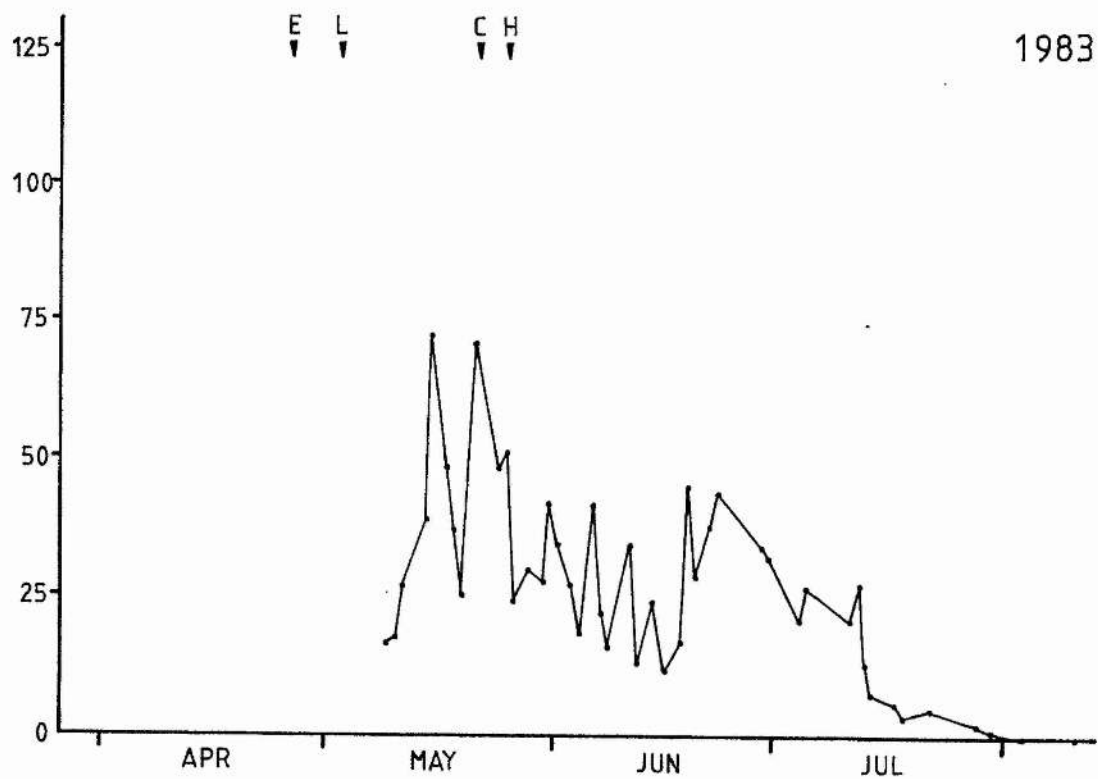


TABLE 6.1 SIGNIFICANT DATES DURING THE BREEDING SEASON

	1982		1983		1984	
	DAY	DATE	DAY	DATE	DAY	DATE
GULLS FIRST SEEN IN THE COLONY	31/3	1	3/4	1	28/3	1
GULLS SETTLED IN THE COLONY	15/4	16	21/4	19	28/3	1
FIRST EGG LAID	26/4	27	25/4	23	20/4	24
PEAK LAYING	?	?	2/5	30	29/4	33
FIRST CHICK HATCHED	20/5	51	21/5	49	14/5	48
PEAK HATCHING	31/5	62	25/5	53	16/5	50
FOX FIRST ENTERED COLONY	31/5	62			21/5	55
GULLS FIRST SEEN LEAVING COLONY	22/6	84	13/7	102	26/6	91
LAST DATE GULLS SEEN IN COLONY	8/7	100	10/8	130	5/7	100



### 6.3 Discussion

From the graphs in Figures 6.1 to 6.6 the impression is obtained that the breeding season started a lot earlier in 1984 than in the other two years, and that more time was spent in the colony by the gulls before egg laying started. In fact this is not strictly true. In 1982 and 1983, disturbances at the beginning of the season frightened the gulls out of the colony during the day until early to mid April. In 1982 my inexperience of black-headed gulls (see Section 3.2) caused me to disturb the gulls each time I used the hide to view them, and they continually left the colony when I arrived until I found a method to avoid disturbing them. In 1983 the Forestry Commission was carrying out a programme of tree felling near the colony at the beginning of the season and the noise of the machinery and passage of vehicles along the track kept the gulls out of the colony while this was in progress. Figure 6.9 shows that the gulls were first seen in the colony on 28th March in 1984 and that this was also the date the gulls settled in the colony. In 1982 and 1983, however, although the gulls were first seen in the colony on 31st March and 3rd April respectively, they did not settle for good until 15 days later in 1982 and 18 days later in 1983 because of the reasons mentioned above. However, it is important to note that two other important dates, the first-egg-laid date and the first-chick-hatched date, occurred at approximately the same time in each year with respect to the date the gulls were first seen in the colony and not the date they eventually settled in the colony. The first egg was laid 26 days after the gulls were first seen in the colony in 1982, 22 days in 1983 and 23 days in 1984, and, the first chick was hatched 50 days after the gulls were first seen in the colony in 1982, 48 days in 1983 and 47 days in 1984. Thus, regardless of the time the gulls spent in the breeding colony, egg-laying occurred at around the same time each year.

The results in this chapter give a general picture of how the gulls spent their time in the colony. At the beginning of the season the total number of gulls on the study area (Figures 6.1 and 6.2) and the number of gulls not sitting on nests (Figures 6.5 and 6.6) were similar as most of the pairs of gulls on the study area set about establishing territories and building nests. The numbers increased to a peak showing the influx of gulls to the colony and to the study area to breed. As the number of gulls sitting

on nests (Figures 6.3 and 6.4) increased, after the first egg was laid, the number of gulls not sitting on nests (Figures 6.5 and 6.6) decreased to a low value. This suggests that once the eggs were laid the gull not sitting on them left the study area. This can also be seen in the decrease in the total number of gulls on the study area at this time (Figures 6.1 and 6.2).

The number of gulls sitting on nests (Figures 6.3 and 6.4) remained high until after peak hatching when it decreased sharply. At the same time the number of other gulls on the study area (Figures 6.5 and 6.6) increased to about the previous value of the number of gulls on nests, indicating that parents stopped continuously brooding their young once they were a few days old, but that one parent still remained on the territory with the chicks. After this, in 1983, the numbers of gulls decreased gradually. This was due in part to the loss of some broods, but in the main to chicks fledging and moving away from their territories. The gradual decline in the total number of gulls after peak laying (Figures 6.1 and 6.2) probably reflects losses of eggs and chicks.

The results for 1982 and 1984, obviously, are different after the entry of the fox into the colony, with a decrease in numbers of all groups after this time. But, up to then the results are very similar to those from 1983. In both 1982 and 1984 the total number of gulls on the study area fell sharply immediately after the fox entered the colony (Figures 6.1 & 6.2). This drop was not so marked in 1984 because the study area was protected from the fox by wire mesh. However, predation by crows which were undeterred by the smaller number of gulls left in the colony resulted in the considerable decline in numbers observed. In 1984 gulls remained on study area B because there were more older chicks in area B which remained in the territories in which they hatched. The few older chicks left in area A moved either to area B or to the area North East of area B where most of the surviving chicks' parents had their territories. In 1983 there was also a rapid drop in the total number of gulls on the study area in mid July (Figures 6.1b & 6.2a). At this time a bird-scarer was in use in a field close to the colony and the noise made the gulls very flighty and probably resulted in an early departure of the remaining gulls from the colony. In 1982 (Figure 6.3a) there was a decrease in the number of gulls sitting on nests at the time of peak hatching (this drop occurred a week after peak hatching in 1983) because of the

entry of the fox into the colony and the resultant loss of broods. In 1984 (Figures 6.3c & 6.4b) this decrease may also have occurred earlier than it would have done had the fox not disturbed the colony. The number of gulls sitting on nests in study area A (Figure 6.3c) dropped to zero in early June in 1984 while the number in study area B (Figure 6.4b) did not reach zero until the end of June. This occurred because there was a high concentration of nesting gulls in and around plot B and the crows preyed on plot A before plot B.

The number of gulls on the water (Figure 6.7) was high at the start of the season, when the gulls initially moved into the colony, and it increased to a peak as more gulls joined them. There was then a fairly rapid decrease in numbers, at the same time as the increase in numbers of gulls on the study area (Figures 6.1 and 6.2), as gulls left the water to establish territories on the nesting areas. The number of gulls on the water began to decrease shortly before the first egg was laid while the total number of gulls on the study area increased showing the movement of gulls from the water onto the breeding areas. After peak laying the number of gulls sitting on nests (Figures 6.3 and 6.4) had reached a plateau while both the number of gulls on the study area (Figures 6.1 and 6.2) and the number of gulls on the water (Figure 6.7) continued to decrease gradually. This suggests that as incubation proceeded the gulls that were not sitting on nests left the study area but spent little time on the water. The number of gulls on the communal, non-nesting areas (Figure 6.8) starts very low and increases to a peak after peak laying. Thus, throughout incubation, the gulls not sitting on eggs must spend some time on these communal areas but probably most of their time out of the colony as the number of gulls on the communal areas is small compared to the number of nesting pairs in the colony.

The number of gulls on the water (Figure 6.7) increased gradually after peak hatching for about two weeks, when it rose to a small peak. This suggests that after the chicks had hatched, the gulls that were not on the territories with their chicks were spending increasingly more time in the colony, than they did during incubation, while they would be expected to be spending more time away from the colony foraging to feed their offspring. However, it may be that this increase is contributed to by gulls that have lost their broods and in fact many of the breeding gulls may be away foraging. Without ringing all

of the gulls on the study area it would be impossible to estimate how many of the gulls present in the colony no longer had eggs or chicks to look after. I did notice, however, that at the end of the breeding season, when there were only a few chicks left in the colony, there were often more gulls in the colony than could have been parents of the remaining chicks. So, it seems likely that gulls no longer breeding may have remained in the colony.

The small peaks observed in the numbers of gulls on the water (Figure 6.7) and on communal areas of ground (Figure 6.8) towards the end of the season probably reflect the movement of the older chicks away from their territories. When chicks had fledged they spent a lot of time away from their territories in the water or on the communal areas. Consequently the adults no longer had to remain on the territories with the chicks and often left them deserted. However, it would appear that although they left the territories they tended to remain in the colony.

The large difference seen in the numbers of gulls on the water in 1983 and 1984 (Figures 6.7a and 6.7b) can be explained by the disturbance that occurred at the beginning of 1983. In 1984 I was able to record the numbers of gulls from the first day that they entered the colony. In 1983, however, the gulls did not settle in the colony properly until 18 days after they were first seen in it because of the disturbance by the forestry workers. However, a lot of the territory choice, mating and nest-building must have taken place in the early morning and perhaps evening and by the time the gulls settled in the colony many of them already had territories to defend and so did not spend time in the water. This is evident when looking at the total number of gulls on study area A in Figures 6.1 and 6.2. In 1983 the number of gulls first seen on the study area was 44% of the maximum number seen at peak laying time, while in 1984 the number first seen was only 20% of the maximum.

Unfortunately, because of the restrictions made on the times of observation (see Chap 3.10) the colony was not regularly observed in the early morning and late evening. Patterson (1965) noted that activity in the black-headed gull colony he studied was at its highest at these times. In this study the colony was

only observed in the early morning or late evening on 12 occasions and there were not sufficient data collected on these occasions for comparison.

The graphs in this section indicate that there is a high degree of synchronisation in the timing of the breeding of the gulls in the colony. Such synchronisation is common in the reproduction of many colonial nesting birds (Darling 1938 (herring gull, and lesser black-backed gull, *Larus fuscus*); Ytreberg 1956, Patterson 1965 (black-headed gull); Feare 1976 (sooty tern, *Sterna fuscata*); Fetterwolf 1984 (ring-billed gull, *Larus delawarensis*); Paynter 1949, Parsons 1971, 1975, 1976 (herring gull); Burger 1974 (Franklin's gull, *Larus pipixcan*); Emlen & Demong 1975 (bank swallow)).

Darling (1938) working on a colony of herring and lesser black-backed gulls suggested that in large colonies of gulls, increased "social stimulation" produces greater breeding synchrony, resulting in an earlier and shorter egg-laying period. Subsequently several authors have presented evidence for increased synchrony with increased colony size (reviewed by Coulson & White 1956) while Weidmann (1956) failed to find any correlation.

Perrins (1970) suggested that synchronisation is beneficial because hatching, for the colony as a whole, occurs over a shorter period and the percentage of chicks taken by predators is less than if the hatching period is extended. Several authors have indeed reported increased breeding success with synchronisation of breeding in bird colonies (Paynter 1949; Emlen & Demong 1975; Parsons 1975, 1976; Feare 1976).

Synchronisation was also very evident in the laying dates of eggs and hatching dates of chicks and the implications of this are discussed more fully in Chapter 7.

## CHAPTER 7 - EGG LAYING, HATCHING AND MORTALITY

### 7.1 Introduction

The nest-building behaviour of the black-headed gull has been described in detail in the past (Kirkman 1937; Moynihan 1955; Ytreberg 1956; Beer 1961). The male appears to choose the potential nest sites and he takes the initiative at the beginning of nest building. The female's contribution to building is quite insignificant, until around the time the first egg is laid, when she begins to assist in earnest. Thereafter both birds maintain and improve the nest throughout the incubation period and they may even cover the eggs and chicks with nest material.

Nest material is often stolen from other gulls' nests and an unguarded nest can disappear entirely as neighbours help themselves to the material. Theft is presumably advantageous because the bird can decrease the time required to gather material, and gulls often steal nest vegetation even when the owners are in the vicinity. This occurs particularly with nests in which birds are busy incubating as a black-headed gull when incubating a complete clutch rarely leaves the eggs to chase away intruding birds in search of nest materials. Black-headed gulls normally lay up to three eggs. Although clutches of up to six eggs have been found, such cases are thought to have resulted because two females have laid in the same nest.

Many factors have been shown to contribute to breeding success in birds. These include timing of laying date with respect to season (Perrins 1970; Nisbet & Drury 1972; Hunt & Hunt 1976), synchronization of laying dates with respect to other birds in the colony (Parsons 1975, 1976; Gochfeld 1980; Fetterolf 1984), clutch size (Lack 1968; Nisbet & Drury 1972), territory position and size (Coulson & White 1956, 1958, 1960; Coulson 1968; Patterson 1965; Hunt & Hunt 1976) and colony size and density (Horn 1968; Parsons 1976; Zykova & Panov 1983). Other factors include the age and physical condition of individuals (Coulson 1968; Horn 1968; Davis & Dunn 1976), predation (Kruuk

1964; Patterson 1965; Tinbergen et al 1967), availability of food (Lack 1966; Hussell 1972; Howe 1976, 1978) and competition and social behaviour (Darling 1938; Lack 1968; Burger 1979a).

In Chapter 5 the effects of predation and territory position on the breeding success of the gulls at Red Myre were described, and in this chapter the effect of the timing of laying , synchronization of laying dates and clutch size will be examined. The methods used are those described in the general account in Chapter 3.



## 7.2 Egg Laying and Chick Hatching Dates

### 7.2.1 Results

The egg laying dates in the study area for 1983 and 1984 are shown in Figure 7.1 and Appendix 10. (Laying dates were not accurately known for 1982.) Figure 7.2 and Appendix 11 show the chick hatching dates for all three years of the study.

The exact date of laying of some eggs was not known because I had either been unable to visit the colony or the weather had been too bad to visit the nests without a serious chilling risk to the chicks. When this occurred the number of eggs known to have been laid during the period concerned was divided by the number of days in that period to obtain the average number of eggs laid per day.

In 1983 peak laying occurred 7 days after the first egg was laid and the graph is skewed to the right (Figure 7.1). In 1984 peak laying occurred slightly later at 9 days after the first egg was laid and again the graph is skewed to the right. The distributions of egg laying for 1983 and 1984 were similar with most of the egg laying occurring in the first half of the egg laying period. In 1983 the main egg laying period lasted 25 days and 53.6% of the eggs were laid in the first 10 days. In 1984 the main period lasted 27 days with 50.4% of the eggs being laid in the first 11 days.

In 1982 peak hatching occurred 11 days after the first chick was hatched (Figure 7.2). There was an abrupt decrease in hatching after the fox had been in the colony with only 19 more chicks hatching from the 92 eggs that had been there when it first invaded. In 1983 peak hatching occurred 4 days after the first chick had hatched, 23 days after peak laying. With no fox disturbance, this graph, like the egg laying graphs, is skewed to the right. In 1984 peak hatching took place 2 days after the first chick had hatched, 17 days after peak laying. Again, there was a decrease in hatching after the fox had been in



FIGURE 7.1

Number of eggs laid on successive 2-day periods in 1983 and 1984. (Insufficient data for 1982.) (Data in Appendix 10)

F - date fox first entered the colony

FIG 7.1

DATES EGGS LAID

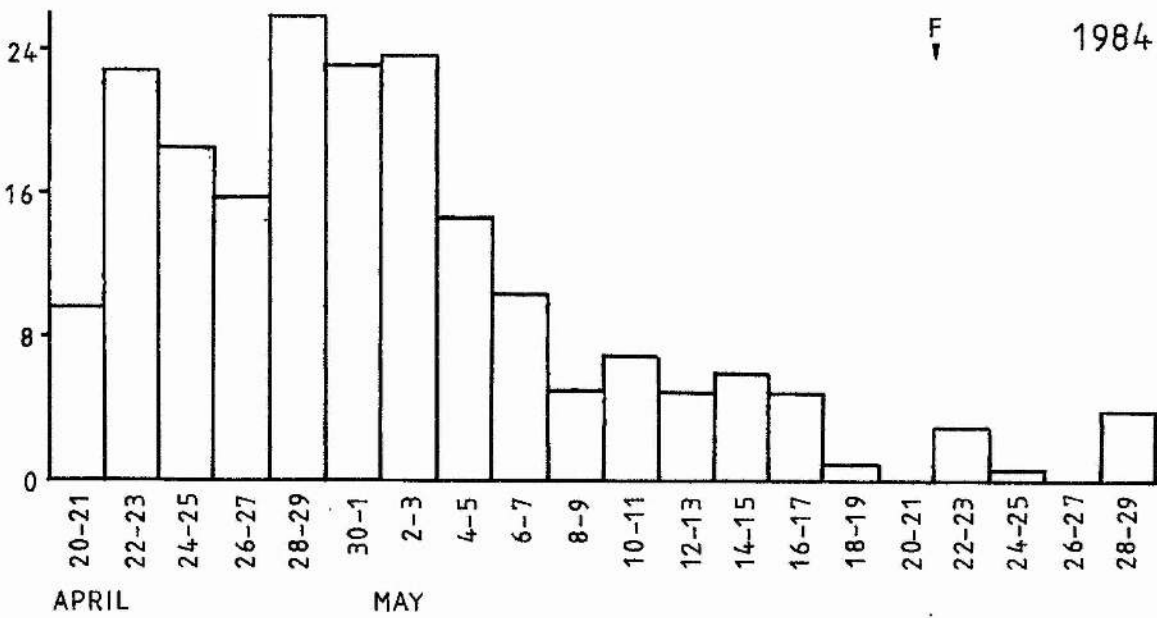
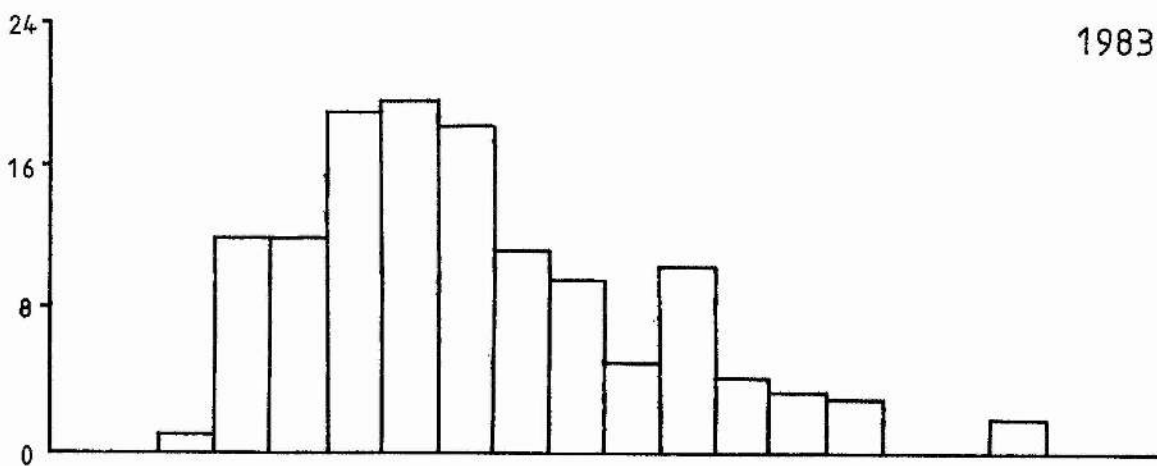


FIGURE 7.2

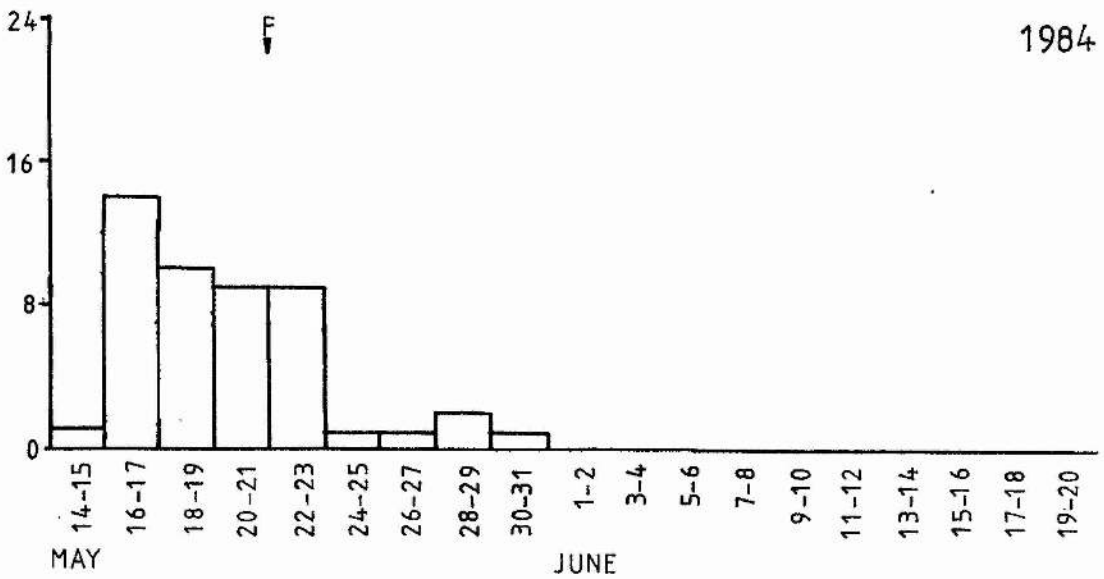
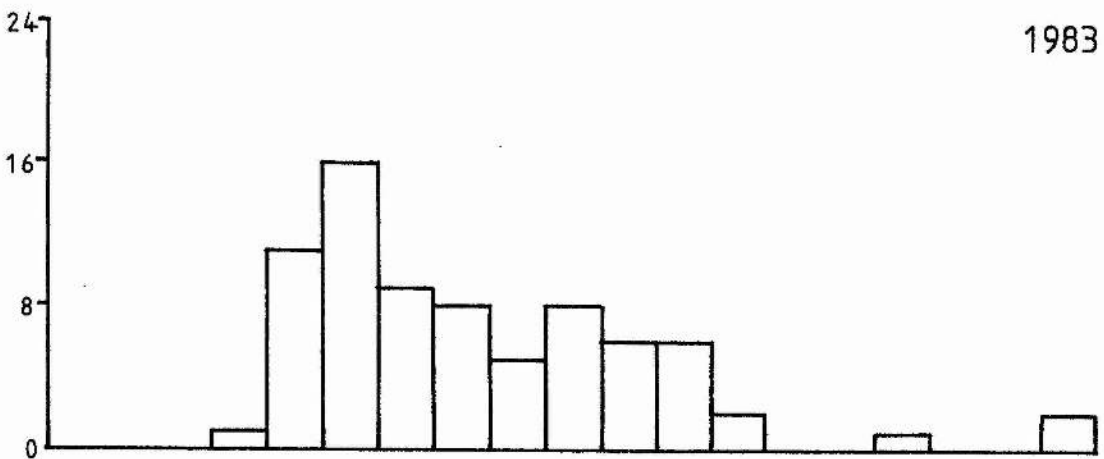
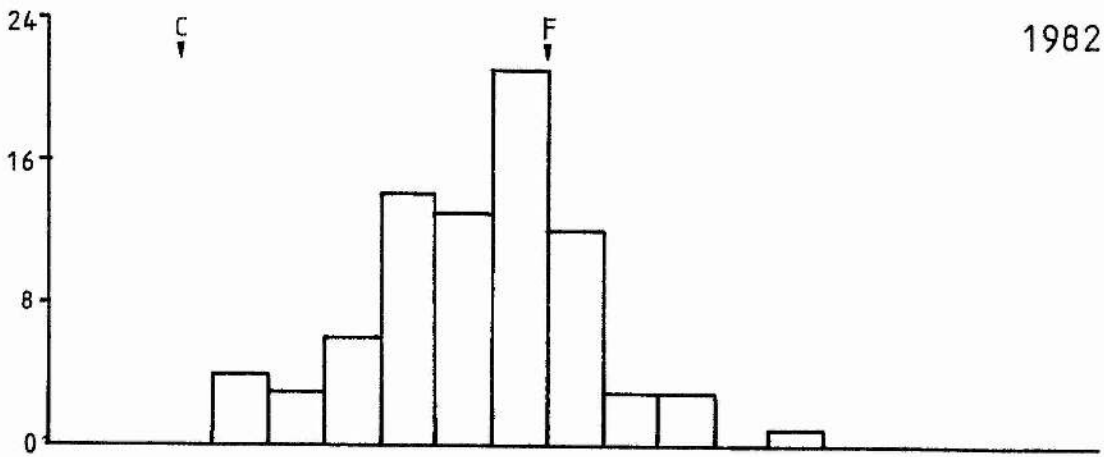
Number of chicks hatched on successive 2-day periods for the three years of the study. (Data in Appendix 11)

C - date children took 36 eggs

F - date fox first entered the colony

FIG 7.2

DATES CHICKS HATCHED



the colony with only 13 chicks hatching from 69 eggs that had been there at that time and a further 8 eggs that were laid later.

In 1983, when there was no fox disturbance, 51.9% of the chicks which hatched did so in the first 8 days of the 19 day hatching period.

### 7.2.2 Discussion

The date of the laying of the first egg on the study area occurred towards the end of April in all 3 years of the study (see Table 6.1). There was only one day's difference in the case of the first dates of laying and the first dates of hatching between 1982 and 1983 and 6 days between 1982 and 1984.

Several researchers have put forward their hypotheses concerning the factors which determine the timing of breeding in birds and these comprise both the functional and the causal aspects. Perrins (1970) considered it common knowledge that birds time the laying of their eggs so that food is generally abundant for the young. Darling (1938), however, maintained that large colonies of gulls start laying earlier and lay their eggs within fewer days than do small colonies, and he suggested that the date of laying depends partly on the amount of stimulation a gull receives from its neighbours' display. Examination of the breeding success of some species of birds shows that there is a strong tendency for the young hatched earliest in the season to have the greatest chance of survival. As natural selection favours parents who have many surviving young the reason why some birds breed late is in question. Perrins (1965) suggested that food supply may limit the females ability to form eggs and thus she may not be able to lay at the optimum time for nestling survival. So, the date of laying may reflect both the foraging ability and the reproductive experience of the parents (Coulson 1966; Perrins 1970; Perrins & Moss 1974). It would seem reasonable also to regard the weather, and primarily the temperature, as a controlling factor influencing egg laying dates, and Kirkman (1937) attributes the late laying of black-headed gulls under study in 1935 to the unusually cold weather.

The time between the date the first egg was laid and the date the first chick was hatched was 24 days in 1982 and 1984 and 26 days in 1983. Although incubation periods as short as 22 days and as long as 28 days were observed the most common incubation period was 24 days.

In both 1983 and 1984, half of the total number of eggs were laid within the first 2/5 of the main laying period and in 1983 half of the total number of chicks hatched within the first 2/5 of the main hatching

period. (The entry of the fox into the colony during the other 2 years of the study reduced the length of the hatching period because of removal of eggs from nests.) In 196 black-headed gull nests studied by Weidmann (1956), first clutches appeared over a period of more than 3 weeks, as they did at Red Myre. However, he found that only 13% of the birds started laying in the first week whereas in this study 35% of the birds started laying in the first week in 1983 and 30% in 1984. Ytreberg (1956) recorded that most of the eggs in several black-headed gull colonies in Norway, were laid in a period of 2 weeks. He too, however, found that only 15-20% of the gulls started laying in the first week of the laying period.

Many researchers have noted the presence of synchronised breeding within colonies of gulls (Darling 1938; Paynter 1949; Patterson 1965; Parsons 1971, 1975, 1976; Parsons et al 1975; Fetterolf 1984) although some research has revealed more synchrony of egg laying in sub-areas of a colony than in the colony as a whole (Burger 1974; Gochfeld 1980), and this supports Darling's theory that the date of laying is affected by stimulation from the behaviour of neighbours.

Parsons (1975) found that both the hatching and fledging success of herring gulls are related to the synchronization of nesting with early and late laying gulls producing fewer fledged young than those breeding during the peak of the season. Nisbet & Drury (1972) also found that early hatched herring gull chicks suffered a markedly lower post fledging survival than those hatching during the peak period.

Feare (1976) suggested that the synchrony he observed in a colony of sooty terns was of social significance since both egg and chick survival were higher where the eggs had been laid at approximately the same time as those in surrounding nests than when the surrounding nests contained partly incubated eggs. He suggested that reduced losses in such cases were due to more effective parental care by birds all at approximately the same stage of breeding. Birds breeding early in the season will hatch chicks when neighbouring pairs are still incubating and relatively tolerant of trespass on outlying portions of their territories (Hunt & Hunt 1976) but more early breeders may lose eggs to predators through being prone to panic flights. Late breeders on the other hand may have reduced

success through laying among birds whose eggs are about to hatch and whose aggressiveness at this time may disturb the incubation of the late birds. Fetterolf (1984) found that aggression was lowest in a synchronous area of a ring-billed gull colony and highest in the asynchronous area. Thus, synchronous nesting in colonial birds may have resulted because early hatching chicks are more prone to predation and late hatching chicks are more likely to be attacked by neighbours.

In 1982 peak hatching occurred just before the fox entered the colony: 209 eggs were laid in this year and about half the eggs had hatched up to this point. Thus, it is likely that peak hatching would have occurred at this time even without disturbance by the fox. However, if the children had not removed 36 of the eggs, many of which may have hatched by this date, then it is likely that peak hatching would have occurred slightly earlier. The hatching success in 1983 (a 'normal' year) was 56.6%, so about 20 of the 36 eggs taken by children would be expected to have hatched. If it is assumed that most of these would have hatched by peak hatching time then peak hatching would have been earlier by one or two days at the very most, ie. 9 or 10 days after the first egg was hatched.

In 1983, a year in which there were no such disturbances, peak hatching occurred 5 days after the first chick was hatched. This is much earlier than the peak hatching 9 to 11 days after the first chick was hatched in 1982. A chi-square test conducted on the frequencies of hatching during 2-day intervals (with the first four days pooled together to make the test feasible) from the first to the 12th day of hatching (up to the date the fox entered the colony in 1982) for 1982 and 1983 showed that the hatching pattern for this period is significantly different for the two years ( $\chi^2=41.67$ ,  $df=4$ ,  $p<0.001$ ). This is an interesting point especially when it is remembered that in 1982 the only chicks that survived the fox were the older ones that were able to take refuge on the open water, ie. those whose parents had started breeding early in the season. In 1983 peak hatching occurred earlier than in 1982 showing that more gulls were breeding earlier in the season in 1983. One explanation for this could be that the gulls which bred early in 1982 and had been successful (at least to some extent) had returned to the colony, and perhaps the same area, in 1983 to breed early again, while some of the gulls that were not successful may have gone elsewhere. There were fewer breeding gulls in 1983 than 1982 which



supports this explanation. I have no way, however, of examining the truth of this suggestion as I only ringed a few adult gulls (those that were difficult to distinguish from their mates) and so I did not know whether or not the gulls were returning to the same area of the colony to breed or even to the same colony.

In 1984 peak hatching occurred only 2 days after the first chick was hatched, 5 days before the fox appeared on the scene. However, had the fox not disturbed the colony, peak hatching might have occurred some days later. There was another problem in 1984 which may also have contributed to this unusual result. During the egg laying period in 1984, while recording details of eggs laid, a lot of eggs were recorded as gone missing without trace or broken. When I was marking a number on one egg it broke up in my hands with very little pressure on it. Unfortunately, the implications of these observations were not realised at the time and it was only a couple of weeks later when it was obvious that nest failure was much greater than in the previous years that the possibility of a thin egg shell problem was realised.

At the time the fox entered the colony in 1984 only 69 eggs were left from 194 previously laid (eight were laid after this date) but only 35 chicks had hatched - a hatching success of only 28.0% over this period compared to a hatching success of 56.6% for the whole of the season in 1983. It is obvious from this that something was wrong in 1984. In Table 7.1 and Figure 7.8, the number of eggs lost through breakage and for unknown reasons before the fox appeared in 1984 was very high at 46.5%. This can be compared to 36.0% for 1983, which was the percentage of eggs lost in this manner during the whole of the breeding season and not just to 8 days after the first chick had hatched as in 1984. In 1983 only 5 (35.7%) of the eggs lost in the breakage/fallen-in-water category were known to have been lost through breaking, while in 1984 17 (94.4%) of the losses in this category were due to breakage ( $\chi^2 = 15.524$ ,  $df = 1$ ,  $p < 0.001$ ).

Black-headed gulls remove egg shells from their nests when the chicks hatch (Ytreberg 1956; Tinbergen et al 1962a, 1962b) and I have also seen gulls eat their own broken eggs or take them in their

bills and drop them in the water. So, many of the eggs that went missing without trace may in fact have been disposed of by the gulls because they were damaged or broken.

Egg shell thickness in birds is known to be effected by several factors. Imperfect diet, especially deficiency of calcium, but also of manganese and vitamin D, causes domestic fowl to lay thin shelled eggs (Sturkie 1965). Thus, shortage of food in a wild bird species could lead to the production of thin shelled eggs. Egg shell thickness has also been inversely correlated with the levels of organochlorines (e.g. DDT, DDE and dieldrin residues) and polychlorinated biphenyls in several species of birds, though mostly in birds of prey (Newton & Bogan 1974, 1978; Klaas et al 1978; Olsen & Olsen 1979; King et al 1980; Newton et al 1980). The majority of such compounds get into the environment through the use of insecticides, although polychlorinated biphenyls are also widely used in the manufacture of plastics and lubricants. They accumulate in the tissues of wild birds, especially birds of prey which are high in the food chain, and effect their ability to form eggs properly. Little information is available, however, on the effects of such compounds on non-raptorial species. It seems unlikely that food availability could be so poor early in 1984, especially in a species that has such diverse eating habits, to be detrimental to egg shell production. Therefore, it can only be suggested that a local food source may have been contaminated by some chemical/insecticide which affected the females' ability to form eggs in some way, resulting in a large number of eggs with thin egg shells being laid in the colony.

TABLE 7.1 NUMBERS OF EGGS LAID AND HATCHED, AND REASONS FOR MORTALITY

	1982		1983		1984	
	No	%	No	%	No	%
<u>NO OF EGGS</u>	209		136		202	
<u>NO OF NESTS</u>	97		62		96	
MEAN EGGS PER NEST	2.15		2.19		2.10	
<u>NO OF NESTS WITH</u>						
1 EGG	20	20.62	15	24.19	24	25.00
2 EGGS	44	45.36	21	33.87	38	39.58
3 EGGS	31	31.96	25	40.32	34	35.42
4 EGGS	2	2.06	1	1.61		
<u>NO OF CHICKS</u>	80		77		48	
<u>NO OF NESTS</u>	47		43		32	
MEAN CHICKS/NEST	1.70		1.79		1.50	
<u>NO OF NESTS WITH</u>						
1 CHICK	22	46.81	16	37.21	20	62.50
2 CHICKS	17	36.17	20	46.51	8	25.00
3 CHICKS	8	17.02	7	16.28	4	12.50
<u>CHICKS FLEDGED</u>	1		36+1		7	
<u>CAUSE OF EGG LOSS</u>						
Children	36	17.22				
Fox	40	19.14			13	6.44
Broken or in water	2	0.96	14	10.29	18	8.91
Failed to hatch	17	8.13	10	7.35	8	3.96
Unknown	34	16.27	35	25.74	115	56.93
(before fox					76	37.62)
(after fox					39	19.31)
<u>CAUSE OF CHICK LOSS</u>						
Fox	*40	50.00			9	18.75
Found dead	20	25.00	9	11.69	2	4.17
Unknown	19	23.75	32	41.56	30	62.50
(before fox	19	23.75			0	0.00)
(after fox	*inc. above				30	62.50)
<u>HATCHING SUCCESS</u>		38.28		56.62		23.76
<u>FLEDGING SUCCESS</u>		1.25		88.31 max		14.58
<u>REPRODUCTIVE SUCCESS</u>		0.48		46.75 min 50.00 max 26.47 min		3.47

### 7.3 Numbers of Eggs Laid and Chicks Hatched

#### 7.3.1 Results

Figure 7.3 shows the numbers of nests with 1, 2, 3, and 4 eggs laid in them and with 1, 2, and 3 chicks hatched in them for the 3 years of the study. The data for these graphs are included in Table 7.1. The results for eggs laid in 1982 are likely to be inaccurate because they were derived from only intermittent checks on the numbers of eggs in the nests. It is likely that more eggs were actually laid in some nests but were laid and lost between two visits and so were not recorded. Therefore, the mean number of eggs laid per nest for 1982 is likely to be lower than it should be. The graphs for 1983 and 1984 are much more accurate, as regular visits were made to the study area in those years. However, some eggs are bound to have been laid and lost between visits especially when bad weather or some other reason prevented me from going out to the study area.

The mean number of eggs laid per nest ranges from 2.10 to 2.19 during the 3 year study. The mean number of chicks hatched per nest, however, ranges from 1.50 to 1.79, with 1.50 a seemingly low value in 1984. Analysis of variance, however, shows no significant differences in the means (eggs -  $F=0.256$ ,  $df=2,252$ ,  $p>0.1$ ; chicks -  $F=1.535$ ,  $df=2,118$ ,  $p>0.1$ ).

In 1982 the largest class of clutch (45.4% of nests) was 2 eggs, but as few trips were made to the study area during the egg laying period of this year it is likely that more gulls than were recorded may have laid 3 eggs. In 1983 the largest class of clutch (40.3% of nests) was 3 eggs and in 1984 the largest class of clutch (39.6% of nests) was 2 eggs, with 3 egg nests a close second at 35.4%. Single egg clutches, however, were in the minority in all three years.

In 1982 the largest class of broods (46.8% of nests) had one chick, with fewest (17.0% of nests) with 3 chicks. In 1983 46.5% of the broods had 2 chicks and again fewest (16.3%) had 3 chicks. In 1984 62.5% hatched only one chick with fewest (12.5%) again hatching 3 chicks. A 3x3 chi-square test of the

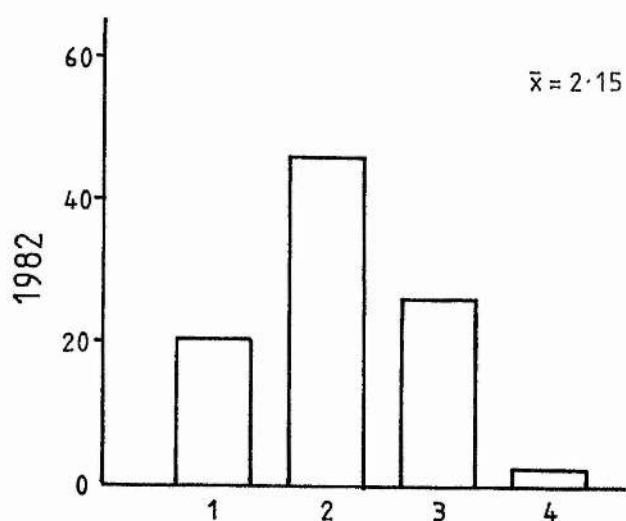
FIGURE 7.3

Percentage of nests containing different numbers of eggs and chicks for each of the study years. The means for each graph are included. (Data in Table 7.1)

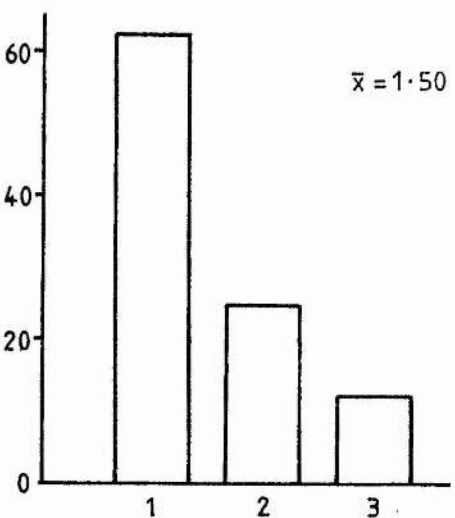
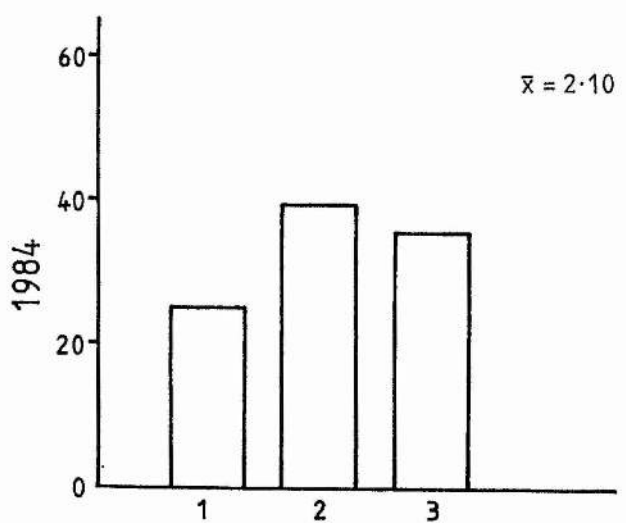
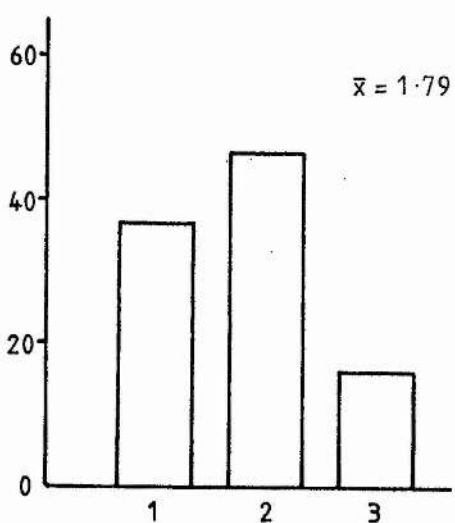
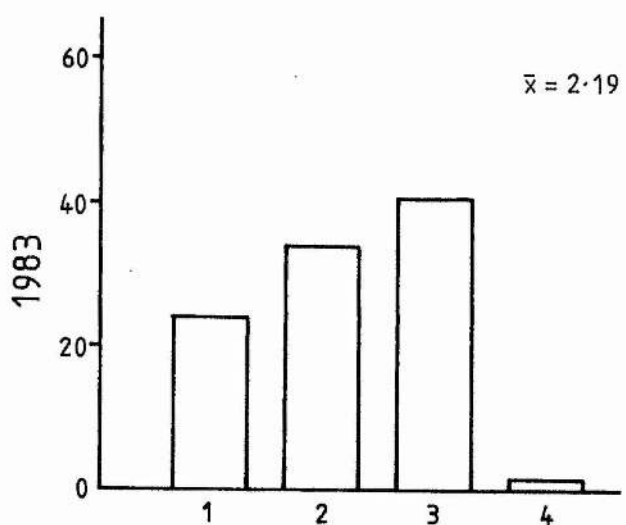
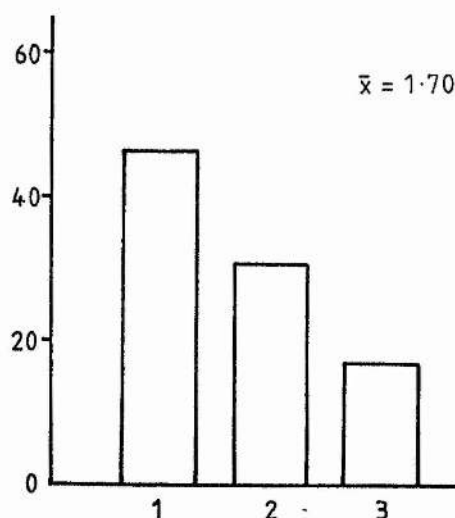
FIG 7.3

% NESTS CONTAINING 1,2,3 OR 4 EGGS AND CHICKS

EGGS



CHICKS



frequencies of different sized broods of chicks hatched during the three years showed that the pattern of brood sizes was the same for all three years ( $\chi^2=5.218$ ,  $df=4$ ,  $p>0.1$ ).

Figure 7.4 and Appendix 12 show the percentage of eggs from different sized clutches that hatched and that produced fledged young, and the percentage of chicks from different sized broods that subsequently fledged. Only the results for 1983 are included here because of the drastic effect the fox had in the other years. The results suggest that single-egg clutches are less likely to produce chicks and fledged young than 2- and 3-egg clutches, but chi-square analysis shows that there is no significant difference in the hatching and fledging success from different sized clutches (hatched -  $\chi^2=2.041$ ,  $df=2$ ,  $p>0.1$ ; fledged(min) -  $\chi^2=0.414$ ,  $df=2$ ,  $p>0.5$ ; fledged(max) -  $\chi^2=1.882$ ,  $df=2$ ,  $p>0.1$ ). There is also no significant difference in the number of chicks fledged from different sized broods (fledged(min) -  $\chi^2=0.356$ ,  $df=2$ ,  $p>0.5$ ; fledged(max) -  $\chi^2=0.130$ ,  $df=2$ ,  $p>0.9$ ).

To see if there was any difference in the numbers of eggs laid, the numbers of chicks hatched and the hatching and fledging success at different times of the season, the egg laying period was divided into three smaller periods of early laying, mid-season laying and late laying. Each of these periods contained approximately equal numbers of clutches. As the laying dates were not known accurately for a lot of the eggs laid in 1982, only the data for 1983 and 1984 were used in this section.

Figure 7.5 and Appendix 13a show the percentage of clutches, laid during the three different periods, which contain different numbers of eggs. Unfortunately the frequencies are generally small making it difficult to draw any significant conclusions from the results. Examination of the graphs of eggs laid in 1983 gives the appearance that there is a tendency for more larger sized clutches to be laid at the beginning of the season. The means for the three periods show a decreasing trend throughout the season but analysis of variance shows that the differences between the means are not significant ( $F=0.074$ ,  $df=2,59$ ,  $p>0.05$ ). The results for 1984 again show a downward trend of the mean number of eggs per nest with seasonal period. Again, however, there are no significant differences between the means ( $F=0.319$   $df=2,59$ ,  $p>0.05$ ). 3x3 chi-square tests of the data for each of the two years show

FIGURE 7.4

(a) Percentage of eggs from clutches of different sizes that were hatched and that produced fledged young in 1983.

(b) Percentage of chicks from different sized broods that subsequently fledged in 1983.

The fledged (min) graphs show the percentage actually known to have fledged, and the fledged (max) graphs show the maximum percentage that may have fledged if all the chicks which disappeared survived in other parts of the colony. (Data in Appendix 12)



FIG 7.4

BREEDING SUCCESS OF DIFFERENT BROOD SIZES

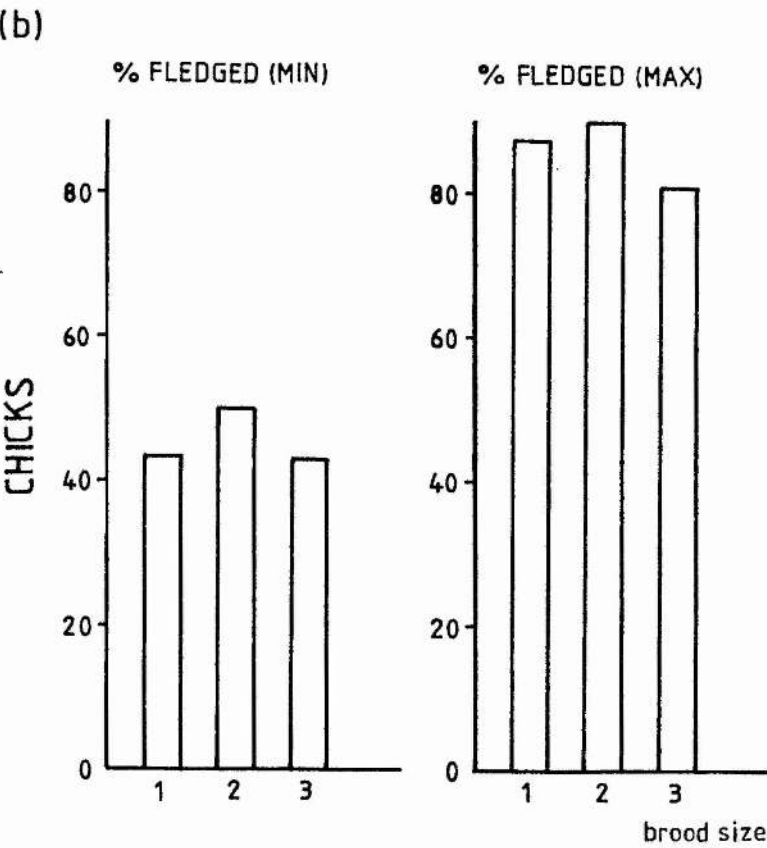
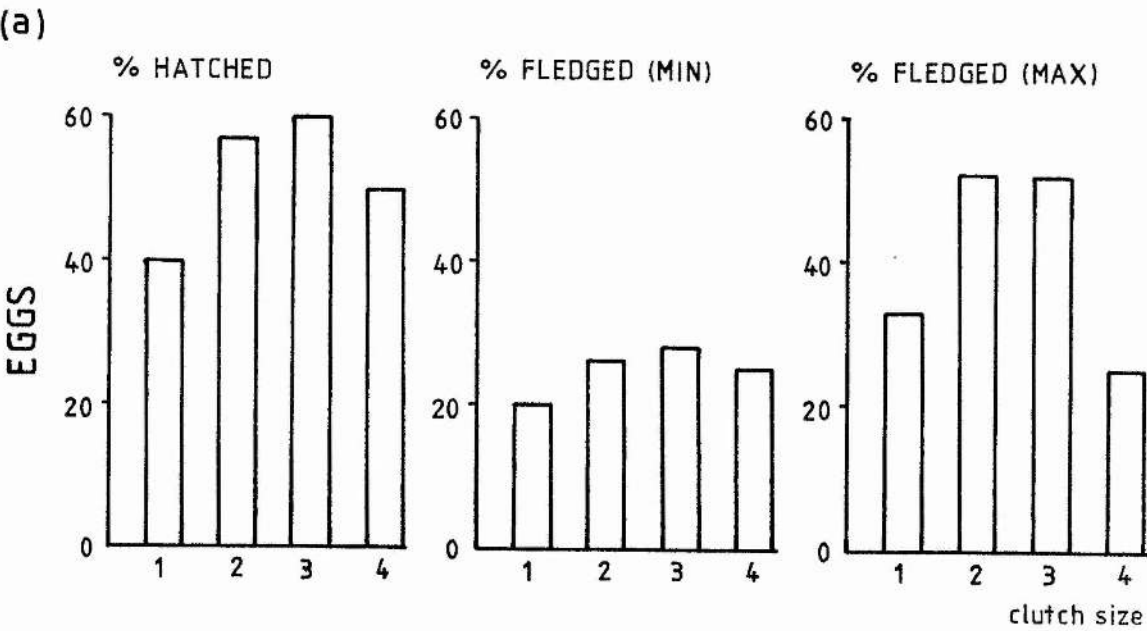
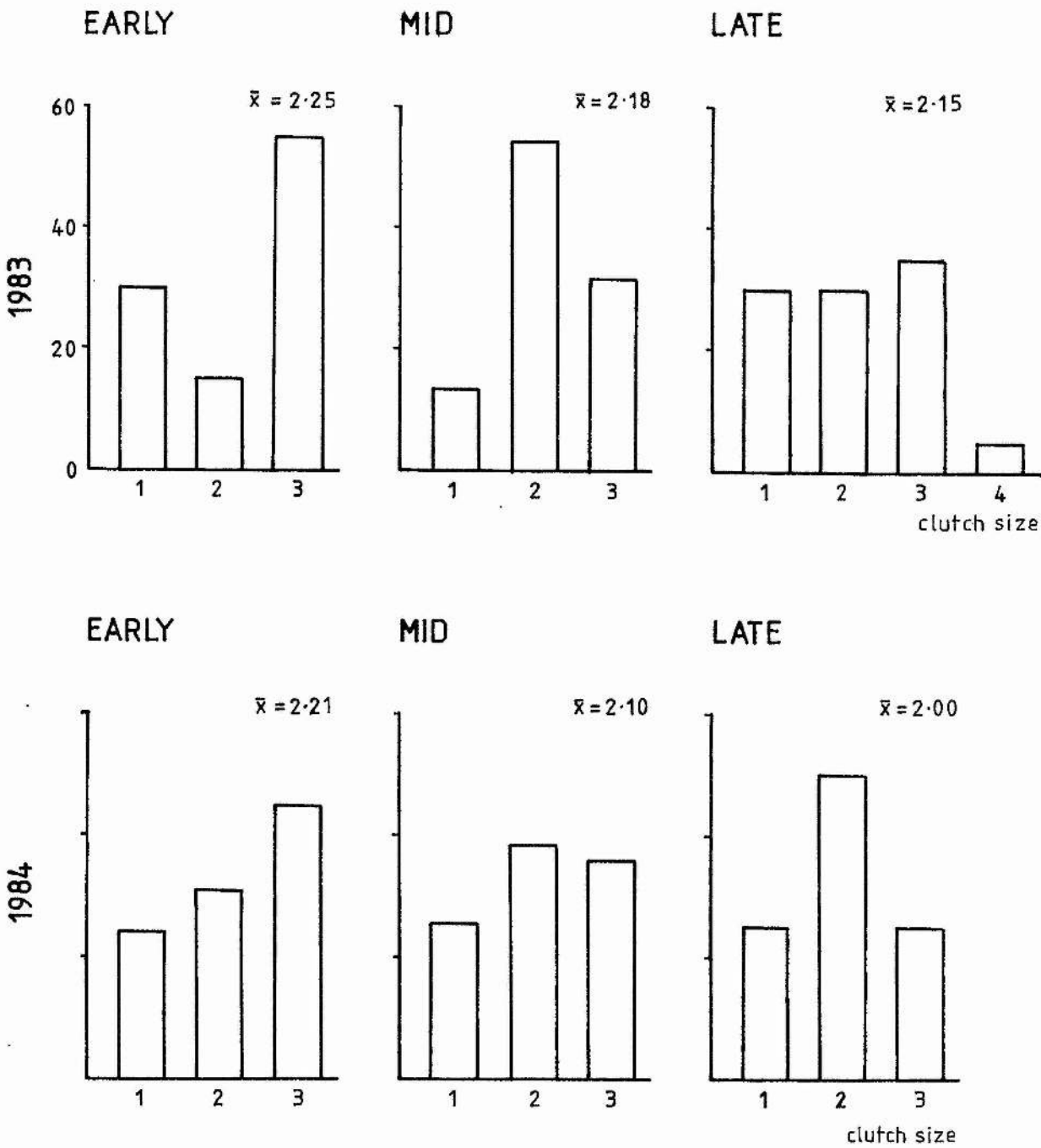


FIGURE 7.5

Percentage of clutches of eggs laid at different times of the season, containing 1, 2, 3 and 4 eggs in 1983 and 1984. (Data in Appendix 13a)

FIG 7.5

PERCENTAGE OF CLUTCHES OF EGGS LAID



that there is no significant difference in the pattern of frequencies between different times of the season in either year ( $1983 - \chi^2 = 8.001, df = 4, p > 0.05$ ;  $1984 - \chi^2 = 2.916, df = 4, p > 0.5$ ).

Figure 7.6 and Appendix 13b show the percentage of broods hatched at different times of the season which contain different numbers of chicks. In 1983 the mean numbers of chicks per nest in the early-season and the late-season periods appeared larger than the mean for the mid-season period. However, this is not significant ( $F = 0.569, df = 2, 40, p > 0.05$ ).

In 1984 the fox got into the colony as the first eggs which were laid in the mid-season period were beginning to hatch. Therefore, few gulls hatched young from eggs laid in the middle of the season and only three pairs hatched young from those laid late in the season. (These have not been included in Figure 7.6 because there are so few.) Over 90.0% of the nests that hatched chicks in mid-season hatched only one chick. In part this is due to the fact that the fox may have plundered nests which had only hatched one chick, and so the other eggs did not have a chance to hatch, but it was also due to the fact that increased losses of eggs through breakage left more nests with single eggs.

The percentage of eggs, laid at different times of the season, which hatched chicks and produced fledged young, is shown in Figure 7.7 and Appendix 14. From the graphs the impression is gained that more chicks were hatched from eggs laid earlier in the season than later but in 1983 this is not statistically significant ( $\chi^2 = 4.614, df = 2, p > 0.05$ ). In 1984 this result is to be expected because of the great loss of eggs after the fox entered the colony.

It is difficult to make deductions from the graphs showing the numbers of young that fledged at different times of the season because the exact number that fledged is not known. Only the minimum number that were seen to have fledged and the maximum number that could have fledged are known. The 1983 graphs give the impression that fewer chicks may have been fledged from eggs laid late in the

FIGURE 7.6

Percentage of broods of chicks hatched at different times of the season, containing 1, 2, and 3 chicks in 1983 and 1984. (Data in Appendix 13b)

FIG 7.6

PERCENTAGE OF BROODS OF CHICKS HATCHED

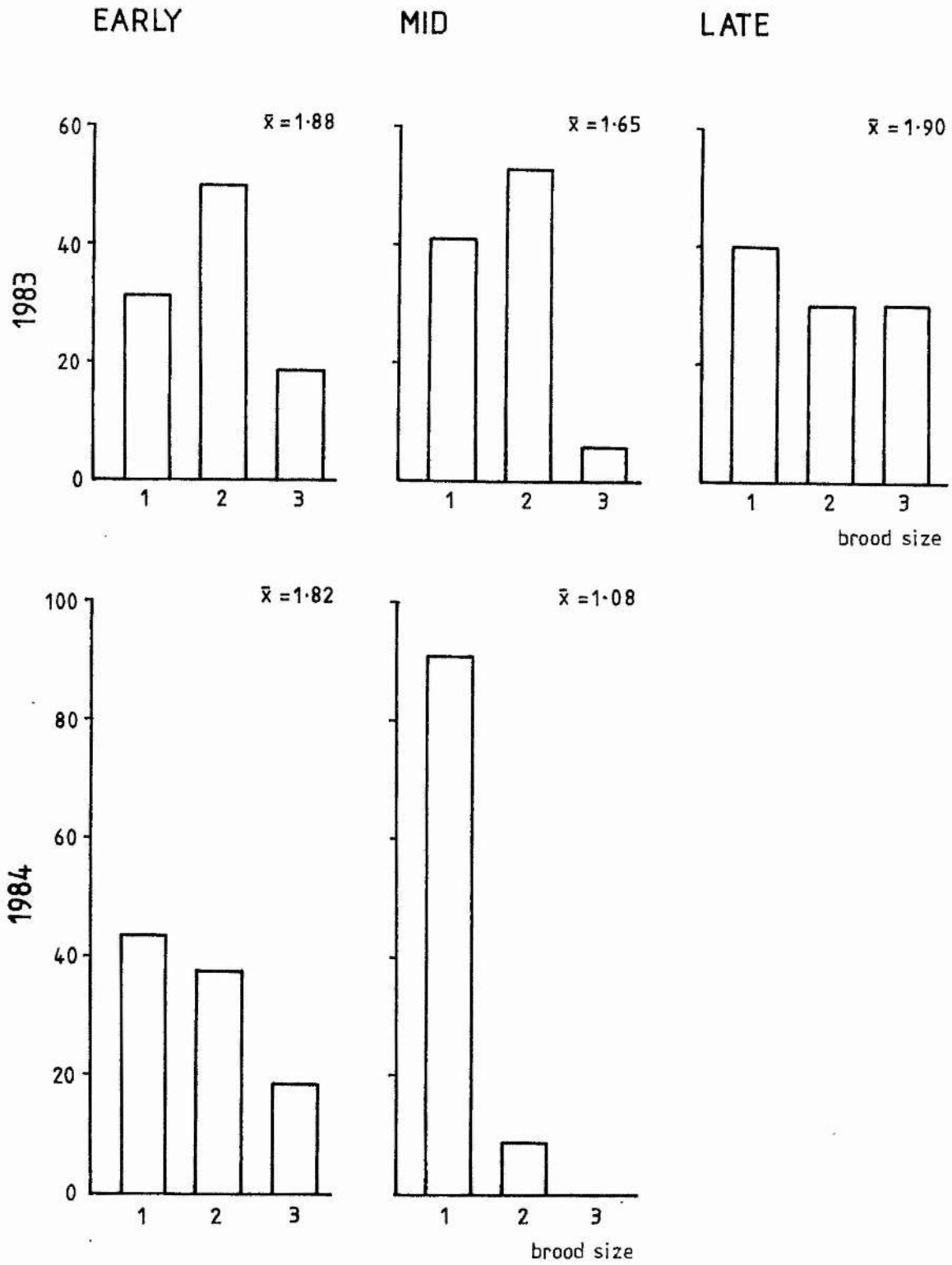


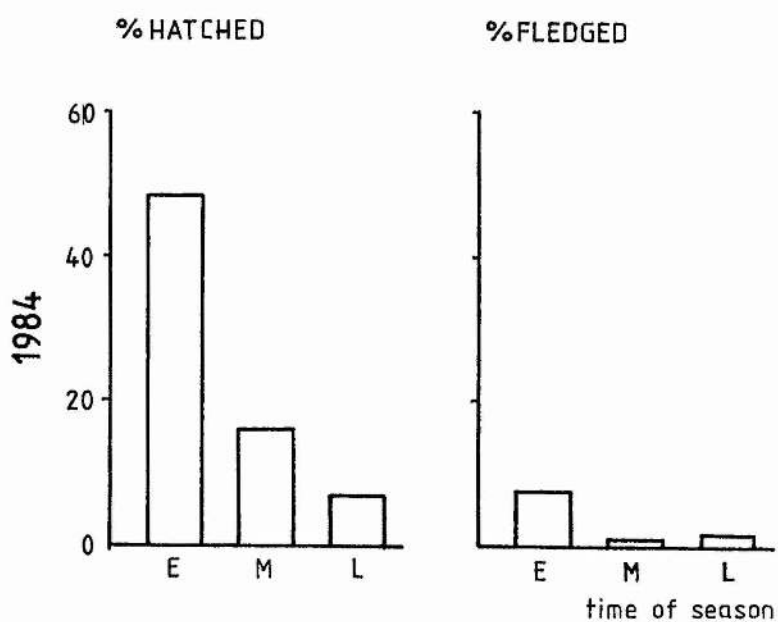
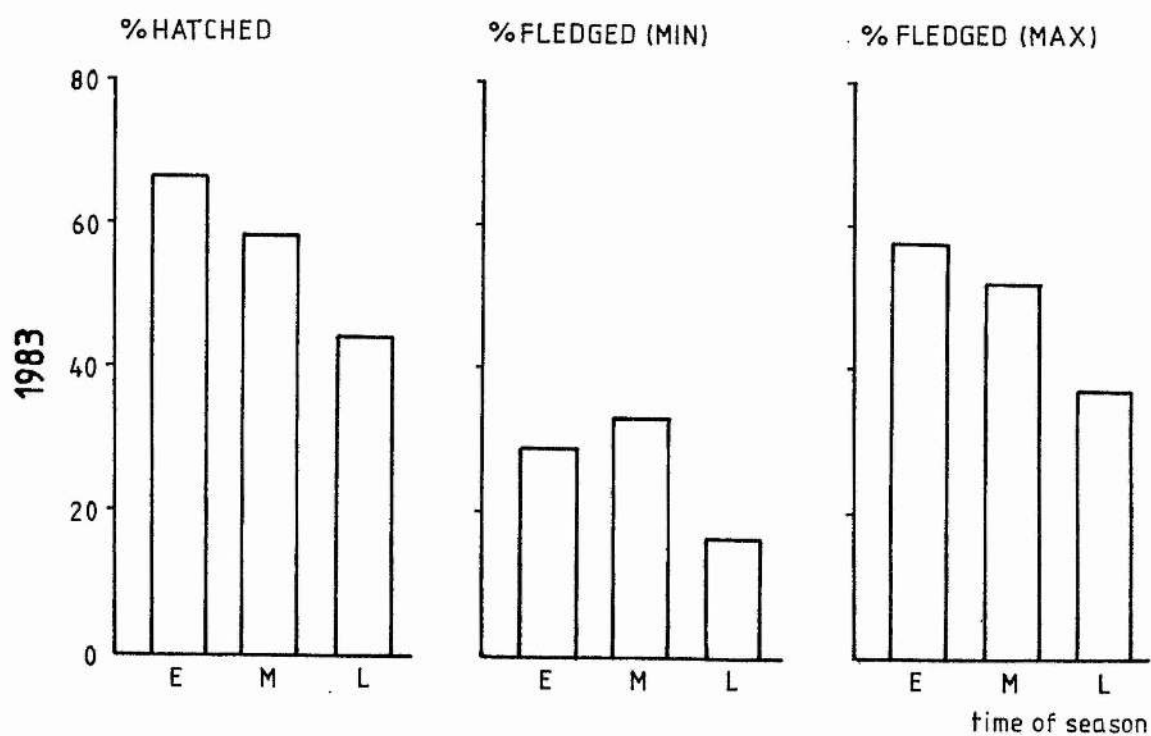
FIGURE 7.7

Percentage of eggs, laid at different times of the season, which hatched chicks and which produced fledged young in 1983 and 1984. (Data in Appendix 14)

In 1983 the fledged (min) graph shows the percentage actually known to have fledged, and the fledged (max) graph shows the maximum percentage that may have fledged if all the chicks which disappeared survived in other parts of the colony.

FIG 7.7

PERCENTAGE OF EGGS LAID





season than early, but this is not statistically significant (fledged(min) -  $\chi^2=3.591$ ,  $df=2$ ,  $p>0.1$ ; fledged(max) -  $\chi^2=3.958$ ,  $df=2$ ,  $p>0.1$ ) and again the results observed in 1984 are to be expected because of the predation on eggs and chicks by the fox.

### 7.3.2 Discussion

According to the literature black-headed gulls normally lay 3 eggs, although examples are found of both smaller and larger clutches. The only year in which the largest group (40.3%) of gulls laid 3 eggs at Red Myre was 1983. In 1982 it is probable that many more 3-egg clutches were in fact laid than were recorded, but in 1984 the number of 3-egg clutches was slightly less (35.4%) than the number of 2-egg clutches (39.6%). Weidmann (1956) reported that 70.1% of black-headed gull clutches contained 3 eggs, while Ytreberg (1956) recorded an average of 88.4% over a three year study. The mean number of eggs per nest ranged from 2.10 in 1984 to 2.19 in 1983 at Red Myre. 2.54 eggs per nest was the average recorded by Weidmann (1956), and Ytreberg (1956) recorded means of 2.81, 2.86 and 2.92 in the three successive years of his study. Thus there appear to have been fewer 3-egg clutches laid at Red Myre than might have been expected.

At Red Myre the study area was visited at most once a day but 2 days or more sometimes elapsed between visits if the weather was wet or if I was unable to visit the colony. Thus it may be that more 3-egg clutches were laid in all 3 years and that a lot of eggs were lost between visits. Ytreberg (1956) frequently noticed that eggs disappeared without trace and commented that it was difficult to decide whether the size of any given clutch gave a true picture of the number of eggs which had been laid, even though the nests may have been inspected twice a day. However, if in fact 70-90% of clutches were 3-egg clutches then approximately 17-25% of all eggs laid would have had to be lost between visits in 1983 and 1984.

Several studies on herring gulls have shown that larger clutches of eggs have a lower egg mortality than smaller ones, the chief cause of egg loss occurring through predation. Paynter (1949), Brown (1967) and Kadlec et al (1969) all show that the hatching success of 2-egg clutches is poorer than that of 3-egg clutches. The results here, although indicating that there may be a tendency for eggs from smaller clutches to be less successful than those from larger clutches, were not significant.

The time of hatching appears to play an important role in the success of raising young. Hunt & Hunt (1976) and Feare (1976) found that chicks hatched early in the season had a higher probability of surviving than those that were hatched later, for glaucous-winged gulls (*Larus glaucescens*) and sooty terns respectively. Paynter (1949) and Vermeer (1970) also found that early nesting herring gulls and california gulls (*Larus californicus*) had the greatest success where the major cause of chick loss was killing by neighbours. Kruuk (1964) and Patterson (1965), however, found that both early and late hatching black-headed gull chicks suffered higher mortality to predators than chicks hatched in mid-season. Mid-season herring gulls' nests were also found to produce more young per nest than did early or late nests (Brown 1967; Kadlec et al 1969; Parsons 1971, 1975) although in one out of the six studies conducted by Kadlec et al the earliest nests were the most productive. In this study, although there is a slight tendency for egg and chick mortality to be lowest for early nesters and highest for late nesters, this is not significant. However, because of the disturbance of the colony by the fox during two years of the study, there were few data available for an examination of this question.

It may be that the differences in breeding success with time of laying and hatching seen in many studies are related in part to the synchronization of breeding. Early and mid-season nesters may have greater success because neighbouring pairs of gulls will either be at the same stage as themselves or still incubating when they are bringing up young chicks, while late nesters will still be trying to incubate when most of their neighbours have chicks and are more aggressive towards other gulls near their territories (Fetterolf 1984). Late nesters will also be caring for very young defenceless chicks when most of the broods around them will be much older. This may be particularly important for the larger gulls which are cannibalistic and suffer most chick mortality from the attacks of neighbouring gulls. Losses to predators in general are greater very early in the season when the gulls are easily disturbed and late in the season when the majority of the chicks are well grown (Kruuk 1964) and leave their territories for much of the time leaving late nesters more exposed on the breeding areas. Therefore, gulls that breed early or especially during the peak period would be expected to be more successful than those breeding later in the season.

Post-fledging survival may also be related to the date of hatching (Perrins 1965, 1966; Lack 1966; Fretwell 1969; Nisbet & Drury 1972). Nisbet & Drury found that early hatched herring gull chicks had a higher post-fledging survival than chicks that were hatched midway through the season or towards the end of it. Perrins (1966) showed that late hatched manx shearwaters (*Puffinus puffinus*) were less likely to return to the same breeding colony in subsequent years than those hatching early in the season. Nisbet & Drury (1972) suggested that early fledged chicks may have dominance over late fledged chicks and that in years of high mortality, the more dominant juveniles are at an advantage.

## 7.4 Reasons for Egg and Chick Mortality

### 7.4.1 Results

Table 7.1 gives details of the numbers of eggs laid and chicks hatched in the three study years, and details of the reasons for any egg and chick losses. The number of nests under study that had eggs laid in them was 97 in 1982 and 96 in 1984 but only 62 in 1983. Of the 62 nests with eggs in 1983, 43 (69.4%) had chicks hatched in them. However, in 1982 and 1984, from 97 and 96 nests respectively only 47 (48.5%) in 1982 and 32 (33.3%) in 1984 hatched chicks because of the fox.

Figure 7.8 gives a graphical representation of the remainder of the table showing the reasons for egg and chick loss. The main points are as follows:-

#### Eggs

1982 The majority of egg losses were attributed to the fox and the children (36.4% of eggs laid) with another 16.3% of eggs lost for reasons unknown. 38.28% of the eggs laid hatched.

1983 Most losses were for unknown reasons (25.7% of eggs laid) while 56.6% of the eggs laid hatched.

1984 Again, most losses were for unknown reasons but to a much greater degree than 1983. A total of 56.9% of eggs laid were lost for reasons unknown, 37.3% before the fox entered the colony and 19.3% after. Only 23.8% of the eggs laid were hatched.

#### Chicks

1982 The majority of chick losses were due to the fox (50.0% of chicks hatched). 23.8% of the chicks disappeared for unknown reasons before the fox appeared (those that disappeared after the fox entered the colony have been included in the 50.0% attributed to the fox) and another 25.0% were found dead, 22.5% after the fox had been and 2.5% before. Only 1.3% (1 chick) survived to fledge.

**FIGURE 7.8**

Percentage of eggs and chicks lost for various reasons during each year of the study. The resulting hatching and fledging successes are also shown for each year. (Data in Table 7.1)



losses occurring before the fox entered the colony



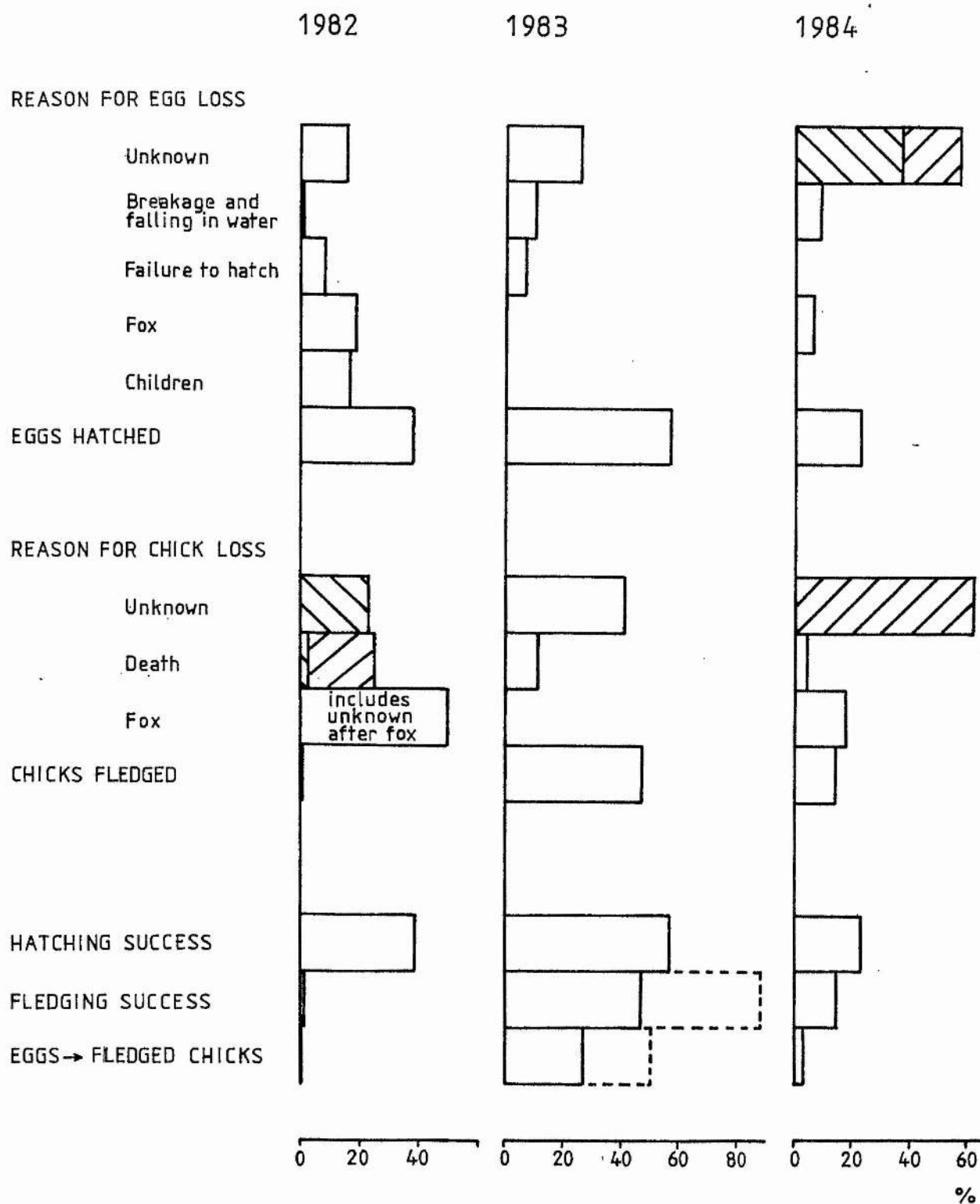
losses occurring after the fox entered the colony



maximum possible fledging success and reproductive success. The solid line here shows the minimum success if all the chicks that disappeared had died or been killed.

FIG 7.8

PERCENTAGE LOSSES OF EGGS AND CHICKS



1983 41.6% of the chicks disappeared for unknown reasons while 11.7% were found dead. 46.8% survived to fledge.

1984 18.8% of the chicks that were lost were attributed to the fox while 62.5% disappeared for unknown reasons after the fox had been in the colony. Only 14.6% survived to fledge.

The eggs lost for reasons unknown could include unseen predation and breakages, and eggs which fell out of the nest and were subsequently removed. In 1982 fewer eggs were lost for unknown reasons (16.3%) but this was for a shorter period because the fox interrupted the season. In 1984 many eggs were lost for unknown reasons (56.9%) and mostly (37.6%) before the fox arrived. This amount could not be attributed to the expected levels of natural breakage and predation and the possibility of thin egg shells as the cause for this loss has already been discussed (Section 7.2.2). In 1984 only a small number (6.4%) of eggs were lost to the fox because after the fox had entered the colony, wire mesh was placed around the study area to keep the fox out. The eggs lost for reasons unknown after the fox first entered the colony in 1984 were probably mostly taken by crows and other predators (see Chapter 5).

In 1982 a number of chicks (23.8%) disappeared for unknown reasons before the fox appeared on the scene and it is likely that some of these may just have moved out of the study area. In 1984 no chicks disappeared before the fox came because it arrived only 7 days after the first chick had hatched. In 1982 a large number of chick losses were attributed to the fox. In this year the whole colony apart from about 20 chicks was wiped out in 3 nights and so all the chicks that disappeared after the arrival of the fox were included as being taken by it. In 1984 only 9 chicks (18.8%) were taken from the study area by the fox and after that it was protected by wire mesh.

On several occasions, I saw chicks move away from their home territory. When this happened the parents usually followed the chick, chasing away any other gulls that came near the chick. In most cases, the chick finally took cover in some vegetation as the barrage of attacks by adult gulls increased. Its parents landed nearby and very often set up a new territory, where they stayed for part or the rest of the season.



I also saw chicks move away from the study area when they got lost after a disturbance. During a disturbance in the colony when the adult gulls took to the air, the chicks ran for cover, and some chicks went well away from their territory before they found somewhere suitable. If they could not find their way back or had to take cover elsewhere from attacks by other gulls they were often found by their parents who heard their calls. They then set up a new territory where they found the chick, or settled nearby if there was a suitable place eg. a deserted nest. On the occasions this was seen to happen, some families appeared back on their original territories a day or two later but others remained where they were for part or the rest of the season. Many of the cases of chick movement I saw happened shortly after I had been out on the study area to check up on the nests, and it is likely that many of these moves occurred as a result of my activity in the colony.

As the breeding season progressed each year the vegetation grew rapidly and by the time most of the chicks had hatched, most of the nests in the colony were hidden from view. The vegetation was kept cut down in front of the nests that were under observation but very few of the other nests in the colony could be seen. Even when chicks were spotted in other parts of the colony it was rare that their legs were ever seen to enable identification by rings if present. So, it was rarely known whether or not chicks that disappeared from the study area had moved to other parts of the colony.

Some of the gulls' nests were built quite high on tufts of rushes and if one chick fell out of the nest and could not get back up to it then it usually died of exposure. If, however, it was an only chick, the parents usually left the nest and built a new nest at the base of the tuft, or moved to a nearby deserted nest. In other cases chicks that had gone too far from the nest and could not find their way back, and were not located by their parents, usually died of exposure. Some chicks were found dead with raw-red heads from the pecks of adult gulls and it is likely that these chicks also lost their way and could not get protection from the pecks of other gulls or get back to their nest.

Pairs of gulls in the study area were seen adopting chicks both from other parts of the study area and from other parts of the colony, and it is likely that some of the chicks that disappeared from the study

area, leaving siblings behind, may have been adopted in other parts of the colony. In nearly all the cases of adoption seen at Red Myre and in many reported by other researchers (Davies & Carrick 1962; Burger 1974; Beer 1979) the adopted chicks appeared to be of comparable age or slightly older than the brood they were adopted into, and the chicks of the adopting pair were usually less than a week old. Gulls with older chicks discriminated between strange chicks and their own and aggressively chased strange ones out of their territory.

Figure 7.9a and Appendix 15 show the percentage of 1st, 2nd and 3rd laid eggs, in 3-egg clutches, which hatched, failed to hatch and were lost before they were due to hatch. The graphs suggest that fewer 3rd chicks hatched than 1st and 2nd and that more 3rd chicks died hatching or failed to hatch. More 1st and 2nd eggs seem to have been lost before they were due to hatch than 3rd eggs. The number of observations of eggs that failed to hatch and of eggs that were lost before hatching are too small for valid statistical analysis. However, the eight recorded cases of third eggs dying while hatching or failing to hatch seems particularly high compared to the single 1st and 2nd eggs that failed to hatch. The difference between the number of 3rd eggs that hatched and the number of 1st and 2nd eggs that hatched, however, is not significant ( $\chi^2 = 1.526$ ,  $df = 2$ ,  $p > 0.5$ ).

Figure 7.9b shows the percentage of 1st, 2nd and 3rd hatched chicks, from 3-chick broods, which were fledged, found dead and which disappeared. This suggests that fewer 3rd chicks were fledged than 1st or 2nd and that more 3rd chicks were found dead than 1st or 2nd. The number of 3-chick broods was only 8 and so with such a small number no significant conclusions can reasonably be drawn from the data.

FIGURE 7.9

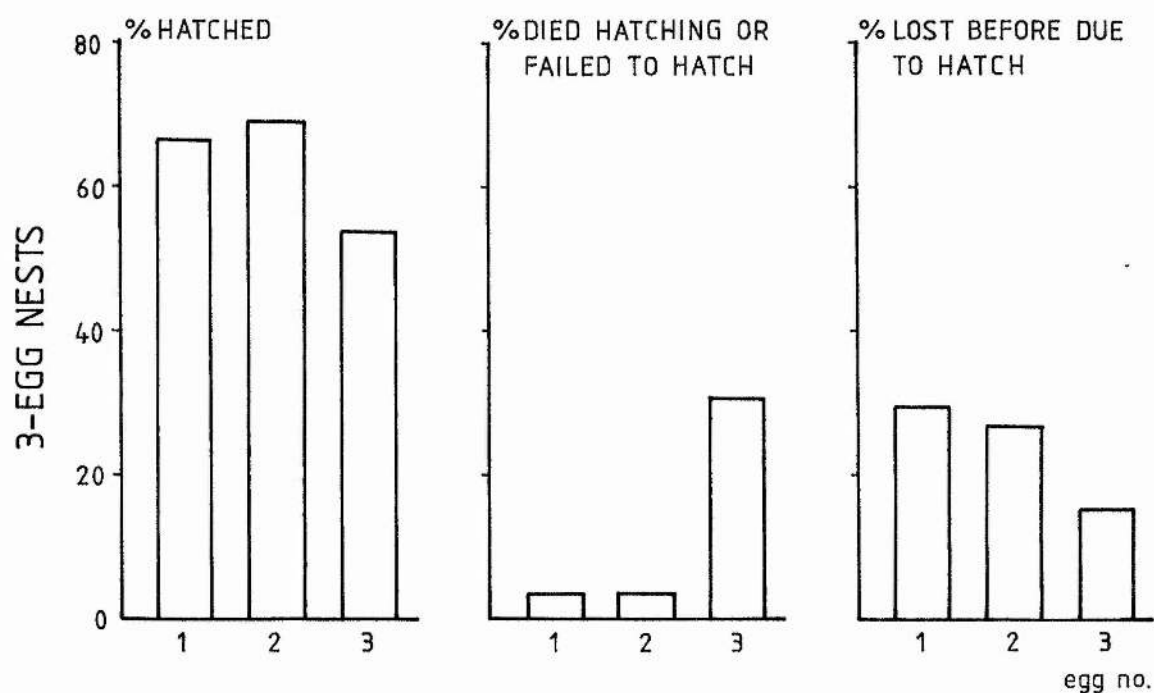
(a) Percentage of first, second and third laid eggs, from three-egg clutches, which hatched, failed to hatch and were lost before they were due to hatch. (Data in Appendix 15)

(b) Percentage of first, second and third hatched chicks, from three-chick clutches, which were fledged, found dead and which disappeared. (Data in Appendix 15)

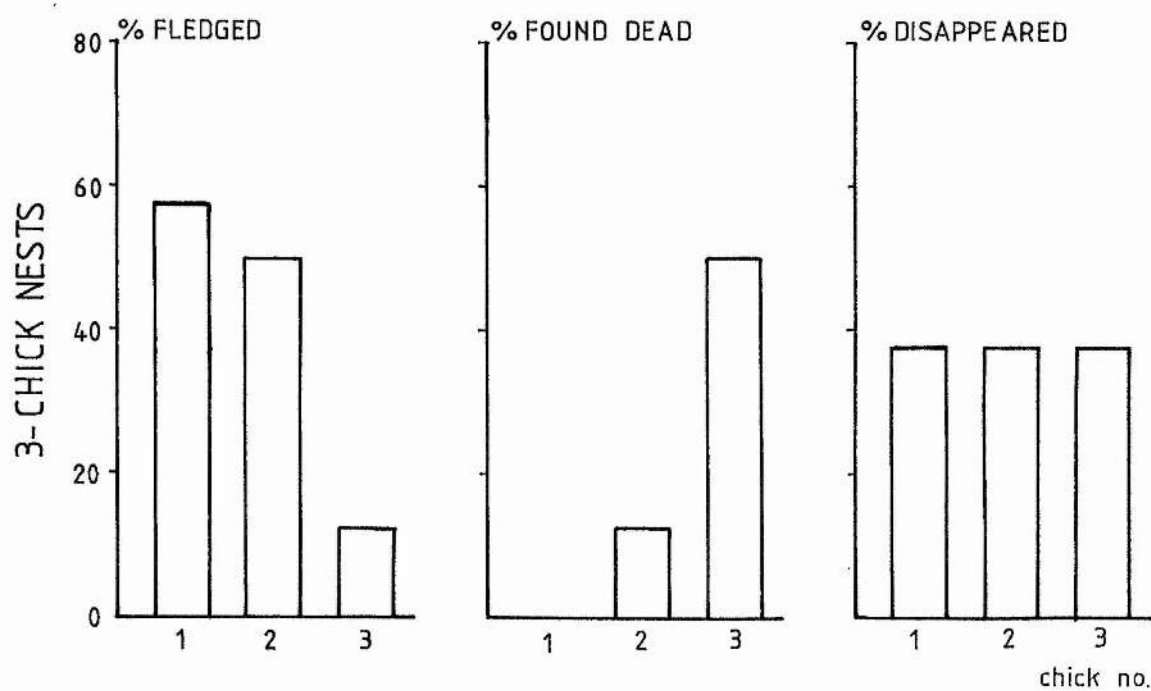
FIG 7.9

PERCENTAGE OF 1ST, 2ND AND 3RD EGGS AND CHICKS

(a)



(b)



#### 7.4.2 Discussion

The net result of the egg losses during the study was that in 1983 56.6% of the eggs laid hatched, compared to 38.3% in 1982 and 23.8% in 1984. Few visits were made to the study area during the egg laying period in 1982 and more eggs may have been laid than were recorded so 38.3% will be the maximum hatching success possible in that year. Ytreberg (1956) found the hatching success of black-headed gulls in two successive years to be 75% and 78%, much higher than the 57% success in 1983 at Red Myre. Kadlec et al (1969) found the hatching success for herring gulls to be 60-80% and Coulson & Wooller (1984) reported a hatching success of 67% for kittiwakes (*Rissa tridactyla*).

In 1983 most chicks disappeared for reasons unknown (46.6%). As chicks were seen moving away from the study area during or after disturbances, it is possible that many of these chicks may have moved to other areas of the colony and subsequently fledged. In 1982 a great number of chicks disappeared after the fox had been in the colony (62.5%). Wire mesh was placed around the study area after the first occasion that the fox had been in the colony, so it is unlikely that it would have taken many of these chicks. Most of them were probably taken by crows and perhaps other avian or small mammal predators (see Chapter 5).

A few chicks were found dead on the study area each year. In 1982 a lot of chicks were found dead after the fox came into the colony. The study area was not protected by wire mesh in this year and so it is likely that most of these were killed and left by the fox. These other deaths recorded occurred for several reasons, the main one probably being exposure after the chicks were separated from their parents.

In large *Larus* gulls, killing of chicks by neighbours is an important cause of chick mortality (Paynter 1949; Drury & Smith 1968; Parsons 1971; Hunt 1972; Panov et al 1980) and many instances of cannibalism have been reported, especially in times of food shortage (Panov et al 1980). Black-headed

gulls are cannibals only of eggs and newly-hatched chicks, although they will attack chicks which stray into their territory and can seriously injure or kill small chicks. Few chicks are killed from such attacks though and at Red Myre there were more instances of death through exposure while hiding from attacking gulls. Many unprovoked attacks on chicks, however, were seen in this study, usually when a chick or brood of chicks decided to move away from its present territory, or when a chick got lost after a disturbance. On these occasions chicks seen wandering in the open, far from the territories of any gulls, were repeatedly attacked by adult gulls. If the parents of the chick were aware of its position then they fended off a lot of the attacks, but the chick was not left in peace until it took cover in some vegetation and was joined by its parents.

Chicks that get separated from their parents and are unable to find their way back to their territory do not always perish. Sometimes such chicks survive by being adopted by other breeding gulls in the colony. The adoption of strange chicks has been reported for several colonial species of gulls (Ytreberg 1956, black-headed gull; Burger 1974, Franklin's gull; Holley 1971, 1981; Graves & Whiten 1980, herring gull; Beer 1979, laughing gull (*Larus atricilla*); Miller & Emlen 1975, ring-billed gull) and several instances were seen in this study.

To achieve maximum reproductive success a parent gull must not only successfully rear its own chicks but must not contribute to the survival of unrelated chicks at the expense of its own offspring. Thus, mechanisms would be expected to have evolved to ensure that parental care will be restricted to the correct offspring. In the main, individual territories probably ensure this during the egg and early chick stage, and as chicks become more mobile individual recognition appears to maintain it (Davies & Carrick 1962; Beer 1969, 1970a, 1970b, 1979; Burger 1974; Miller & Emlen 1975). It is evident, however, that these devices do not always work, as many instances have been recorded of gulls rearing unrelated chicks. It was evident at Red Myre that many such instances probably arose as a direct result of disturbance by myself, and in an undisturbed colony the adoption of strange young may be a rare occurrence. Normally the study area was visited once a day to number eggs and ring chicks, and by 2-3 days of age, chicks left the nest to look for cover during the disturbance. However, on one occasion

when a visit was not made to the study area during a period of 2 days, many of the young chicks up to 5 days of age did not leave the nests until they saw me approaching. Thus, it would appear that the regular visits to the colony caused increased motility of the chicks with the consequent increase in the numbers of chicks straying away from their own territories.

One interesting point to note is that the occurrence of chick adoption selects for greater reproductive success in early rather than late breeders. Early breeders will be rearing chicks when their neighbours are still incubating or have younger chicks than their own. It is unlikely, therefore, that many of the chicks in the colony will be old enough to stray far from their parents before the early breeders have developed the ability to identify their own chicks. Also, if their own chicks get lost, the chances of them being adopted and reared by another pair of gulls is high because other gulls in the colony will not be at the stage of discriminating between strange chicks and their own. Also, two instances were seen in this study of incubating gulls with no hatched chicks adopting young chicks that arrived in their territories. Late breeders, on the other hand, will be much more likely to rear strange chicks at a cost to their own, as they will still be incubating or rearing young chicks when most of the other gulls in the colony have mobile chicks. One pair of gulls on the study area neglected the incubation of their egg when a chick, which had fallen from its nest on a high tuft of rushes and was unable to get up to it again, moved into their territory. They paid all their attention to the chick over the next two days and when the chick then returned to its own parents their egg was found to be bad and they had lost the chance to rear a chick of their own. Equally, when a pair of gulls receives a strange chick into their brood, their own chicks are likely to get less food now that there are more mouths to feed, and if the parents do manage to increase the amount of food that they produce for the chicks, they will be using up a lot more energy to obtain it so decreasing their chances of surviving to breed in future years. The chicks of late breeders are also much less likely to get adopted, if they get lost, than the chicks of early breeders. Most of the gulls in the colony will have older chicks than the late breeding pairs and will be able to identify strange chicks. Therefore, most of the late bred chicks that do get lost will die.

Many of the chick deaths that occurred through exposure and from attacks by other gulls may have done so because of my presence in the colony. Chicks on high tufts sought cover down into the rushes when there was a disturbance and often had a great struggle to get back up afterwards. Disturbances also caused some chicks to run far from their territories looking for cover with the risk of getting lost or injured by other gulls on their return. Therefore, it is likely that without my presence there would not have been so many of such casualties.

Several researchers have concluded that a proportion of egg and chick mortality may be attributed to their own disturbance of the colony (Kadlec et al 1969; Ellison & Cleary 1978; Anderson & Keith 1980). Ellison & Cleary showed that the hatching success of double crested cormorants (*Phalacrocorax auritus*) was related to the frequency at which nests were checked with losses primarily due to nest abandonments and predation on the eggs. Hunt (1972) found that the hatching success of herring gulls was greatly affected by disturbance of the colony. When a colony is disturbed the adults leave the eggs unprotected and thus more susceptible to predation. Also, as gulls eggs are sensitive to overheating (Drent 1967) such displacements could be lethal if they involve eggs or chicks at stages particularly susceptible to heat stress. Equally, disturbance in cold and wet weather could result in mortality of eggs and young chicks through chilling.

Anderson & Keith (1980) reported that during disturbances young Heerman's gulls (*Larus heermanni*) and Western gulls (*Larus occidentalis*) were displaced into adjacent territories where they were harassed and often killed. Hunt & Hunt (1976) suggest that this infanticide is typical even in undisturbed colonies, but it obviously increases with human disturbance. Breeding Western gulls that lose their eggs or chicks apparently practice conspecific predation whether or not humans are present (Hand 1980) thus increasing the effects of human intrusion on the success of the colony. Unfortunately for a lot of gull research, measures of breeding success are required to be known. This involves obtaining accurate measures of the numbers of eggs laid and hatched which requires frequent visits to the colony. These visits cause disturbance which results in increased egg and chick mortality and so decreases the breeding success under study.



The net result of all these losses was that in 1983 46.8% of the chicks hatched survived to fledge, compared to 1.3% in 1982 and 14.6% in 1984. However, many of the chicks that simply disappeared in 1983 may have just moved to other areas of the colony and it is likely that some of them survived to fledge. If all the chicks that disappeared had survived, then the fledging success would have been 88.3% and if none of them had survived it would have been 46.8%.

The fledging success of the kittiwakes studied by Coulson & Wooller (1984) was very high at 87%. However, Kadlec et al (1969) found that only about 50% of the herring gull chicks which hatch live to fledge, and Paynter (1949) reported a fledging success of about 58% for herring gulls. Several studies show that on average a pair of herring gulls succeeds in rearing 1 chick to fledging each year (Kadlec & Drury 1968; Brown 1967) but others have recorded a value of 0.6 fledglings per pair (Harris 1964; Holley 1971). In this study the minimum number of chicks known to have fledged from study nests in 1983 is 36, which gives an average of 0.6 fledglings per breeding pair of gulls, and the maximum number that could have fledged is 67 giving an average of 1.0 fledgling per pair.

The breeding success observed for clutches of three eggs and broods of three chicks suggests that more third laid eggs may fail to hatch than first or second and that fewer third hatched chicks may survive to fledge than first or second. However, there was so little data available that it was not feasible to conduct statistical analysis on it. Reports of mortality of the youngest or smallest nestlings are common among altricial birds (blue tits (*Parus caeruleus*) and great tits, Gibb 1950; swifts (*Apus apus*), Lack & Lack 1951; starlings (*Sturnus vulgaris*), Dunnet 1955; goldfinches (*Carduelis carduelis*), Holcombe 1969a, 1969b; house martins (*Delichon urbica*), Bryant 1975, 1978; common grackle (*Quiscalus quiscula*), Howe 1976, 1978) and the mortality of chicks hatching from the third egg of the typical 3-egg clutch of many gulls (Parsons 1970, 1971, 1975; Graves et al 1984) and common terns (*Sterna hirundo*, Nisbet 1973) is higher than those hatching from first or second laid eggs. Graves et al (1984) reported that during two seasons in which the nests were undisturbed only 8% of the 74 pairs of herring gulls hatching all three eggs managed to fledge three chicks. Parsons (1970) reported that the hatching success in herring gulls is the same for all three eggs. Ytreberg (1956), however, observed that some

black-headed gull chicks die because they are unable to free themselves from their shells, and he noticed that such cases are nearly always third eggs. He attributed this to insufficient incubation resulting in either the cold or too much heat reducing the ability of the hatching chick to work its way out of the egg quickly enough, thus giving the down time to dry and stick to the shell. He also suggested that the presence of young in the nest may have resulted in poor incubation of the last egg.

In many gull species the third laid egg is distinctly smaller than the first two and produces a lighter weight chick at hatching (Coulson 1963; Parsons 1970, 1972, 1975; Graves et al 1984). Parsons (1970) found that the smaller last egg had reduced lipid and yolk content compared with the other eggs, and he experimentally demonstrated higher mortality of herring gull chicks hatching from the third egg even when the hatching sequence was altered. For the first week after hatching, he showed that there is a significant positive correlation between egg size and chick survival. This relationship is similar for first and second eggs in a clutch but the survival is 10% lower for third chicks of the same size.

Hatching asynchrony within a brood of chicks is produced by the parents initiating incubation before all eggs are laid, and varies in degree between and within bird species. In some species parents deter effective incubation until after completion of laying, thereby establishing an even start for embryonic development and subsequent hatch synchrony of the brood. In others, by initiating incubation early in the laying process, parents can give a developmental headstart to those eggs already in the nest, producing hatching intervals of comparable length to laying intervals.

Ytreberg (1956) observed that brooding in the black-headed gull does not become effective until after the second egg is laid because the gulls have a decided tendency to leave the first laid egg and carry on building the nest. He recorded that the majority (41.2%) of 3-egg nests hatched the first and second eggs on the same day and hatched the third egg one day later, and in 10.3% of the nests the third chick hatched two days later than the first two. Thus, not only is the third chick disadvantaged by its smaller size at hatching but it is further disadvantaged by being the last to hatch and having to compete for food against two distinctly larger and older chicks.

There have been several theories put forward to explain the reason for hatching asynchrony within the broods of some bird species.

### 1) Brood-reduction hypothesis

By producing offspring of different ages and sizes, parents can rely on sibling competition for food to adjust the number of offspring to that which can be reared given the level of food availability (Lack 1947, 1954, 1966, 1968; Ricklefs 1965; Howe 1976, 1978; O'Connor 1978; Mock & Parker 1986). A situation is created in which late hatching birds, in which least parental time and energy has been invested, may be starved if the food available is insufficient to raise an entire healthy brood. Thus, the production of more chicks than are normally reared exploits a fluctuating food supply when it is plentiful. A massive outbreak of inchworms provided young common grackle under study by Howe (1976) with unusually abundant food. The weight of some 12 day old young were reported as by far the heaviest recorded in the species. Therefore, it proved a great advantage in having more chicks than are normally raised with a species for which food conditions within a season are not correlated with time. Gibb (1950) showed that hatching is synchronous in first broods of the great tit but asynchronous in second broods. He associated this with high levels of food availability and fledging of the entire brood early in the season in contrast to a scarcity of food to feed the young and frequent brood reduction late in the spring.

### 2) Insurance hypothesis

By laying eggs asynchronously and laying more than the number that are usually fledged, parents have an insurance against the infertility or accidental loss of any of the other eggs. This hypothesis is usually applied to species such as raptors which are characterised by small clutches and long nesting periods (Stinson 1979). Two eggs are laid when only one young will be reared, and should both eggs hatch then the extra one is lost through sibling competition or fratricide (Ingram 1959; Meyburg 1974; Stinson 1979). The brown booby (*Sula leucogaster*) and the white booby (*Sula dactylatra*) usually lay two asynchronously hatching eggs but never fledge more than one chick (Nelson 1978). A much higher fledging rate is produced by 2-egg clutches than 1-egg clutches, as a replacement for the first egg is left

if it should fail to hatch or die in early life. Nelson suggested that this second egg acts simply as an insurance against such a loss.

### 3) Predation hypothesis

By initiating incubation before the completion of the clutch, parent birds shorten the period between the laying of the first egg and the time when the first chick leaves the nest and this will reduce the average loss to predators (Hussell 1972; Clark & Wilson 1981, 1985; Bancroft 1985). If predation is common and avoidable by means of growth (via chick mobility or when the predator is gape limited), the older siblings may be able to reach a safe minimum size more quickly, thereby obtaining at least partial success for the parents. Hussell (1972) observed that after a visit of an arctic fox (*Alopex lagopus*) to a snow bunting (*Plectrophenax nivalis*) nest, when the young were 8-10 days old, the smallest chick, which was a day younger than any of the others, had disappeared, but the other four were still present. At this stage the young are becoming active and move out of the nest into the recesses of the nest cavity when disturbed, and it seems quite possible that the older young escaped because of their more advanced development. It is unlikely that they would have survived if incubation had started when the last egg was laid.

### 4) Peak load reduction hypothesis

By spreading out hatching times, parents also spread out the peak food demands of individual offspring (Hussell 1972). If the food requirements of the young reach a marked peak at a certain age, asynchronous hatching might stagger the maximum demand for food so that parents can meet the needs of the entire brood more effectively than if all siblings attained peak energy demands simultaneously. This might be important when parents are limited by the amount of time per day during which they can forage regardless of food supply. The death of late hatching young, under this hypothesis, would be an incidental effect of another adaptation.

##### 5) Sibling rivalry hypothesis

By producing asynchronous hatching young, parents benefit from competitive differences within the brood because they help reduce the potential costs of sibling rivalry (Hamilton 1964; Hahn 1981; Mock & Ploger 1987). By giving each offspring a headstart over its later hatched siblings parents reduce the amount of sibling aggression required to form stable dominance relationships. Hahn (1981) showed that asynchronously hatching 3-chick broods of laughing gulls had greater whole brood successes (all three chicks fledging) than experimentally synchronized broods and speculated that the asynchrony may have permitted more efficient use of parental resources. Fujioka (1985) and Mock & Ploger (1987) showed that artificially synchronized broods of cattle egrets (*Ardeola ibis*) fought significantly more than asynchronous broods and that the parents of synchronous broods were solicited more often and provided more food to the chicks. They did not, however, produce more surviving young than parents with asynchronous broods (Mock & Ploger 1987).

These hypotheses are not exclusive, and each must be evaluated in relation to the species and circumstances under consideration.

Very little sibling aggression was seen in the black-headed gull chicks in this study, even in 2-chick broods in which both were hatched on the same day. However, without testing experimentally if aggression is higher in synchronized broods of three chicks, it is difficult to comment on the possibility of a reduction in sibling rivalry being mediated by asynchronous hatching.

Black-headed gull chicks begin hatching in mid May and are nearly all fledged by early August, giving their parents full advantage of the long day-length for foraging. Parents that did manage to raise three chicks to fledging managed to provide them all with enough food to do so, while most gulls only had one or two chicks to feed. There was no evidence of food shortage in any of the three years of the study. Black-headed gulls exploit a wide range of food sources, eg. fish, insects, worms and foodscraps, and while chicks were dying in newly hatched broods of three many gulls were adequately providing

fully grown broods of two chicks. Thus there is no evidence that asynchronous hatching served to reduce the brood size because of low food availability.

Predation accounts for a major portion of egg and chick losses in the black-headed gull. It was noticeable, however, that only very young chicks were taken from the colony by crows. Also, chicks that were old enough to take to the water when the fox was present survived while younger chicks were taken or killed by the fox. Therefore, any mechanism that reduces the time between egg-laying and fledging, or decreases the time for chicks to reach a safe size more quickly, is likely to increase their survival. Asynchronous hatching, therefore, may well act to reduce chick mortality from predation.

Mechanistically, the insurance hypothesis is equivalent to the brood reduction hypothesis. It differs in that the survival of the first laid eggs or first hatched chicks more than the food availability is uncertain. The death of the late-hatching chick is common in many gulls and terns (parsons 1970; Nisbet 1973) and its presence could be viewed as insurance against infertility of early eggs or early death of the first hatched chicks. Unfortunately there were only eight pairs of gulls on the study area which hatched three chicks in 1983 when there was no disruption of the breeding success by foxes. However, in half of these nests the third chick was found dead in the first few days of life and only one third chick survived to fledge. This chick was from a nest in which the older two chicks got separated from their parents and were adopted by other gulls when the third chick was only four days old. Several cases were also seen of third chicks dying in the process of hatching because they got stuck to the egg shell as it dried out. This probably occurred because of poor incubation by the parents (Ytreberg 1956). The presence of two chicks in the nest moving about and begging is likely to cause the parents to sit on the remaining egg less efficiently

Thus, in conclusion, while asynchronous hatching could be said to have reduced predation on the chicks it appears that it may be more important in insuring against the loss of any of the other eggs or young chicks.



## CHAPTER 8 - TIME SPENT ON THE TERRITORY AND TIME SPENT INCUBATING AND BROODING

### 8.1 Introduction

In this and the following two chapters, various aspects of the behaviour of the black-headed gulls on their territories are examined: the time they spend on the territory, incubating eggs and brooding chicks, their reactions towards intruders on their territories, and their behaviour while feeding their chicks. All these behaviours play an important role in the determination of the breeding success of the gulls, and all are forms of parental investment since they require time and energy from the parents which might decrease the possibility of them investing in future offspring.

Before their eggs are laid, when they are establishing territories in the breeding colony, black-headed gulls must spend enough time on the territory to maintain it and to prevent other pairs of gulls from displacing them or stealing nesting material. When there are eggs and young chicks in the nest at least one of the gulls must be present at all times to protect the eggs and chicks from predators, as crows and coots are quick to take advantage of any unattended nests (see Chapter 5). Thus, it is obvious that the time that individual gulls spend on the territory and the time that they spend incubating their eggs and brooding their chicks could be an important factor for the breeding success of the gulls.

The budgetting of various aspects of parental care is an important part of the overall breeding strategy, and so an examination of the apportioning of nest attendance between males and females was also made in this chapter.

## 8.2 Methods

The arrival and departure times, on the territories, of all the adult gulls under observation were recorded throughout the breeding season in 1983 and 1984. Using this information, calculations were made of the time each gull had spent on the territory during the observation period, and the amount of time that both gulls were present on the territory together and that both gulls were absent from the territory together.

In 1984 the times that gulls started to and stopped incubating and brooding were also recorded and so in this year it was also possible to calculate the time each bird had spent sitting on eggs or brooding chicks and the amount of time that the eggs were left uncovered. The number of periods of presence on the territory and periods of incubation or brooding during the observation period were also calculated.

The periods of observation of groups of nests were not always the same length, and so the time spent on the territory and the time spent incubating and brooding were calculated as a percentage of the time the territory was watched. The mean values then calculated were the means of the percentage-attendance values of individual pairs of gulls throughout the period in question. The number of periods of presence on the territory and the number of periods of incubation and brooding were calculated as the number of periods per hour observed.



## 8.3 Results

### 8.3.1 Time Spent on the Territory

The results were divided into four sections as follows:

- 1) No-egg - the results acquired from pairs of gulls during the pre-egg-laying stage which failed to lay eggs and subsequently left the study area.
- 2) Pre-egg - the results acquired from gulls during the pre-egg-laying stage which did subsequently lay eggs on the territory.
- 3) Egg - The results obtained from pairs of gulls with eggs in their nests.
- 4) Chick - The results obtained from gulls with chicks.

The mean percentage of time spent on the territory, and the mean numbers of periods of presence per hour are shown in Appendix 16 and plotted in Figures 8.1 to 8.4. In 1983 there were only five records obtained from no-egg gulls and 13 from pre-egg gulls and so analysis of these stages was not possible in most cases for this year.

In 1984 (Figure 8.3) there was no significant difference between the amount of time male and female gulls from either the no-egg or pre-egg groups spent on the territory ( $F=3.622$ ,  $df=1,188$ ,  $p>0.5$ ), although there was a tendency for both males and females from pre-egg pairs to spend more time on the territory than no-egg gulls ( $F=4.720$ ,  $df=1,188$ ,  $p<0.05$ ; however Tukey  $p>0.05$ ). Both gulls of a pair tended to spend less time together on the territory in the no-egg group than the pre-egg group ( $F=3.928$ ,  $df=1,94$ ,  $p$  just  $>0.05$ ) and there was a significant difference in the amount of time that both gulls were absent from the territory, with no-egg gulls being absent together more often than pre-egg gulls ( $F=7.313$ ,  $df=1,94$ ,  $p<0.01$ ).

No-egg males spent their time on the territory in more periods (ie. they went to and from the territory more often) than their partners ( $F=16.501$ ,  $df=1,188$ ,  $p<0.01$ ; Tukey  $p<0.05$ ) (Figure 8.4) and there

was an interaction between the sex of the gull and the group ( $F = 4.555$ ,  $df = 1,188$ ,  $p < 0.05$ ) with no-egg males going to and from the territory more often than pre-egg males (Tukey  $p < 0.05$ ) while the females from the two groups did not differ (Tukey  $p > 0.05$ ).

The comparison between gulls observed during the pre-egg and egg stages of 1984 (Figure 8.3) shows that there was no significant difference in the time males and females spent on the territory between the two groups ( $F = 2.985$ ,  $df = 1,356$ ,  $p > 0.05$ ) but during the egg stage male gulls spent significantly more time on the territory than females ( $F = 9.051$ ,  $df = 1,356$ ,  $p < 0.01$ ; Tukey  $p < 0.05$ ). Both gulls spent significantly more time on the territory together during the pre-egg stage than they did during the egg stage ( $F = 44.161$ ,  $df = 1,178$ ,  $p < 0.01$ ) and the territory was left unattended more often during the pre-egg stage than the egg stage ( $F = 19.770$ ,  $df = 1,178$ ,  $p < 0.01$ ). This last result was also found in 1983 (Figure 8.1) ( $F = 42.283$ ,  $df = 1,155$ ,  $p < 0.01$ ) but there were no other significant differences found in that year during these stages.

In both 1983 (Figure 8.2) and 1984 (Figure 8.4) both males and females went to and from the territory more often during the pre-egg stage than the egg stage (1983 -  $F = 10.233$ ,  $df = 1,310$ ,  $p < 0.01$ ; 1984 -  $F = 37.780$ ,  $df = 1,356$ ,  $p < 0.01$ ; Tukey  $p < 0.05$ ). During the egg stage of 1984 only, males were found to go to and from the territory significantly more often than females (1984 -  $F = 9.839$ ,  $df = 1,356$ ,  $p < 0.01$ ; Tukey  $p < 0.05$ ; 1983 -  $F = 0.154$ ,  $df = 1,310$ ,  $p > 0.05$ ).

In 1983 (Figure 8.1) a comparison between the results obtained from gulls observed during the egg stage and the chick stage shows that both males and females spent more time on the territory during the egg stage than the chick stage ( $F = 10.568$ ,  $df = 1,558$ ,  $p < 0.01$ ; Tukey  $p < 0.05$ ) but there is no significant difference between the time males and females spent on the territory during either stage ( $F = 2.054$ ,  $df = 1,558$ ,  $p > 0.05$ ). In 1984 (Figure 8.3), however, there is an interaction between the sex of the territory holder and the season ( $F = 6.209$ ,  $df = 1,320$ ,  $p < 0.05$ ). Females spent less time on the territory during the egg stage than their partners but more time during the chick stage (Tukey  $p < 0.05$ ).

### KEY FOR GRAPHS IN CHAPTER 8

♂	males only
♀	females only
♂+♀	both males and females
⊖	none (no male, no female)

NE	pre-egg-stage gulls that failed to lay eggs
PE	pre-egg-stage gulls that did subsequently lay eggs
E	gulls with eggs in their nests
C	gulls with chicks

— * —	denotes a significant difference between the means indicated
— (*) —	denotes a difference between means which is just not significant

### FIGURE 8.1

Mean percentage and standard error of the time observed that the gulls spent on the territory during different stages of reproduction in 1983. (Data in Appendix 16)

### FIGURE 8.2

Mean number and standard error of periods of presence per hour spent on the territory during different stages of reproduction in 1983. (Data in Appendix 16)

FIG 8.1

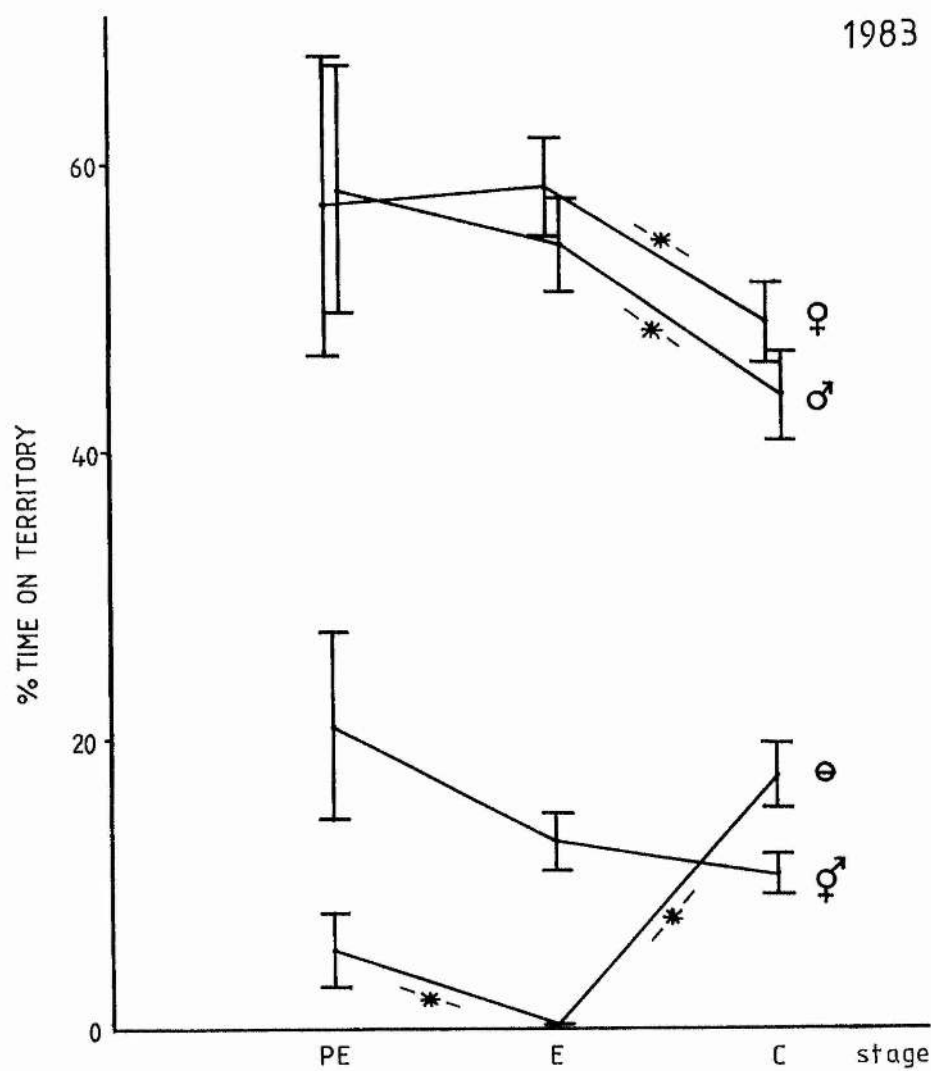


FIG 8.2

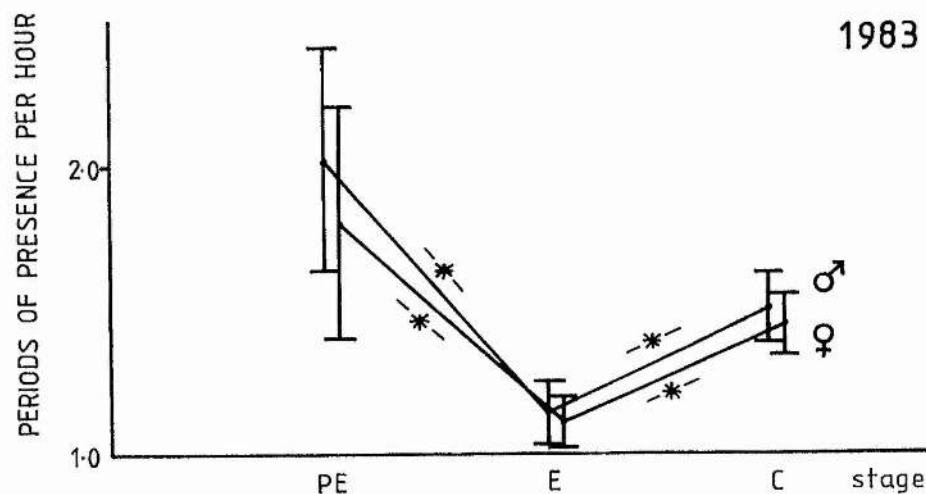


FIGURE 8.3

Mean percentage and standard error of the time observed that the gulls spent on the territory during different stages of reproduction in 1984. (Data in Appendix 16)

FIGURE 8.4

Mean number and standard error of periods of presence per hour spent on the territory during different stages of reproduction in 1984. (Data in Appendix 16)

FIG 8.3

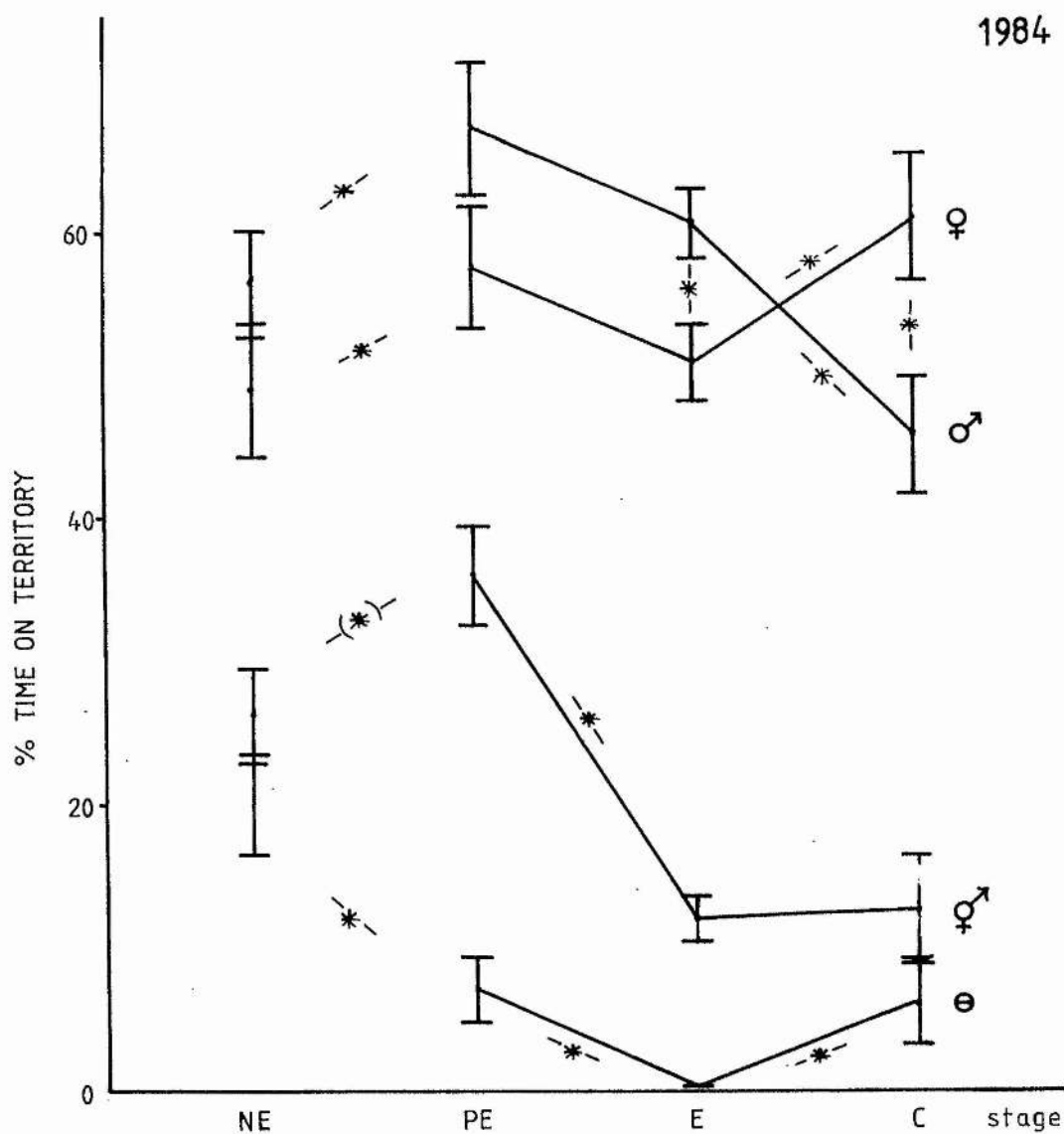
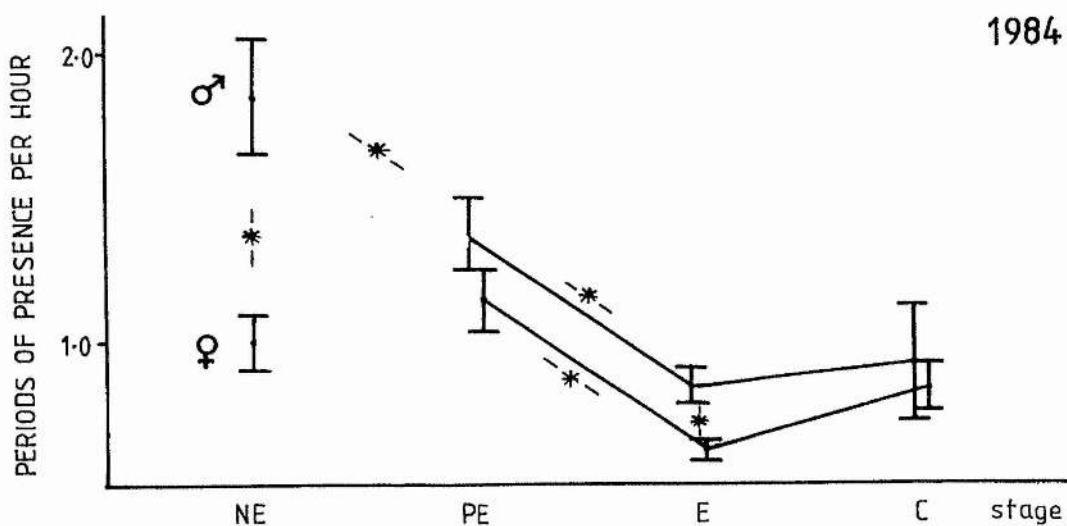


FIG 8.4



and females spent more time on the territory during the chick stage than the egg stage while males spent more time on the territory during the egg stage than the chick stage (Tukey  $p < 0.05$ ).

Both sexes spent the same amount of time together on the territory during the egg and chick stages of both 1983 and 1984 (1983 -  $F = 1.020$ ,  $df = 1,279$ ,  $p > 0.05$ ; 1984 -  $F = 0.025$ ,  $df = 1,160$ ,  $p > 0.05$ ) and both gulls were virtually never absent together from the territory during the egg stage but were absent significantly more often together during the chick stage (1983 -  $F = 53.931$ ,  $df = 1,279$ ,  $p < 0.01$ ; 1984 -  $F = 11.074$ ,  $df = 1,160$ ,  $p < 0.01$ ).

In 1983 (Figure 8.2) males and females went to and from the territory less often during the egg stage than the chick stage ( $F = 10.874$ ,  $df = 1,558$ ,  $p < 0.01$ ; Tukey  $< 0.05$ ). However, in 1984 (Figure 8.4) there was no significant difference ( $F = 0.361$ ,  $df = 1,320$ ,  $p > 0.05$ ).

The data collected during the chick stage differed between 1983 and 1984. In 1983, data were collected from gulls with chicks of all ages, but in 1984, because of the disruption of the colony by the fox, data were only collected from gulls with chicks of up to nine days of age. To examine how the behaviour of the gulls changed as the chicks grew, the data for the chick stage of 1983 were divided up into four sections - the first four weeks during which the gulls had chicks. These data are shown in Appendix 17 and plotted in Figures 8.5 and 8.6.

From Figure 8.5 it can be seen that both males and females spent less time on the territory during each successive week of their chicks' lives. In fact there was a significant negative correlation between the age of the chicks and the time spent on the territory by both sexes (males -  $r = -0.240$ ,  $p < 0.02$ ; females -  $r = -0.370$ ,  $p < 0.001$ ). Figure 8.5 also shows that the time both gulls spent on the territory together decreased as the chicks grew older, until during the fourth week they were virtually never on the territory together, and the territory was left unattended increasingly more often as the chicks aged. Analysis showed that there was a significant negative correlation between the time both gulls were on their territory together and the age of their chicks ( $r = -0.310$ ,  $p < 0.005$ ), and a significant positive

FIGURE 8.5

Mean percentage and standard error of the time observed that gulls with different age groups of chicks spent on the territory in 1983. (Data in Appendix 17)

FIGURE 8.6

Mean number and standard error of periods of presence per hour spent on the territory by gulls with different age groups of chicks in 1983. (Data in Appendix 17)



FIG 8.5

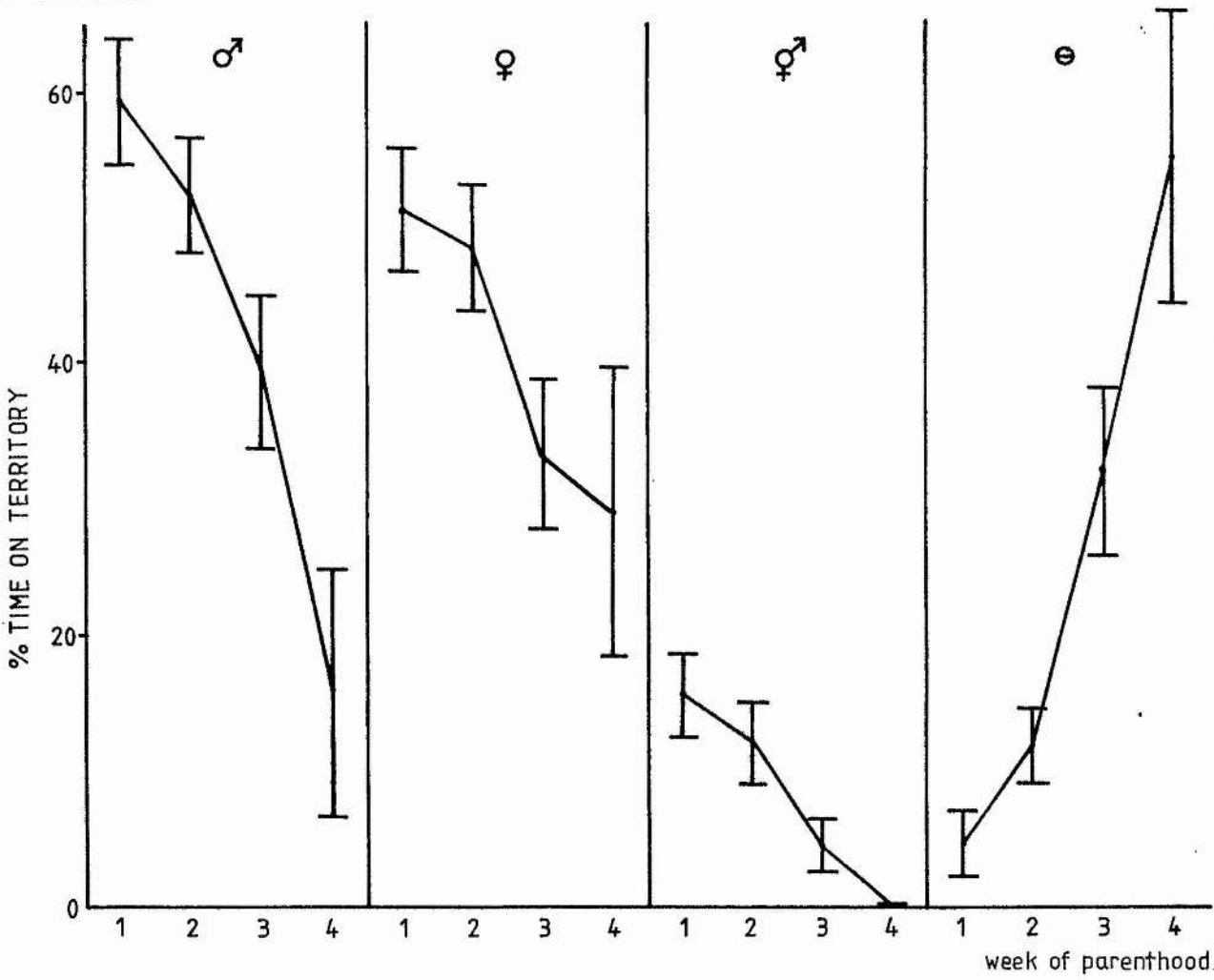
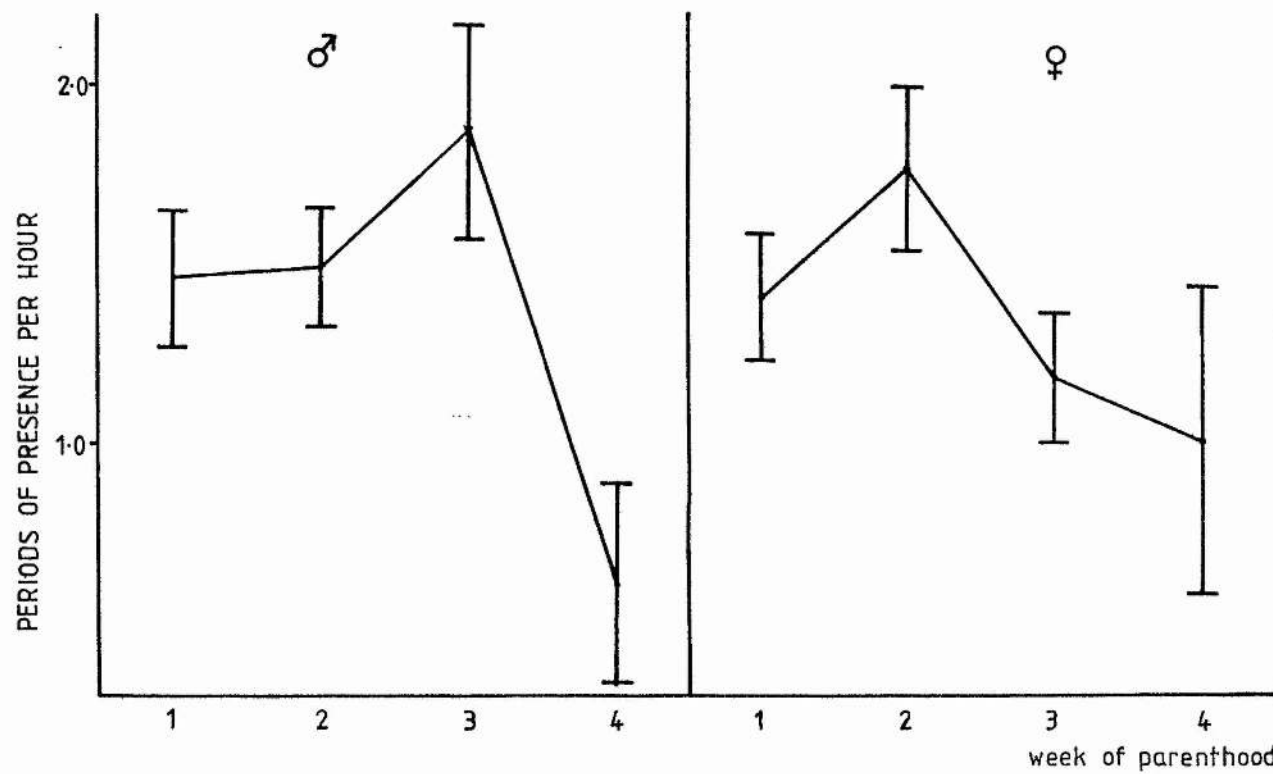


FIG 8.6



correlation between the time that the territory was left unattended and the age of the chicks ( $r=0.508$ ,  $p<0.001$ ).

Figure 8.6 shows the number of periods of presence spent on the territory by males and females during the first four weeks of their chicks' lives. Analysis of variance showed that there was no change in the number of times the parents went to and from the territory as the chicks grew (males -  $F=2.356$ ,  $df=3,133$ ,  $p>0.05$ ; females -  $F=1.630$ ,  $df=3,133$ ,  $p>0.05$ ).

### 8.3.2 Time Spent Incubating and Brooding

Appendix 18 contains the means of the percentage of time spent incubating and brooding and the number of periods of incubation and brooding per hour in 1984, and Figure 8.7 shows graphs of these results. Analysis of variance showed that there was an interaction between the amount of time spent on the nest by the two sexes and the season of reproduction ( $F=4.749$ ,  $df=1,310$ ,  $p<0.05$ ). Female gulls spent less time incubating the eggs than male gulls (Tukey  $p<0.05$ ) and male gulls spent more time incubating the eggs than they spent brooding the chicks (Tukey  $p<0.05$ ). The difference observed in the amount of time the two sexes spent brooding the chicks, however, was not significant. The nests were virtually never left uncovered when they contained eggs, but they were left uncovered significantly more often when they had chicks in them ( $F=61.357$ ,  $df=1,155$ ,  $p<0.01$ ).

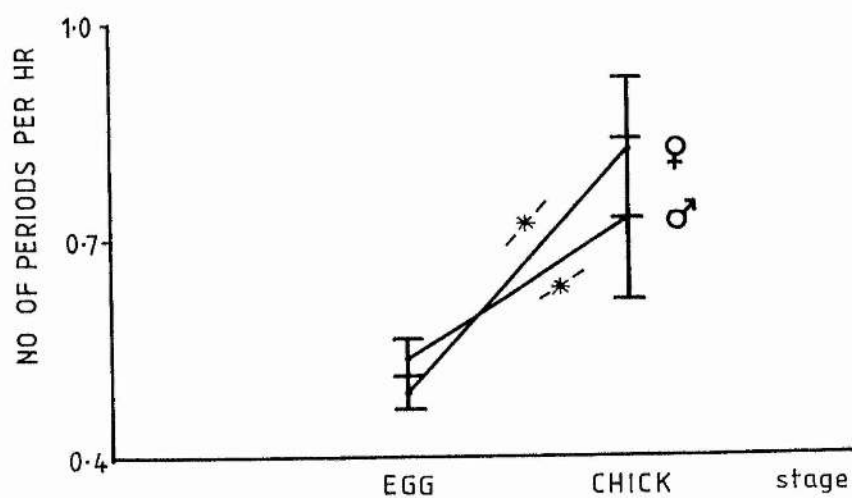
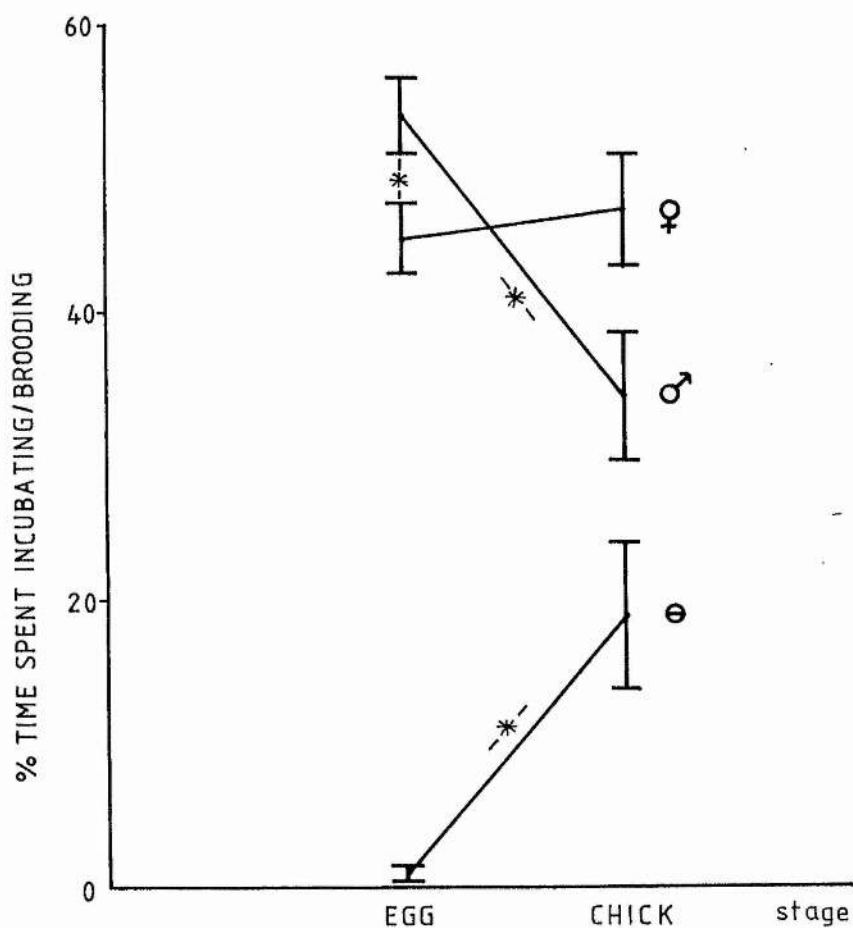
There was no significant difference in the number of periods of incubation and brooding per hour between males and females during either the egg or the chick stage ( $F=0.565$ ,  $df=1,310$ ,  $p>0.05$ ). However, both males and females brooded the chicks in significantly more periods than they incubated the eggs ( $F=18.947$ ,  $df=1,310$ ,  $p<0.01$ ; Tukey  $p<0.05$ ) i.e. they went on and came off the chicks in the nest more often than they did the eggs.

FIGURE 8.7

Mean percentage and standard error of the time observed that the gulls spent incubating eggs and brooding chicks, and the mean number and standard error of periods of each observed per hour in 1984. (Data in Appendix 18)

FIG 6.7

TIME SPENT INCUBATING AND BROODING



### 8.3.3 Comparison of the Time Spent on the Territory and the Time Spent Incubating and Brooding

To discover if there was any significant difference between the amount of time that the gulls spent on the territory during the egg and chick stages and the amount of time they spent incubating and brooding, a comparison was made of the means calculated for the egg and chick stages of 1984. Appendix 19 shows the means used in this comparison and these are plotted in Figure 8.8.

Analysis of variance showed that there was a difference between the time the sexes spent on the territory and the time they spent incubating ( $F=5.989$ ,  $df=1,552$ ,  $p<0.05$ ). However, a post-hoc Tukey test showed no significant difference for females and a difference just not significant for males. Both male and female gulls spent more periods on the territory than they spent periods incubating ( $F=25.584$ ,  $df=1,552$ ,  $p<0.01$ ; Tukey  $p<0.05$ ). During the chick stage both sexes appeared to have spent more time on the territory than they spent brooding the chicks ( $F=8.960$ ,  $df=1,78$ ,  $p<0.01$ ). However, a post-hoc Tukey test showed that while this difference is significant for females it is not quite significant for males. There was no significant difference between the number of periods of presence and periods of brooding for either males or females ( $F=0.630$ ,  $df=1,78$ ,  $p>0.05$ ).

FIGURE 8.8

A comparison of the mean percentage and standard error of the time observed that the gulls spent incubating or brooding and the mean percentage and standard error of the time that they spent on the territory in 1984. (Data in Appendix 19)

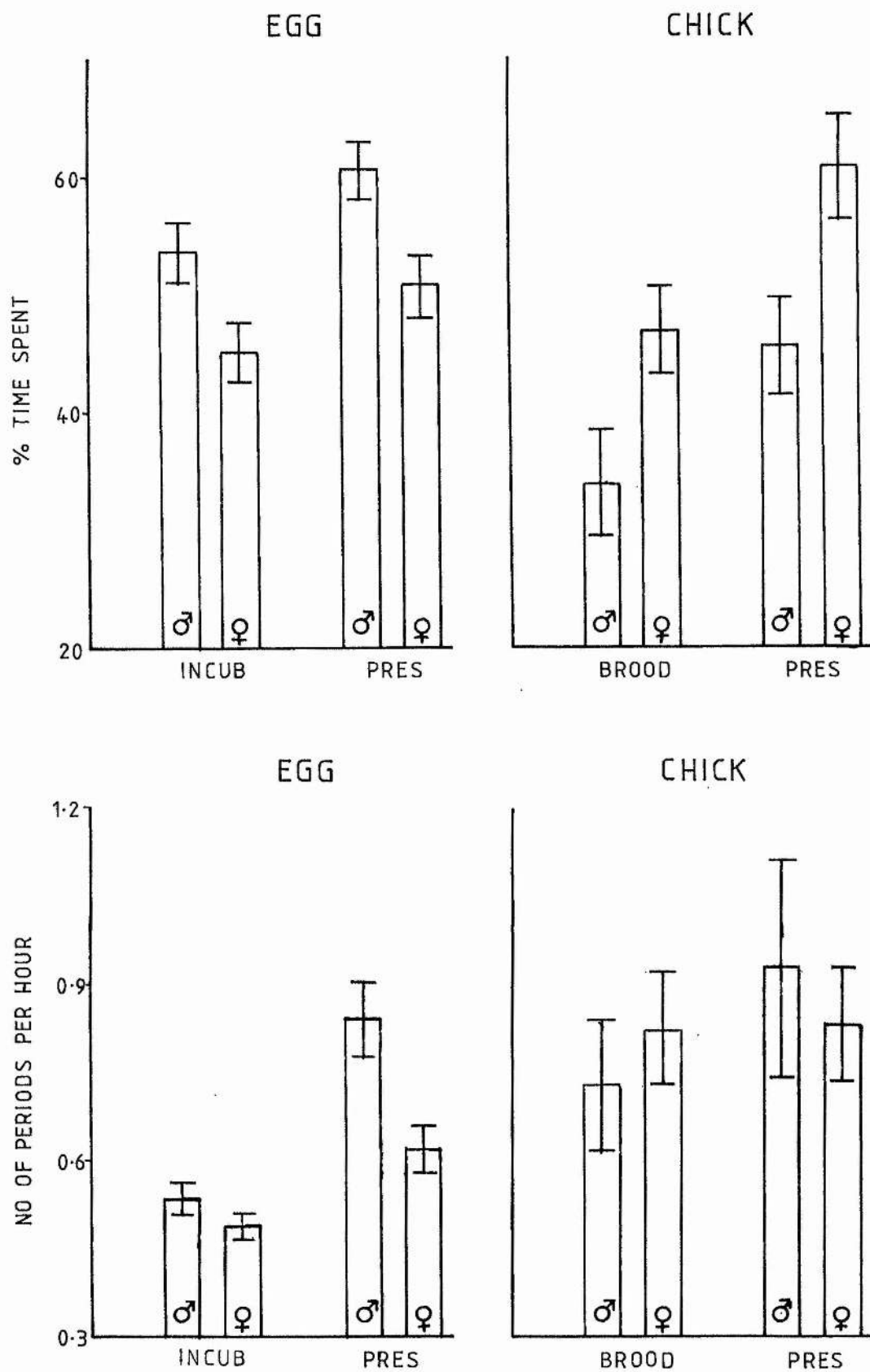
INCUB      time incubating

BROOD     time brooding

PRES       time present

FIG 8.8

COMPARISON OF TIME SPENT INCUBATING/BROODING AND  
TIME SPENT ON TERRITORY



#### 8.4 Discussion

The comparison of gulls that set up territories on the study area at the beginning of the season but failed to lay eggs there, and the gulls that did subsequently lay eggs (Figures 8.3 & 8.4) showed that there was a tendency for both males and females that failed to produce eggs to spend less time on the territory than pairs that did produce eggs. This difference is not significant. However, both gulls were shown to be absent from the territory together more often in the no-egg group than the pre-egg group. Thus, the failure of the no-egg gulls to remain on the territory and to lay eggs may have occurred because of this difference in behaviour. The fact that the no-egg gulls left the territory undefended for 20% of the time would have increased the chances of other gulls managing to take possession of it in their absence. Although female gulls from both groups spent their time on the territory in a similar number of shifts, the males from no-egg pairs went to and from the territory more often than their partners and more often than the males from pre-egg pairs. In Chapter 9 it will be shown that the males were responsible for the majority of the defence of the territory during this stage, the females only playing a minor role when necessary, and it may be that the failure of the no-egg gulls to breed on the study area was a result of ineffective defence by the 'restless' males and the frequent abandonment of the territory by both gulls, enabling other gulls to displace them. However, there is also the possibility that these gulls were simply moving between two potential nesting sites and that they chose to establish themselves on the one outside the study area.

The main differences in the attendance behaviour of the gulls between the pre-egg and incubation stages (Figures 8.1 to 8.4) were the time that both gulls spent on the territory together and the time that the territory was left unattended. During the pre-egg stage, when nest-building, courtship and mating were the main activities, both gulls were present together on the territory over 35% of the time. This decreased to 12% during the egg stage when the main concern of the gulls was to incubate the eggs and protect them against intruders and predators. At this time partners tended to meet only when they changed over incubation duties (Ytreberg 1956; Coulson & Wooller 1984). Thus, there was a switch in



behaviour with both gulls being present together a considerable amount of time during the pre-egg stage, but only one gull being present most of the time during the incubation stage.

During the egg stage the territory was hardly ever left unattended (0.2% of the time) while during the pre-egg stage both gulls were absent together 7% of the time. Although it was important for the gulls to be present on their territory for most of the day during the pre-egg stage to ensure that other gulls did not displace them or expand their territories into theirs, it was more important for at least one of the gulls to be present during the egg stage to incubate and protect the eggs.

The results for this comparison differ slightly between 1983 and 1984 but virtually all the differences can be attributed to the shortage of data collected during the pre-egg stage of 1983.

In both years the number of shifts of presence per hour was greater both for males and females in the pre-egg stage than the egg stage. During the pre-egg stage the gulls went to and from the territory collecting nesting material, but during the egg stage they spent longer periods on the territory incubating the eggs and nearly all the additional nest-building at this time was done during changeovers (Ytreberg 1956; Fogden 1964; Beer 1965).

In 1984 male gulls spent more time on the territory than the females during the egg stage and went to and from the territory more often. In 1983, however, there was no such result. No adequate explanation can be given for this difference as there were over 140 records made in both years and these records were collected throughout the whole of the incubation period.

A comparison of the time the gulls spent on the territory during the egg and chick stages (Figures 8.1 to 8.4) shows that the gulls did not spend significantly more or less time together on the territory during the chick stage than they did during the egg stage. However, the territory was left unattended significantly more often during the chick stage. As the chicks grew they became more able to defend themselves against intruders while the eggs had to be protected all the time. This observed difference

was greater during 1983 where the mean was calculated from data obtained from gulls with chicks of all ages. In 1984 the data were obtained only from gulls with young chicks in the nest and these were not left alone on the territory as often as older chicks.

In 1984 male gulls spent more time on the territory during the egg stage than the chick stage and females spent less time on the territory during the egg stage than the chick stage. In 1983, however, both gulls spent more time on the territory during the egg stage than the chick stage. There was a difference here in the data collected during the chick stage between the two years so it was possible that this could have led to the difference in the results. A comparison was made of the time that male and female gulls with chicks in their first week of life spent on the territory during 1983 (most of the data collected in 1984 were from gulls with chicks in their first week of life) and the time that gulls with eggs spent on the territory. The results, however, showed that males and females did not differ at all between the two stages in 1983 ( $F=0.058$ ,  $df=1,380$ ,  $p>0.05$ ) - still a different result from that found in 1984. It was also shown in 1984 that males spent less time on the territory than the females did during the chick stage but during 1983 both males and females spent a similar amount of time on the territory with chicks of up to one week of age ( $F=1.701$ ,  $df=1,380$ ,  $p>0.05$ ). Thus this is another unexplained difference in behaviour between these two years of the study.

Burger (1981b) found that male black skimmers (*Rynchops niger*) spent more time on the territory during the chick stage than the females did, exactly the opposite from the results found in this study for 1984. However, in another paper (Burger 1981c) she stated that both sexes spent equal amounts of time on the territory during both the egg and chick stages, so here too there must have been some variability.

There was also a difference recorded in the number of periods of presence observed between the two years. In 1984 males and females went to and from the territory a similar number of times during both the egg and chick stages, while in 1983 both sexes were shown to come and go more often during the chick stage. However, this difference can be explained by the difference in the data collected between

the two years. An analysis of variance of the number of shifts observed during the egg stage and the number of shifts observed in gulls during their first week of parenthood showed that there was a significant difference between the two stages ( $F=4.838$ ,  $df=1,380$ ,  $p<0.05$ ); however a post-hoc Tukey test showed that the differences between the two stages for the two sexes were not significant, a similar result to that observed in 1984.

Both males and females spent less and less time on the territory as the chicks grew older (Figure 8.5). During the first week of the chicks' lives both male and female parents were present on the territory over 50% of the time and this decreased to just over 15% for males with chicks in their fourth week of life and to just under 30% for females. Both gulls were also present on the territory together less often as the chicks grew until during the fourth week of the chicks' lives they were virtually never on the territory together. Also, both gulls were increasingly absent from the territory together. In the first two weeks the territory was left unattended less than 15% of the time but this increased to 55% of the time in the fourth week.

During their first week of life black-headed gull chicks are rarely left alone and at least one parent is usually present to protect them and brood them. As they grow older and larger they are increasingly able to protect themselves against intruding gulls and by their fourth week of life some of the chicks start to spend time away from the territory. Thus the parents are required to stay on the territory less and less as the chicks grow.

Data on the incubation and brooding behaviour of the gulls were only collected in 1984 (Figure 8.7) and so included only the brooding of gulls with chicks of 1-9 days of age. Male gulls were found to incubate the eggs more than the females and more than they brooded the chicks while the females spent a similar amount of time both incubating and brooding. Males have been shown to do more incubation of eggs than females in several species of birds (Ytreberg 1956, black-headed gull; Drent 1967, herring gull; Burger 1981b, 1981c, black skimmers) but Coulson and Wooller (1984) found that the opposite was the case in kittiwakes. Burger (1981b, 1981c) also reported that male black skimmers

brooded the chicks more than females. In this study, however, although there was no significant difference the tendency was for females to brood 1-9 day old chicks more than males.

During the incubation stage the nest was hardly ever (only 1% of the time) left uncovered (Ytreberg 1956; Drent 1967; Burger 1974, Coulson & Wooller 1984). In fact, close examination of the data revealed that the few occasions when nests were left uncovered occurred during the first or second day after the first egg was laid. Ytreberg (1956) also observed this in black-headed gulls and noted that during the first day or two that there were eggs in the nest the gulls frequently interrupted the incubation of the eggs to carry out nest building, but that the intensity of incubation increased rapidly when the last egg was laid. This was also the case in kittiwakes studied by Coulson & Wooller (1984). The results of this behaviour were discussed in Chapter 7 when it was noted that very often the first and second chicks hatched on the same day because effective incubation of the first egg often did not begin until after the second egg was also in the nest.

Although the eggs were virtually never left uncovered the 1-9 day old chicks were not brooded nearly 20% of the time. Ytreberg (1956) observed that when the eggs began to hatch brooding was continued with the same intensity as the eggs were incubated and thereafter decreased as the chicks grew (see also Beer 1979; Burger 1981b; Bedard & Meunier 1983).

The average number of shifts of brooding observed per hour was significantly more than the average number of shifts of incubation per hour, both for males and females. During very early incubation it was noticed that the gulls alternated fairly often but the shifts became longer as time proceeded (Burger 1974; Feare 1976; Coulson & Wooller 1984). However, after the chicks had hatched the gulls alternated more rapidly again (Coulson & Wooller 1984). The lengths of the incubation shifts were determined by the off-duty bird, as the incubating bird would not leave the eggs until its mate arrived to relieve it. Thus the number of shifts per day tended to be small. During the chick stage, however, the off-duty bird returned much sooner in order to feed the chicks with the food it had collected while away foraging.

The comparison of the time spent incubating and brooding and the time spent on the territory (Figure 8.8) showed that there was a tendency for the gulls to spend time on the territory when they were not incubating. Incubating gulls rarely leave their nests to chase away intruders and the advantages of the presence of the second bird of a pair on the territory at times to chase off intruders and maintain territorial boundaries are discussed in Chapter 9. The gulls also tended to spend more time on the territory during the chick stage than they spent brooding chicks, although this was only significant for females. This difference occurred, however, because there was usually a parent present on the territory but the chicks were not necessarily brooded all the time.

During the egg stage both males and females spent fewer shifts incubating the eggs than they spent on the territory. This may have occurred in part because of their tendency to spend time on the territory when they were not incubating, but is more likely to have occurred because of their behaviour during changeovers of adding nesting material to the nest (Ytreberg 1956). On many occasions an off-duty gull was seen arriving with nesting material and flying to and from the nest several times with additional material before finally relieving the incubating bird. During the chick stage, however, there was no difference observed between the numbers of shifts of brooding and presence. The large standard error bars here indicate that there was great variability in the numbers of shifts observed from different pairs of gulls.

## CHAPTER 9 - AGGRESSION ON THE TERRITORY

### 9.1 Introduction

Fetterolf (1984) reported that relationships between aggression and fledging success in ring-billed gulls suggested that breeding success was lowest in the gulls that engaged in the most aggression. He suggested that the energy used in aggression towards intruders could affect the ability of the parents to nourish the chicks both by direct energy expenditure and by using time otherwise available for foraging. However, there are several possible evolutionary advantages however for breeding-season aggression. These include the protection of parentage, nest-site defence and guarding against intraspecific predation (Burger 1974, 1980a, 1981a, 1981b, 1981c; Gowaty 1981; Blancher & Robertson 1982).

To ensure that the offspring raised are infact their own, male gulls must prevent any other males from mating with their partners. Thus aggression aimed at the protection of parentage should be greatest during copulatory periods and there should be a lot of aggression between male territory holders and intruders during the pre-egg-laying and perhaps also the egg-laying stages. Therefore, in this section the number of interactions seen involving different sexes of territory holders were examined, with a special emphasis on the interactions seen when both male and female territory holders were on the territory together. Male territory holders would be expected to be involved in the majority of these interactions especially when the females were also on the territory. The numbers of interactions seen involving different sexes of intruders and territory holders were also examined, as more aggression would be expected between male intruders and male territory holders during the copulatory stages.

The defence of the nesting site should evoke an aggressive response to intruders over the three stages of the nesting cycle, and the protection of the eggs and chicks against predation will result in aggression during these two stages. However, in all these cases the aggression should vary depending on the threat posed by individual intruders. Thus, this study investigated the number of interactions seen

involving different intruder types at the different stages of reproduction to examine which types of intruders were either more common or posed a greater threat at each stage of reproduction. To analyse the reaction of the territory holders towards the intruders in more detail, two aspects were examined. Firstly, what was the distance of an intruder from the nest when the territory holder reacted to it. Intruders that posed the least threat should be allowed closer to the nest before being chased off, while those posing a greater threat would be expected to be reacted to at a greater distance from the nest. Secondly, the intensity of the reaction of the territory holder was examined. Territory holders should react less aggressively towards the intruders which posed little threat, however, when a gull is incubating eggs or brooding chicks a balance has to be struck between the need to chase an intruder off and the need to protect the eggs and chicks from predation by remaining on top of them. Thus this study looked at the difference between those gulls that were incubating or brooding, and those gulls that were not, when an intruder entered their territory.

## 9.2 Methods

All instances of intrusion by other gulls on to any of the territories under direct observation were recorded. The information collected on each one in 1982 and 1983 was as follows:

- 1) Date and time
- 2) Territory number where intrusion occurred
- 3) Sex of the territory holder which reacted towards the intruder
- 4) How the territory holder reacted towards the intruder
  - a) ignored it
  - b) displayed at it without moving towards it
  - c) jabbed at it with its beak but did not move towards it
  - d) walked towards it
  - e) ran towards it
  - f) flew at it
  - g) chased it out of the territory and flew after it
  - h) made contact with it and fought with it
- 5) Identity of intruder
  - a) Neighbouring gull
  - b) Strange gull
  - c) Immature gull
  - d) Other species of bird

[A neighbour was defined as a gull which had a territory adjacent to the gulls under consideration, and a stranger was a gull which did not have a territory adjacent to the pair concerned.]



- 6) How intruder reacted to action taken by territory holder towards it
- a) ignored it
  - b) was flying over the territory holders nest
  - c) displayed at it
  - d) left the territory
  - e) was chased away by another territory holder

In 1984 additional data were collected as follows:

- 7) Estimated distance in feet that intruder was from nest when territory holder reacted to its presence.
- 8) Whether or not the territory holder was incubating or brooding at the time.
- 9) Whether or not the territory holder's mate was present
- 10) Whether or not the mate was incubating or brooding at the time
- 11) What the mate's reaction towards the intruder was
- a) to h) of section 4) above plus
  - i) did not see it
  - j) ignored it
  - k) watched it
  - l) moved away
  - m) left the territory

In an interaction the territory holder was recorded as the member of a pair that reacted most aggressively towards the intruder and the mate was recorded as the one which reacted least aggressively. Also, the reaction recorded for the territory holder was the most aggressive action taken by it during the interaction.

The information required from each interaction was recorded using a Hewlett Packard HP-41C alphanumeric programmable calculator (Whiten & Barton 1988) After a day's observation the data were stored on magnetic tape and subsequently transferred to one of the University's Vax 11/780 computers for analysis.

The data collected were divided up into different stages of reproduction on the basis of the stage of the individual pairs of gulls concerned. In 1982 data were collected for pairs during the 'egg and chick stages of reproduction only. In 1983 a small number of data were also collected for the pre-egg stage and in 1984 a lot of data were collected for the pre-egg and egg stages, but few were collected from pairs during the chick stage because of the disruption of the colony, before many of the eggs had hatched, by the fox. The data collected from territories before egg-laying occurred were divided into two groups; no-egg data which were collected from pairs of gulls which established territories but then left at some later date without laying eggs, and pre-egg data collected from pairs that did subsequently lay eggs.

### 9.3 Results

#### 9.3.1 Number of Interactions Involving Different Intruder Types at Different Times of the Season

Appendix 20 and Figure 9.1 show the frequencies of interactions observed which involved different types of intruders during different stages of the breeding season for the three years of the study. In 1982 neighbouring gulls were involved in more interactions during the egg stage than the other three intruder types. During the chick stage, however, neighbours and strangers were involved in a similar number of interactions. In 1983 and 1984 strangers were involved in more interactions than the other three types of intruders in all the reproductive stages.

Chi-square tests were carried out on the frequencies for all stages recorded for each individual year. In 1982, because of the low frequencies, the data for immatures and other species were pooled together. The number of interactions involving immatures and other species was smaller than expected during the chick stage of 1982 ( $\chi^2=15.417$ ,  $df=2$ ,  $p<0.001$ ) but there were no other significant differences seen in that year. In 1983 there was no significant difference in the patterns of frequencies seen during the three stages ( $\chi^2=9.865$ ,  $df=6$ ,  $p>0.1$ ). In 1984, however, a difference was found in the pattern of interactions observed involving different types of intruders ( $\chi^2=65.708$ ,  $df=9$ ,  $p<0.001$ ). Neighbours were involved in more reactions than expected with no-egg gulls while strangers were found to be involved in more interactions than expected with pre-egg stage gulls and fewer than expected with egg stage gulls. Other species were involved in fewer than expected interactions both with no-egg gulls and with pre-egg stage gulls, and involved in more interactions than expected during the egg and chick stages.

Chi-square tests were then carried out on the data collected for all three years during each individual stage. During the pre-egg stage there was found to be no difference in the pattern of frequencies observed between 1983 and 1984 ( $\chi^2=5.963$ ,  $df=3$ ,  $p>0.1$ ). The pattern of interactions for egg and

#### KEY FOR GRAPHS IN CHAPTER 9

N neighbouring gull

S strange gull

I immature gull

OS other species

E egg stage of reproduction

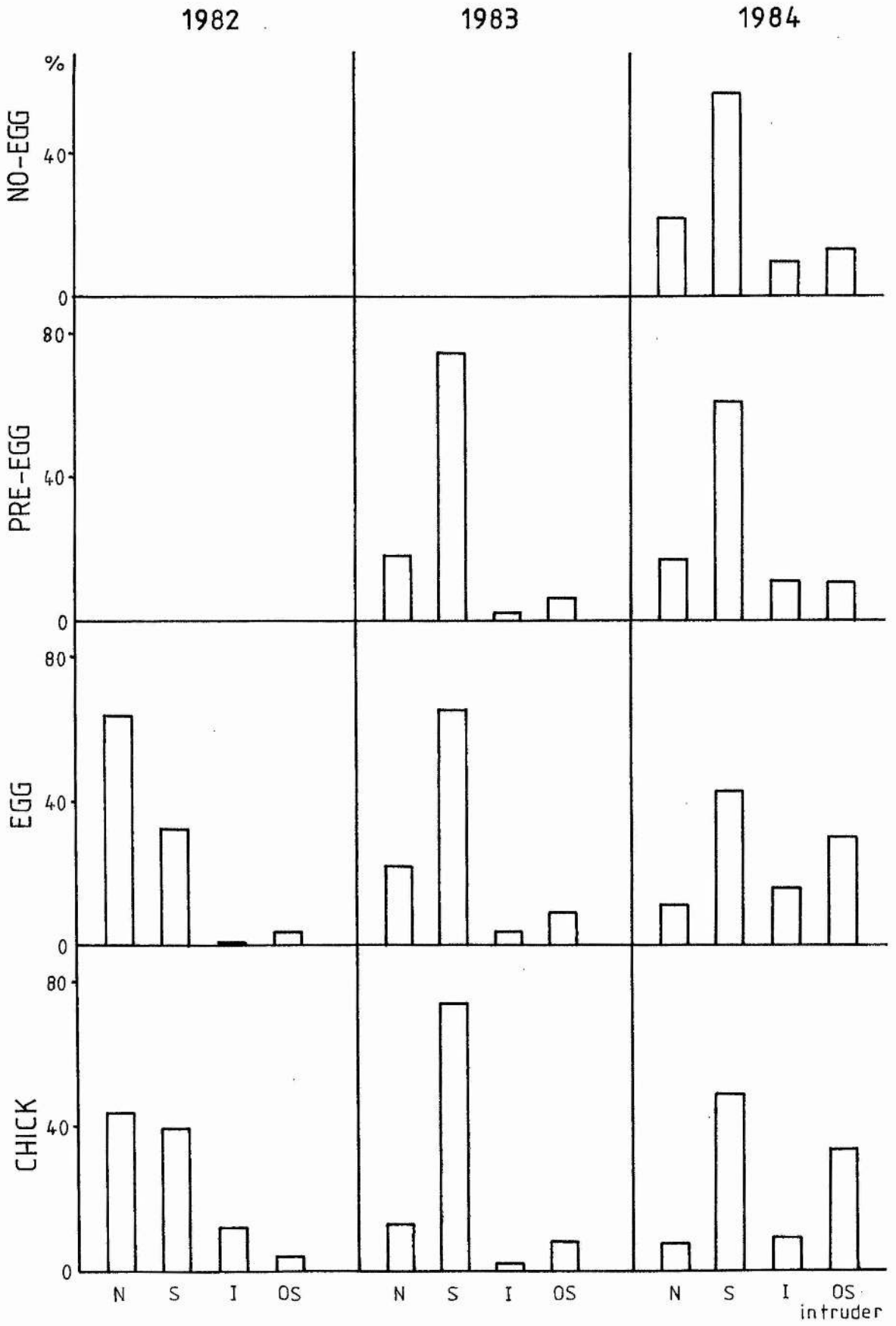
C chick stage of reproduction

#### FIGURE 9.1

Percentage of interactions involving different intruder types during different stages of reproduction for the three years of the study. (Data in Appendix 20)

FIG 9.1

PERCENTAGE OF INTERACTIONS WITH DIFFERENT INTRUDER TYPES



chick stage gulls, however, is very different between years (egg -  $\chi^2=258.877$ ,  $df=6$ ,  $p<0.001$ ; chick -  $\chi^2=109.341$ ,  $df=6$ ,  $p<0.001$ ). During the egg stage neighbours were involved in more interactions in 1982 and fewer in 1984 than expected and strangers were involved in fewer interactions in 1982 and more in 1983 than expected. Both immatures and other species were involved in fewer interactions in 1982 and 1983 and more interactions in 1984 than expected. During the chick stage neighbours were involved in more interactions than expected during 1982 and fewer during 1983 and 1984. Strangers, as was the case during the egg stage, were involved in fewer interactions than expected during 1982 and more than expected during 1983. Immatures were involved in more interactions in 1982 and fewer in 1983 than expected while other species were only involved in more than expected during 1984.

In 1982 the nests on the study area were much more closely packed together than they were during the following two years (see Chapter 3). This is reflected in the results here with a larger percentage of the interactions observed involving neighbours than strangers in 1982, a year when there was little undefended ground on the study area for strange gulls to loiter on. In the following two years, when the nesting was less dense and there was quite a lot of free space around nests, there was a much larger percentage of interactions observed involving strange gulls than neighbouring gulls. It was noted that there was an increase in the percentage of interactions which involved strange gulls and a decrease in the percentage of interactions seen involving neighbours in the chick stage of 1982, compared to the percentage recorded during the egg stage. Territories were deserted at this time due to loss of eggs or chicks, leaving undefended areas that strangers could enter.

The results for 1983 and 1984 are very similar but there is a difference in the number of interactions observed involving immatures and, particularly, other species. In 1983 many more chicks were fledged than in 1982 and if these chicks have a tendency to return to the breeding colony in which they were born then more immatures would be expected to be present in the colony in 1984 than in 1983. The results here suggest that this may be so: however, the numbers of immatures sighted in the colony as a whole were not recorded in 1982 and 1983 so a comparison cannot be made. It was apparent throughout the study that the numbers of other species of birds in the colony (moorhens, coots and

ducks) increased each year and a greater percentage of interactions were observed involving other species in 1984, especially during the gulls' egg and chick stages when the other species were moving about the colony with their own young and so more likely to be disturbing the gulls and themselves being more aggressive in the protection of their own youngsters.

In 1984 strangers were seen to be involved in more interactions than expected with pre-egg stage gulls and fewer than expected with egg stage gulls. This may have occurred because during the pre-egg-laying stage gulls were looking for suitable nesting sites or for nesting materials. Thus there were likely to be more strange gulls landing in nesting areas for these purposes than there would be during the incubation period.

### 9.3.2 Number of Interactions Involving Males and Females of Territory-holding Pairs During Different Stages of Reproduction.

Appendix 21 and Figure 9.2 show the frequencies of interactions observed which involved male and female territory holders during different stages of reproduction for the three years of the study. In 1984 no-egg males were involved in many more interactions than females (binomial,  $p < 0.001$ ). During the pre-egg stage in both 1983 and 1984 males were also involved in more interactions than females (binomial,  $p < 0.05$ ,  $p < 0.001$ ). During the egg stage, however, males were involved in more interactions than females in 1984 and 1982 (binomial,  $p < 0.001$ ), but not in 1983, and during the chick stage males and females were involved in a similar number of interactions in 1983 and 1984. (There were not enough data where the sex of the territory holder involved in the interaction was known during the chick stage of 1982.)

Males and females did not spend the same amount of time on the territory as each other and this needs to be taken into account for the correct analysis of the data in this section. Therefore, the expected number of interactions involving males and females was calculated on the basis of the relative amount of time that they spent on the territory during the different reproductive stages (see Chapter 8). A chi-

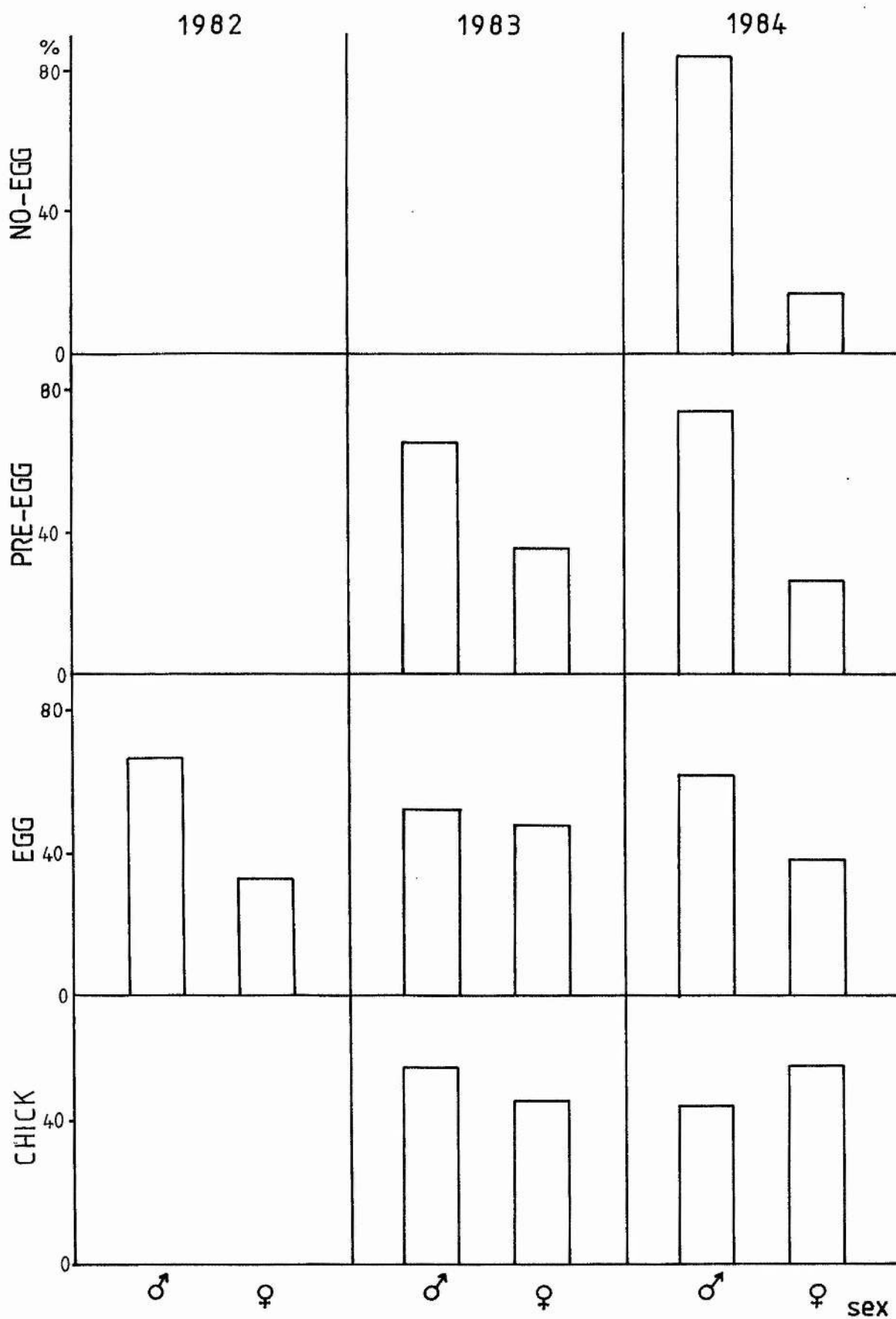
FIGURE 9.2

Percentage of interactions involving male and female territory holders during different stages of reproduction for the three years of the study. (Data in Appendix 21)



FIG 9.2

PERCENTAGE OF INTERACTIONS INVOLVING MALE AND FEMALE  
TERRITORY HOLDERS



square test of these calculated frequencies for all the seasons of 1983 and 1984 showed that in fact there were no significant differences between the observed and expected frequencies (1983 -  $\chi^2=0.125$ ,  $df=2$ ,  $p>0.9$ , 1984 -  $\chi^2=2.928$ ,  $df=3$ ,  $p>0.1$ ) and so the differences seen as reported above are a result of the two sexes spending unequal amounts of time on the territory.

### 9.3.3 Number of Interactions Involving Male and Female Territory Holders when Both Gulls are Present on the Territory - 1984.

In Appendix 22 and Figure 9.3 the numbers of interactions observed which involved male and female territory holders when both gulls of a pair were on the territory together are shown for 1984. During the no-egg, pre-egg and egg stages males were involved in more interactions than females when both gulls were on the territory together (binomial  $p<0.001$ ). (There were too few data available for analysis of this for the chick stage.) However, during the egg stage the males were involved in only five (out of the 44 interactions recorded) when they were incubating, and females in only three (out of the 12 interactions recorded) when incubating. In Chapter 8 it was shown that males had a tendency to spend more time on the territory than they did incubating and were thus often present when the females were incubating. On these occasions therefore the non-incubating males dealt with any intruders on the territory leaving the females to incubate the eggs.

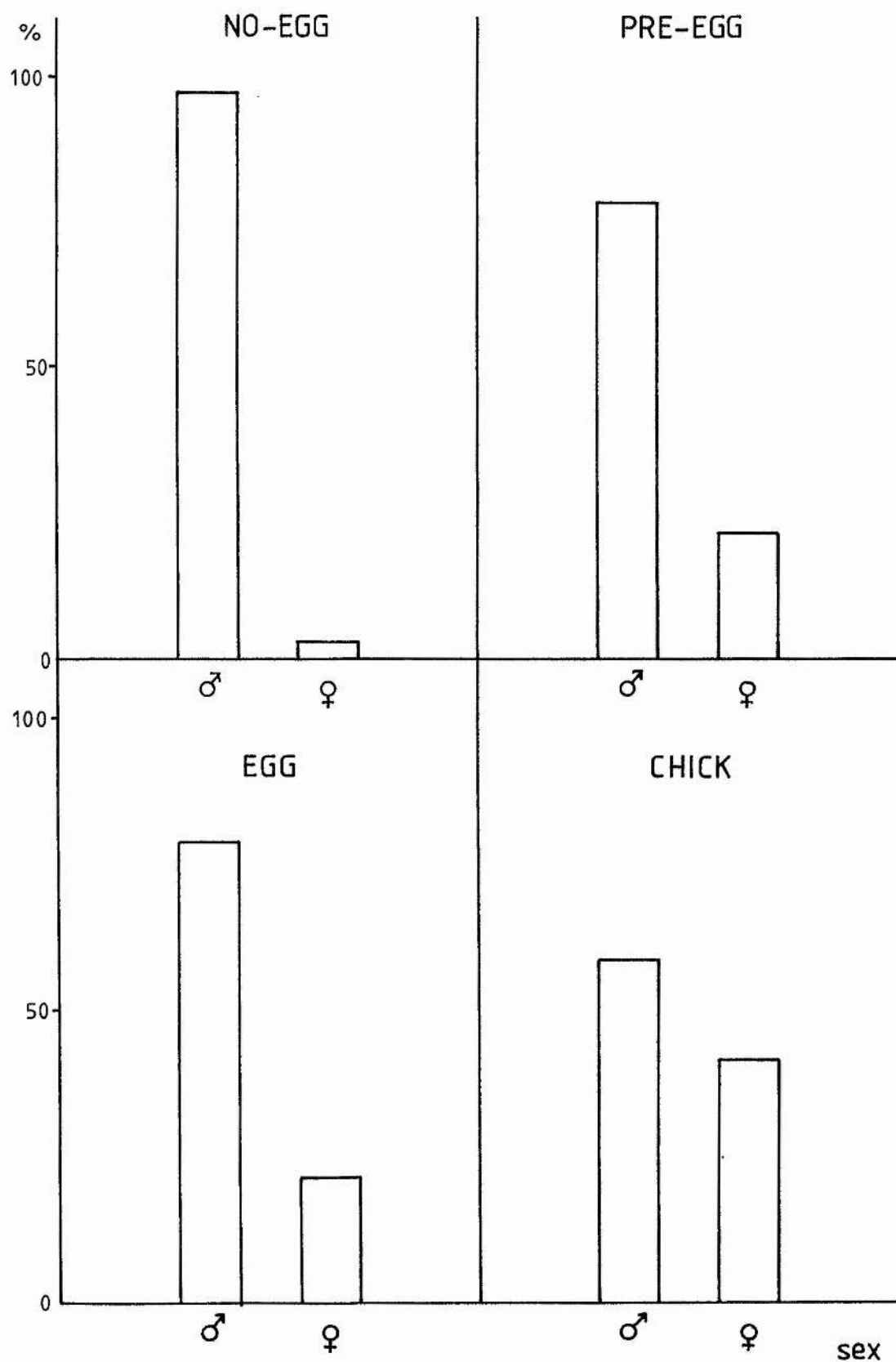
A chi-square analysis of the frequencies observed during the no-egg and pre-egg stages shows that no-egg females were involved in fewer interactions than expected, while pre-egg females were involved in more interactions than expected ( $\chi^2=17.146$ ,  $df=1$ ,  $p<0.001$ ). However, there were no significant differences in the observed and expected frequencies of interactions in a chi-square test of the pre-egg, egg and chick stages ( $\chi^2=2.505$ ,  $df=2$ ,  $p>0.1$ ).

FIGURE 9.3

Percentage of interactions involving male and female territory holders when both gulls were on the territory together during different stages of reproduction in 1984. (Data in Appendix 22)

FIG 9.3

PERCENTAGE OF INTERACTIONS INVOLVING MALE AND FEMALE  
TERRITORY HOLDERS WHEN BOTH GULLS ARE ON THE  
TERRITORY TOGETHER



#### 9.3.4 Number of Interactions Between Different Sexes of Intruders and Territory Holders - 1984.

Appendix 23 and Figure 9.4 show the frequencies of interactions observed between different sexes of intruders and territory holders in 1984. During all three stages where there were sufficient interactions recorded for analysis (no-egg, pre-egg and egg) there were many more interactions between male territory holders and male intruders than between any other combination of sexes. In Section 9.3.2 it was shown that male territory holders were involved in more interactions than females during these three stages and it would appear from the results here that there are more male intruders than female.

The identities of many neighbouring gulls were recorded because they belonged to the groups of gulls selected for detailed observation. Therefore, it was easier to identify the sex of some of the neighbouring intruders than it was a strange intruder. It might be expected that this could have biased the results as most of the neighbouring intruders were likely to be males considering the results found in Section 9.3.3. In fact, in all the stages of reproduction concerned, the results used in this section comprised equal numbers of interactions involving neighbours and strangers. Section 9.3.1 shows the total numbers of interactions observed which involved different types of intruders and the numbers involving strangers were 2-4 times the numbers involving neighbours. Therefore, the fact that it was easier to identify the sex of neighbours has had some effect on the data collected. A chi-square test conducted on all the data, excluding the female versus female interactions which were too few for analysis, for the no-egg, pre-egg and egg stages, showed that during the egg stage there were more interactions involving female territory holders and male intruders than expected ( $\chi^2 = 11.939$ ,  $df = 4$ ,  $p < 0.05$ ). This also appears to be the case during the chick stage, and in fact more interactions were seen during this stage between female territory holders and male intruders than for any other combination. There were only 15 interactions recorded during this stage however, when the sex of the two gulls involved was known, which is too few for statistical analysis. Despite this there is a strong suggestion that female territory holders are playing a much larger part in defence than they did during any of the other stages.

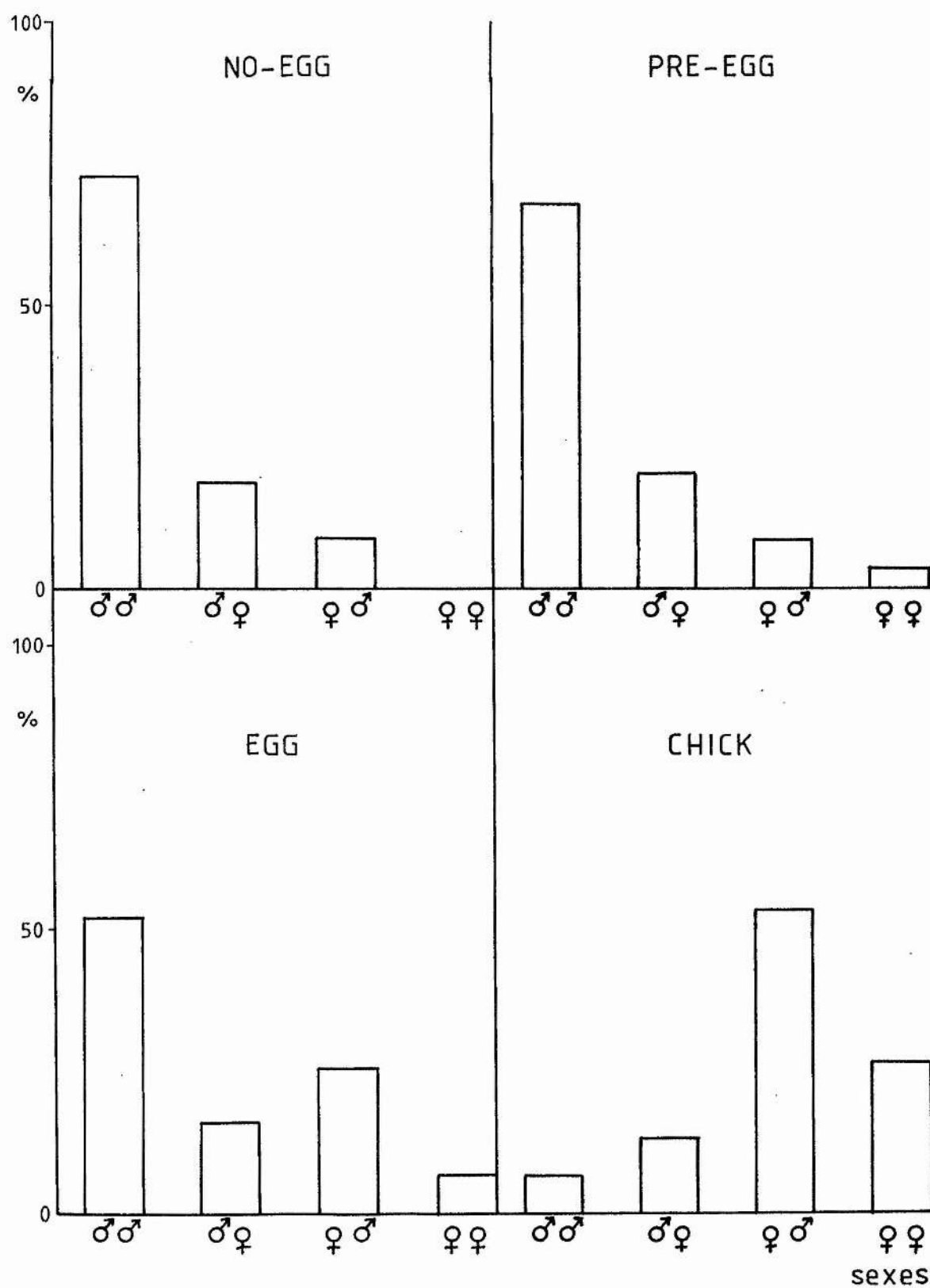
**FIGURE 9.4**

Percentage of interactions involving different sexes of territory holders and intruders during different stages of reproduction in 1984. (Data in Appendix 23)

- |    |   |
|----|---|
| ♂♂ | both male territory holder and intruder   |
| ♂♀ | male territory holder and female intruder |
| ♀♂ | female territory holder and male intruder |
| ♀♀ | both female territory holder and intruder |

FIG 9.4

PERCENTAGE OF INTERACTIONS INVOLVING DIFFERENT SEXES  
OF TERRITORY HOLDERS AND INTRUDERS



### 9.3.5 Distance of the Intruder from the Nest when the Interaction Occurred - 1984.

Appendix 24 and Figure 9.5 show the mean distances that different intruder types were from a nest when they were reacted to by the territory holders. The data are divided up into different stages of reproduction. Analysis of variance tests were carried out on the data collected for each of the reproductive stages followed by Tukey's post-hoc HSD tests.

No-egg gulls allowed neighbouring gulls to get closer to the nest than any of the other three groups of intruders before reacting to their presence ( $F=4.948$ ,  $df=3,228$ ,  $p<0.01$ ; Tukey  $p<0.05$ ). During the pre-egg stage the results look similar but neighbouring gulls were allowed significantly closer to the nest only than strange gulls before being reacted towards ( $F=2.638$ ,  $df=3,214$ ,  $p<0.05$ ); Tukey  $p<0.05$ ). During the egg stage, however, neighbours were again allowed closer to the nest than the other 3 intruder types ( $F=7.084$ ,  $df=3,378$ ,  $p<0.01$ ; Tukey  $p<0.05$ ). During the chick stage there are very few data for interactions with neighbours and immature gulls. However, the statistical analysis showed that both neighbours and strangers were allowed closer to the nest than other species, and strangers were allowed closer than immature gulls ( $F=2.880$ ,  $df=3,61$ ,  $p<0.05$ ; Tukey  $p<0.05$ ).

Appendix 25a and Figure 9.6a show the mean distances of intruders from the nest during the egg and chick stages when they were reacted to by territory holders that were incubating and brooding and by those that were not incubating or brooding. Analysis of variance showed that territory holders which were incubating eggs and brooding chicks allowed intruders to get closer to the nest than territory holders that were not incubating or brooding ( $F=26.216$ ,  $df=1,446$ ,  $p<0.01$ ). The data were subdivided to show the mean distances for different types of intruders (Appendix 25b and Figure 9.6b). Unfortunately there were too few data for analysis of the chick-stage results but analysis of variance was carried out on the egg-stage results. This showed that there was a difference between the reactions of incubating and non-incubating gulls ( $F=26.294$ ,  $df=1,376$ ,  $p<0.01$ ) and that there was an interaction between the state of the territory holder and the type of intruder ( $F=18.461$ ,  $df=3,376$ ,  $p<0.01$ ). In fact, neighbours, strangers and immature gulls were all reacted towards at a greater



FIGURE 9.5

Mean distance and standard error of different intruder types from the nest when reacted towards by the territory holder during different stages of reproduction in 1984. (Data in Appendix 24)

FIG 9.5

MEAN DISTANCE OF INTRUDERS FROM THE NEST WHEN REACTED TO BY THE TERRITORY HOLDER

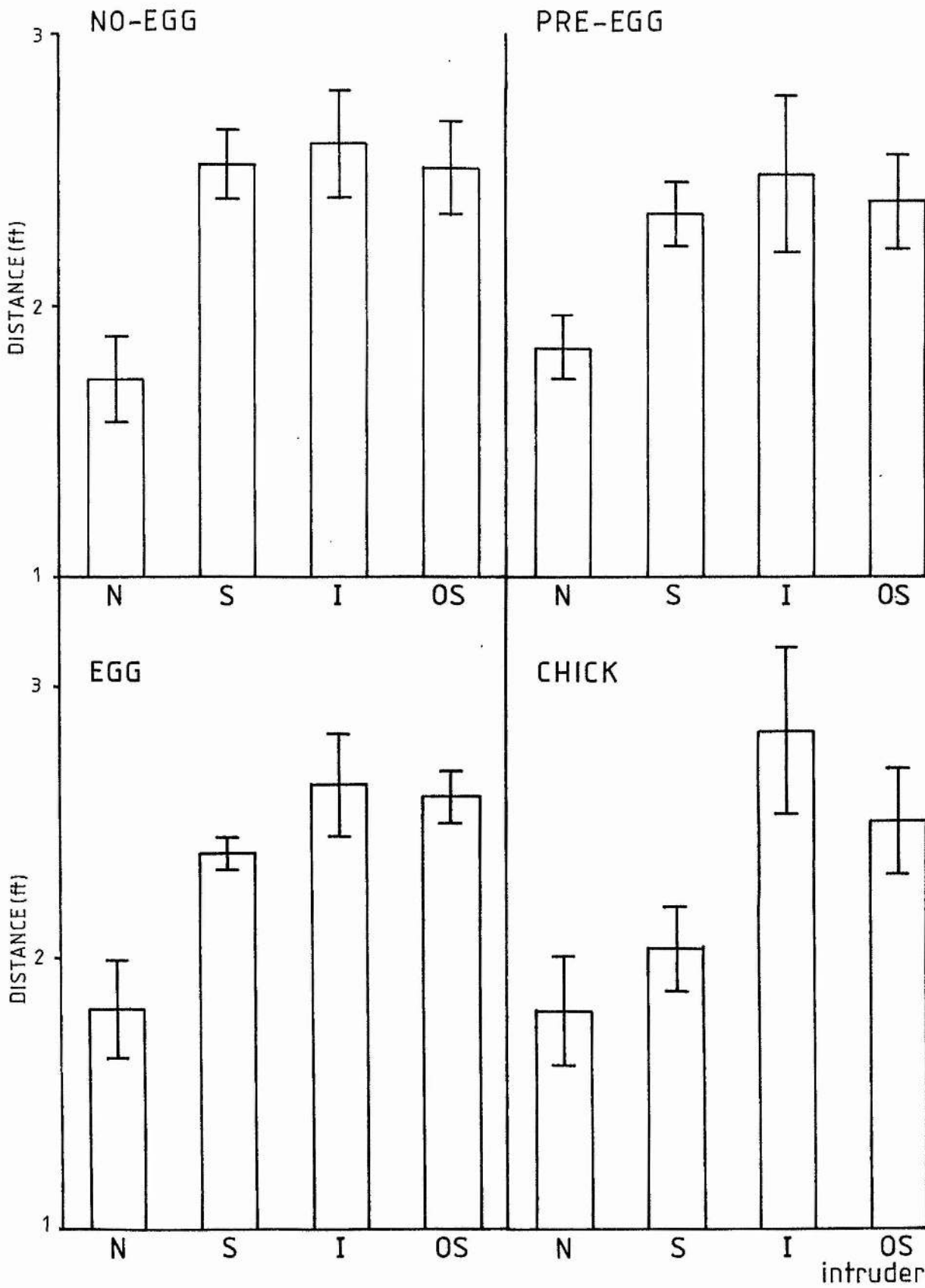


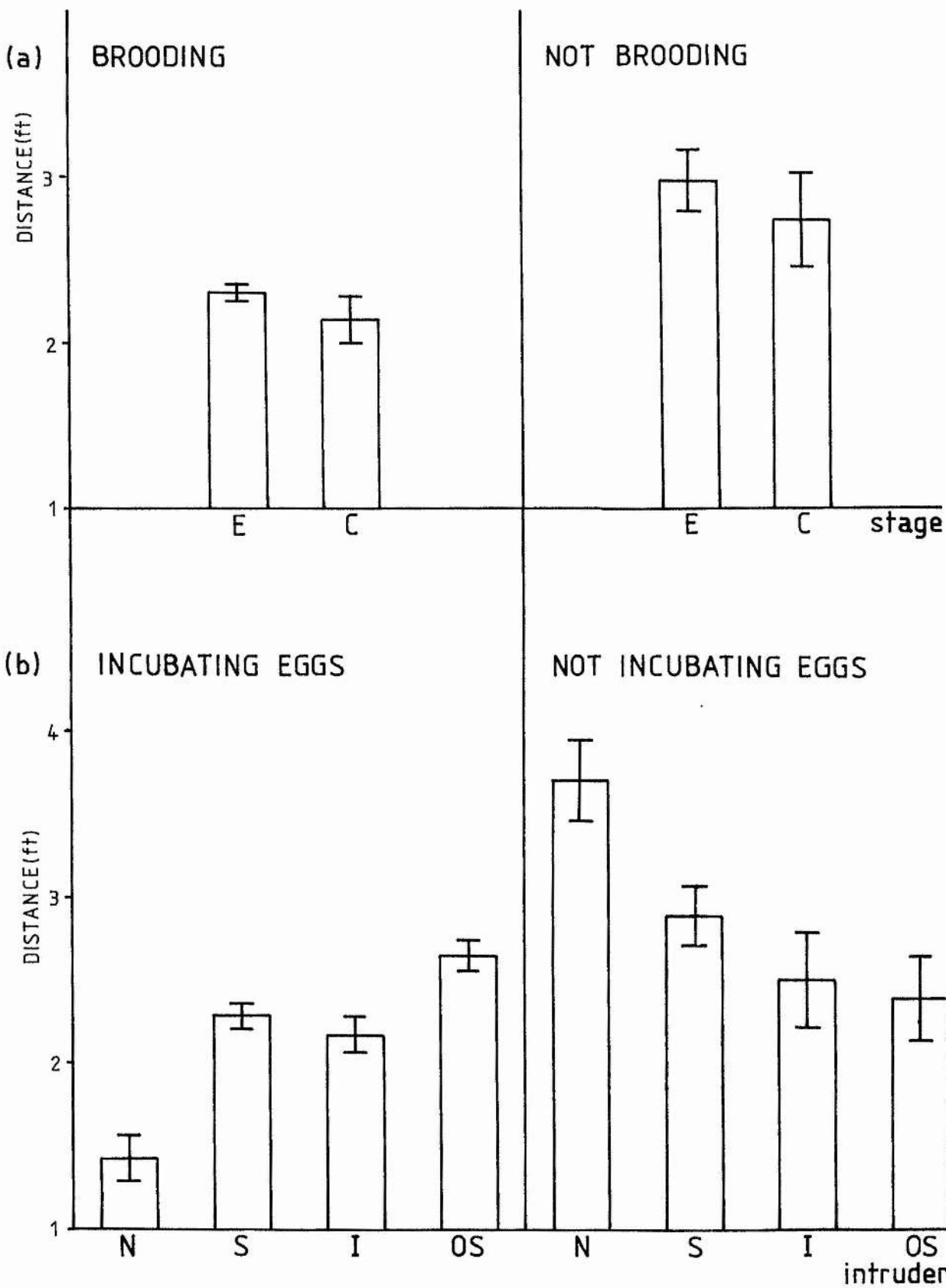
FIGURE 9.6

(a) Mean distance and standard error of intruders from the nest when reacted towards by the territory holder during the egg and chick stages of 1984 when the territory holder was brooding and not brooding. (Data in Appendix 25a)

(b) Mean distance and standard error of different intruder types from the nest when reacted towards by the territory holder during the egg stage of 1984 when the territory holder was brooding and not brooding. (Data in Appendix 25b)

FIG 9.6

MEAN DISTANCE OF INTRUDERS FROM THE NEST WHEN REACTED TO BY THE TERRITORY HOLDER



distance from the nest by non-incubating gulls than by incubating gulls, while other species of birds were allowed closer to the nest by non-incubating territory holders (Tukey  $p < 0.05$ ). When the territory holder was incubating the eggs, neighbours were allowed closer to the nest before being reacted to than the other three intruder types and other species were reacted to at a greater distance from the nest than the other three intruder types (Tukey  $p < 0.05$ ). However, when the territory holder involved was not incubating, neighbours were reacted to by it at a greater distance from the nest than both strangers and other species. In approximately 50% of the interactions observed which involved a non-incubating gull the other bird of the pair was sitting on the eggs. In 25% the other bird was present on the territory but not incubating and in 25% it was not present at all. Thus during 50% of these interactions the eggs were not protected at the time. This seems a very high proportion considering that in general the eggs were rarely left uncovered for any length of time at all. They were, however, necessarily uncovered when there was a changeover of gulls on the nest and, although no records were made, the impression was gained that any gulls in the vicinity of the nest were reacted to aggressively during changeovers. As these were most likely to be neighbours on their own territories, this could explain why it appeared that neighbours were being reacted to at greater distances from the nest than other intruders.

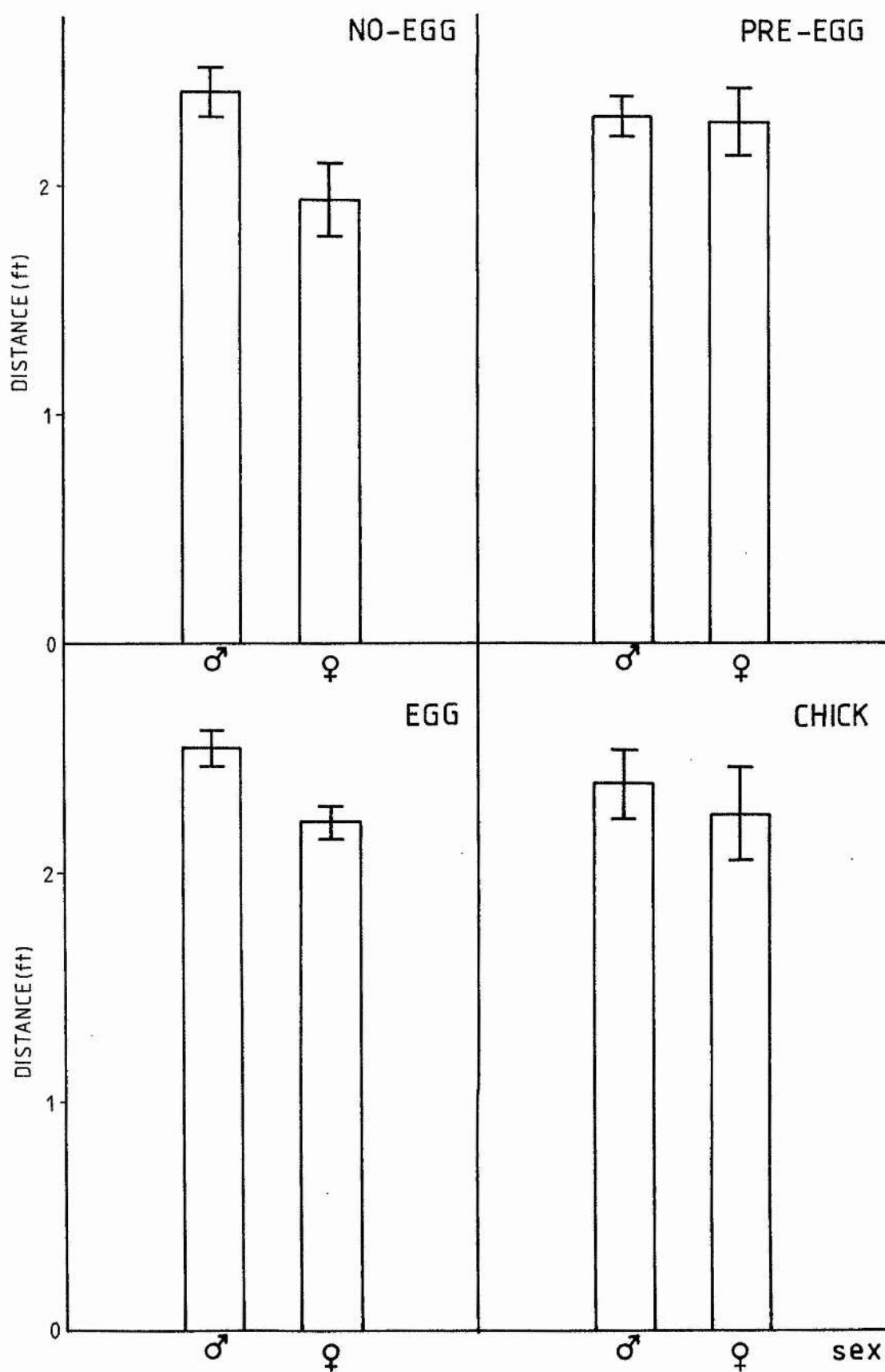
Analysis of the distance of intruders from the nest when reacted to by males and by females (Appendix 26, Figure 9.7) shows that no-egg females allowed intruders to get closer to the nest before reacting to them than no-egg males ( $F = 4.124$ ,  $df = 1,225$ ,  $p < 0.05$ ). During the egg stage this also occurred ( $F = 8.130$ ,  $df = 1,350$ ,  $p < 0.01$ ), but during the pre-egg and chick stages there was no significant difference found between males and females.

FIGURE 9.7

Mean distance and standard error of intruders from the nest when reacted towards by male and female territory holders during different stages of reproduction in 1984. (Data in Appendix 26)

FIG 9.7

MEAN DISTANCE OF INTRUDERS FROM THE NEST WHEN  
REACTED TO BY THE TERRITORY HOLDER



### 9.3.6 Number of Interactions Occurring for Different Intensities of Reactions by Territory Holders Towards Intruders

The information collected about the reaction of a territory holder towards an intruder was divided into five levels of increasing intensity of reaction as follows:

- 1) intruder ignored by territory holder
- 2) intruder displayed or jabbed at without any move being made towards it by the territory holder
- 3) intruder walked or run towards by the territory holder
- 4) intruder flown at or chased and followed out of the territory
- 5) intruder attacked and fought with

In some cases the frequencies in some of the levels, especially in levels 1 and 5, were too low for valid chi-square analysis so in these cases some of the levels, usually levels 1 and 2 and levels 4 and 5, had to be pooled together. (Where this was the case the results were reported with the numbers grouped together ie. 'levels 4 & 5' means that levels 4 and 5 were pooled together, while 'level 4 and level 5' means that levels 4 and 5 were treated individually.)

#### 9.3.6.1 The Pattern of Intensity of Interactions During Different Periods of Reproduction

Appendix 27 and Figure 9.8 show the frequencies of the above levels of reactions observed during all stages of reproduction for the three years of the study. To examine whether or not there were any differences between years, chi-square tests of the pre-egg, egg and chick stages were done for all three years.

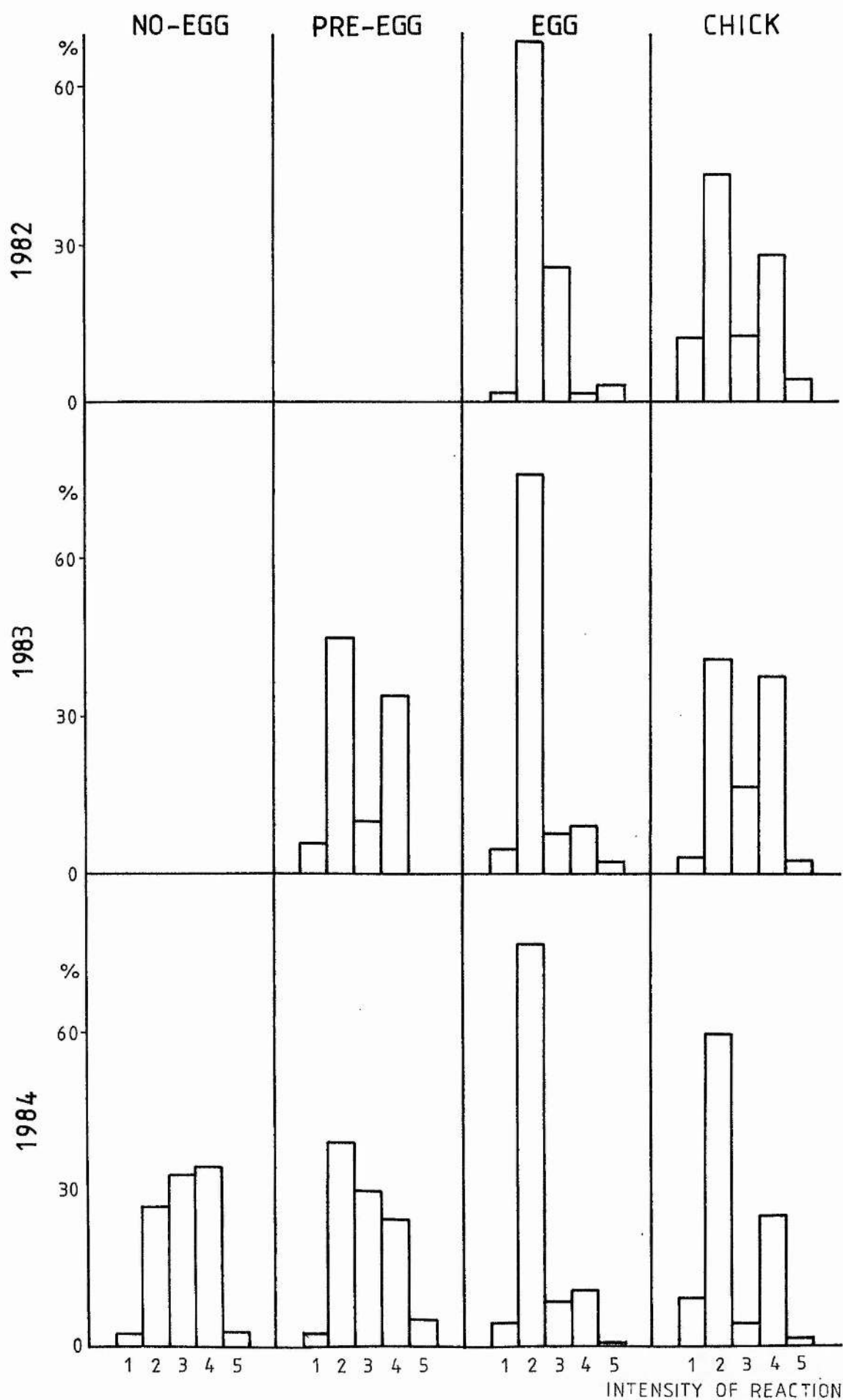
During the pre-egg stage it was found that fewer level 3 reactions were observed than expected in 1983 ( $\chi^2 = 13.177$ ,  $df = 4$ ,  $p < 0.05$ ). However, there were comparatively few data collected for this stage in



**FIGURE 9.8**

Percentage of interactions, of different intensities of reaction, of territory holders towards intruders, during different stages of reproduction for the three years of the study. (Data in Appendix 27)

FIG 9.8



this year. During the egg stage there were more level 3 reactions and fewer level 4 reactions observed than expected in 1982 ( $\chi^2=55.701$ ,  $df=8$ ,  $p<0.001$ ). During the chick stage intruders were ignored more often than expected in 1982 and less often than expected in 1983 ( $\chi^2=26.228$ ,  $df=8$ ,  $p<0.005$ ).

To look at the differences in the intensity of aggression at different times of the season, chi-square tests were done on no-egg and pre-egg frequencies, pre-egg and egg frequencies and on egg and chick frequencies for each year where possible.

The no-egg/pre-egg test results showed that there was a significant difference in the pattern of interactions for the two groups ( $\chi^2=10.458$ ,  $df=4$ ,  $p<0.05$ ) with fewer level 2 reactions from no-egg gulls and more level 2 reactions from pre-egg gulls than expected. Thus the pre-egg gulls are less aggressive than the no-egg gulls.

The only difference found in the pre-egg/egg test for 1983 was that there were more level 4 & 5 reactions observed during the pre-egg stage than expected ( $\chi^2=18.870$ ,  $df=3$ ,  $p<0.001$ ) implying that the gulls were more aggressive during the pre-egg stage than the egg stage. In 1984 the same test showed that there were fewer level 2 reactions observed than expected and more level 3, level 4 and level 5 reactions than expected during the pre-egg stage, while during the egg stage there were more level 2 reactions and fewer level 3, level 4 and level 5 reactions observed than expected ( $\chi^2=102.862$ ,  $df=4$ ,  $p<0.001$ ). Thus, in this year too the gulls were more aggressive during the pre-egg stage than the egg stage.

The egg/chick test for 1982 showed that fewer level 1 and level 4 reactions were observed than expected during the egg stage while more level 1 and level 4 reactions and fewer level 2 reactions were seen than expected during the chick stage ( $\chi^2=58.740$ ,  $df=4$ ,  $p<0.001$ ). Thus, although the gulls ignored intruders more often during the chick stage than the egg stage, when they did react to them they did so more aggressively. As suggested above, the gulls probably ignored intruders more than expected during the chick stage of this year because the data were collected from parents with only

young chicks. In 1983, the year when the data were collected from parents with chicks of all ages, more level 2 and fewer level 3 and level 4 reactions were observed than expected during the egg stage, while during the chick stage fewer level 2 and more level 3 and level 4 reactions were recorded than expected. Therefore, here too chick stage gulls were more aggressive than egg stage gulls. In 1984 there were fewer level 4 & 5 reactions observed during the egg stage than expected and during the chick stage there were more level 4 & 5 reactions recorded than expected. So, in this year also the gulls were more aggressive during the chick stage.

To summarise; no-egg gulls were more aggressive towards intruders than pre-egg stage gulls and both pre-egg and chick stage gulls were more aggressive towards intruders than egg stage gulls.

#### 9.3.6.2 Differences in Reaction towards Different Intruder Types.

In Appendix 28 the frequencies of different reaction levels recorded for four different types of intruders are shown. In Figure 9.9 the percentages for the main two types of intruders (neighbours and strangers) have been plotted. Chi-square tests were done on the frequencies for each stage for each of the study years to discover if there were any significant differences in the patterns of interactions observed towards neighbours and strangers.

In 1984 no-egg gulls were found to react to neighbours with more level 1 & 2 reactions than expected ( $\chi^2=9.586$ ,  $df=2$ ,  $p<0.01$ ), ie. they reacted less aggressively to neighbours than to strangers. During the pre-egg stage of 1984 the gulls again reacted to neighbours with more level 1 & 2 reactions than expected ( $\chi^2=13.390$ ,  $df=3$ ,  $p<0.01$ ) but in 1983 there was no significant difference found between the observed and expected frequencies ( $\chi^2=2.475$ ,  $df=1$ ,  $p>0.05$ ). However, there were very few records made during the pre-egg stage of 1983. So, for this group of gulls also, the reactions towards neighbours intruding on the territory were less aggressive than the reactions towards strangers.

FIGURE 9.9

Percentage of interactions, of different intensities of reaction, of territory holders towards neighbouring and strange gull intruders, during different stages of reproduction for the three years of the study.

(Data in Appendix 28)



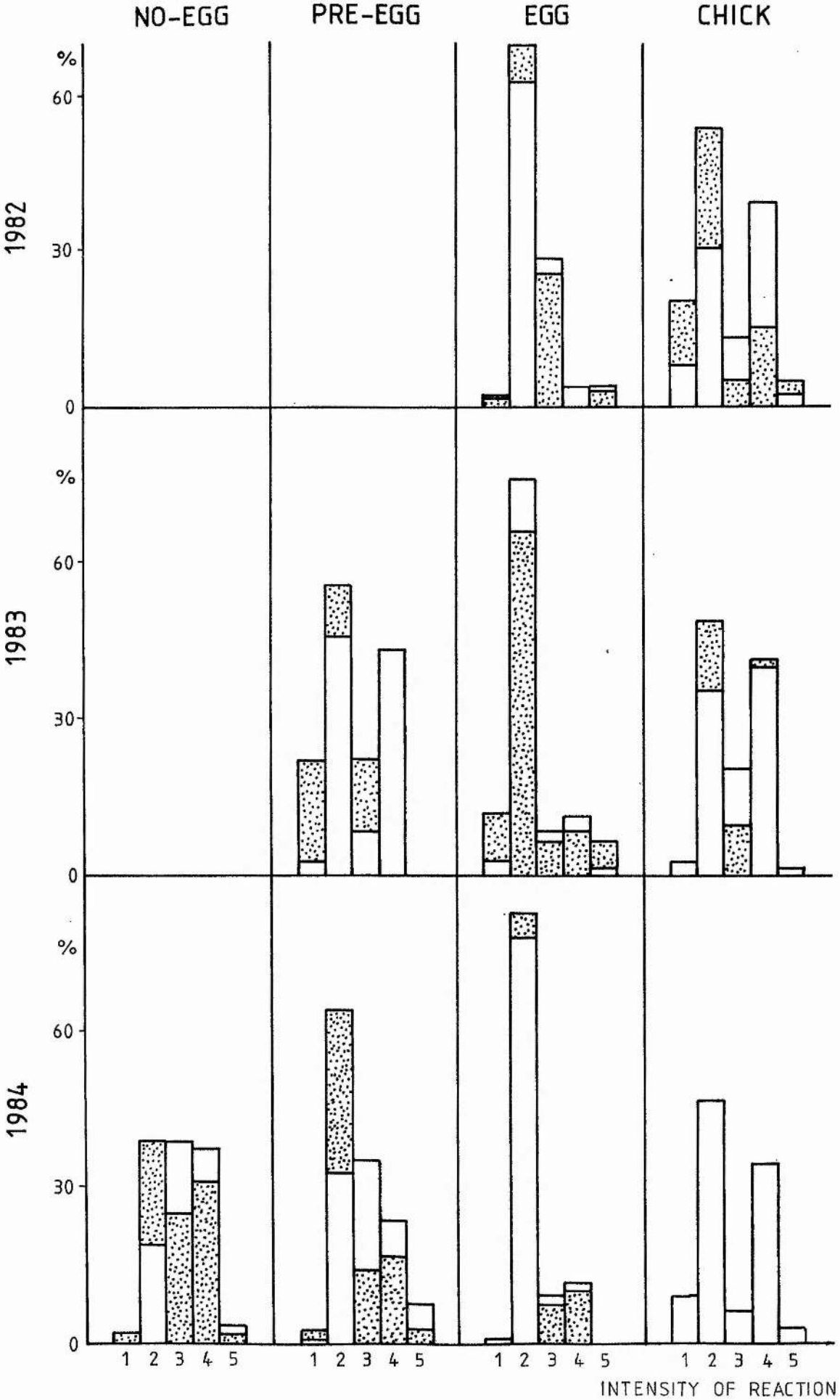
Neighbouring gulls



Strange gulls

(N.B. In this figure and in Figure 9.11 each graph contains percentages for two groups of gulls and these percentages all read from the x-axis.)

FIG 9.9



During the egg stage there were no significant differences found between the observed and expected frequencies in any of the three years of the study (1982 -  $\chi^2=2.184$ ,  $df=2$ ,  $p>0.05$ ; 1983 -  $\chi^2=0.433$ ,  $df=2$ ,  $p>0.05$ ; 1984 -  $\chi^2=0.307$ ,  $df=2$ ,  $p>0.05$ ). During the chick stage there were too few data for analysis in 1984. In 1983 there were no significant differences found between the recorded and the expected frequencies ( $\chi^2=3.016$ ,  $df=2$ ,  $p>0.05$ ) but in 1982 there was a tendency for gulls to react to neighbours with fewer level 3, 4 & 5 reactions than expected and to strangers with more level 3, 4 & 5 reactions than expected ( $\chi^2=9.794$ ,  $df=2$ ,  $p<0.01$ ).

Therefore, during the no-egg and pre-egg stages and during the chick stage of 1982 but not 1983 the gulls reacted less aggressively towards neighbours on their territory than they did towards strangers. During the egg stage of all three years there was no difference in the reactions of the gulls towards the two intruder types, and during the chick stage there was no difference in the reactions in 1983 but in 1982 there was a tendency for gulls to react less aggressively towards neighbours than strangers. Again, this last result has probably occurred because of the difference in the data collected during the chick stage of these two years. In 1982 the data were collected from gulls with only young chicks and these would have been brooded for a lot of the time. Thus, it might be expected that while the chicks were safe in the nest a familiar gull would not have posed as great a threat as a strange one. In 1983, however, the data were collected from nests with chicks of all ages and it would appear that all intruding gulls are seen equally as a threat.

In 1984 there were enough data collected to look at the differences in reaction towards all four intruder types for no-egg, pre-egg and egg stage gulls (Appendix 28, Figure 9.10). Chi-square tests were carried out on the frequencies observed for all four intruder types during each of the three stages of reproduction. No-egg gulls reacted to strange gulls with fewer level 1 & 2 reactions than expected ( $\chi^2=16.259$ ,  $df=6$ ,  $p<0.05$ ) and pre-egg gulls reacted to neighbours with more level 1 & 2 reactions than expected ( $\chi^2=15.679$ ,  $df=6$ ,  $p<0.05$ ). During the egg stage immatures were reacted to with more level 4 & 5 reactions than expected ( $\chi^2=15.398$ ,  $df=6$ ,  $p<0.05$ ).

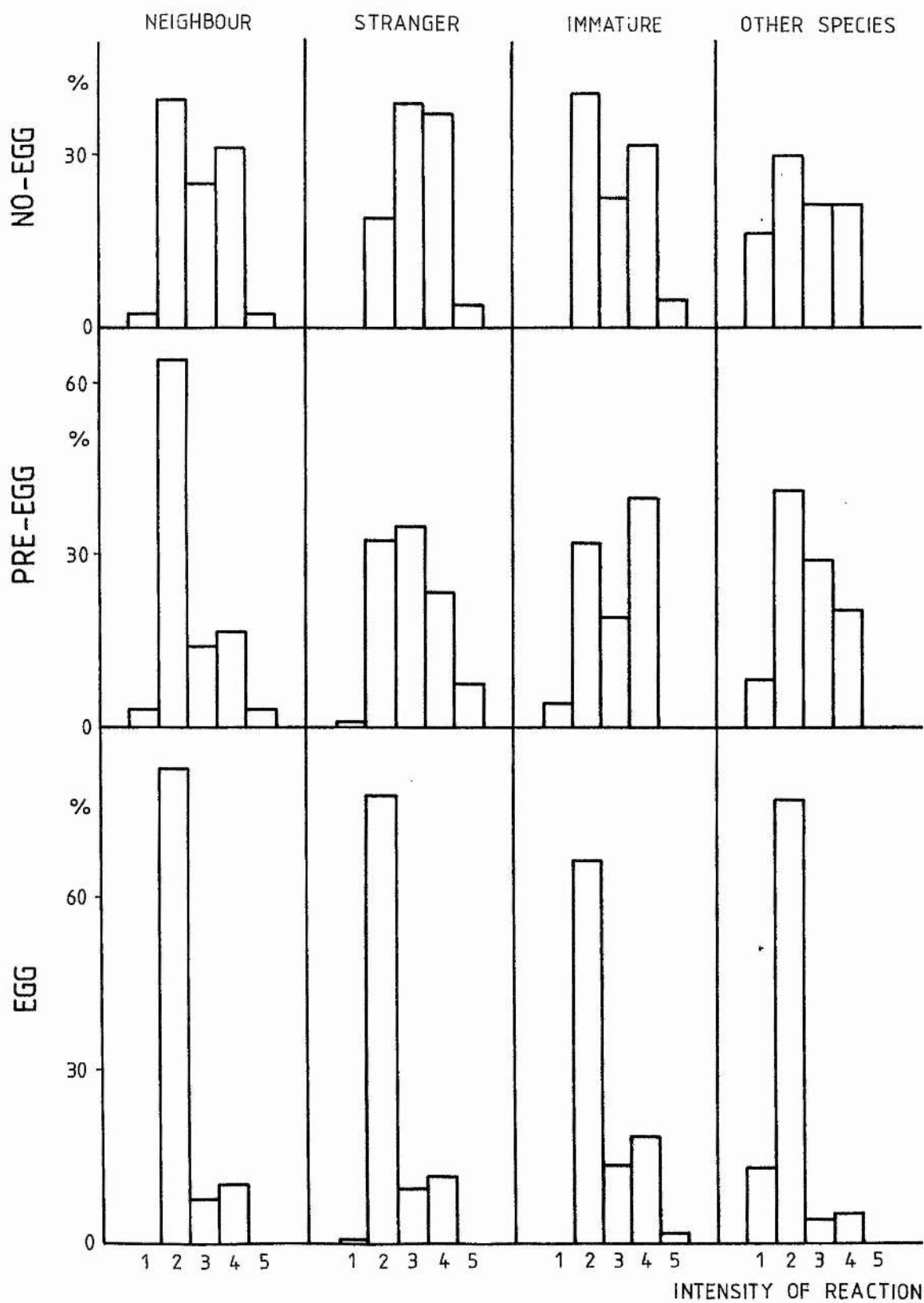
**FIGURE 9.10**

Percentage of interactions, of different intensities of reaction, of territory holders towards different intruder types, during different stages of reproduction in 1984. (Data in Appendix 28)



FIG 9.10

1984



Thus, no-egg gulls reacted more aggressively to strangers than the other groups, pre-egg gulls reacted less aggressively to neighbours than the other three groups and egg-stage gulls reacted more aggressively towards immatures than the other types of intruders.

In Section 9.3.6.1 it was observed that no-egg gulls appeared to be more aggressive towards intruders than pre-egg gulls. This is also suggested here in the graphs for all four intruder types (Figure 9.10). Chi-square tests were done on the frequencies for no-egg and pre-egg gulls for each of the intruder types. There was no significant difference found in the reactions of the two groups towards neighbours ( $\chi^2 = 5.159$ ,  $df = 2$ ,  $p > 0.05$ ), immatures ( $\chi^2 = 0.122$ ,  $df = 2$ ,  $p > 0.05$ ) or other species ( $\chi^2 = 0.249$ ,  $df = 2$ ,  $p > 0.05$ ), but there was a difference found in their reactions towards strangers ( $\chi^2 = 11.201$ ,  $df = 3$ ,  $p < 0.05$ ) with a tendency for no-egg gulls to react to them more aggressively than pre-egg gulls.

#### 9.3.6.3 Differences in Reaction of Male and Female Territory Holders towards Intruders.

Appendix 29 and Figure 9.11 show the frequencies of the five different levels of reactions of male and female territory holders at different stages of reproduction. Chi-square tests were carried out on the data for male and female territory holders for each stage of reproduction in each year of the study, where possible. (There were too few data available with known sexes of territory holders for the chick stage of 1982 and too few data for the pre-egg stage of 1983 for analysis.)

No-egg males and females were found to differ significantly in the pattern of aggression shown towards intruders ( $\chi^2 = 17.291$ ,  $df = 2$ ,  $p < 0.001$ ) with female gulls reacting with more level 1 & 2 reactions and fewer level 4 & 5 reactions than expected. No significant difference was found between the sexes during the pre-egg stage but during the egg stage there was a difference found in 1984 ( $\chi^2 = 20.681$ ,  $df = 3$ ,  $p < 0.001$ ). In this year male gulls reacted with more level 4 & 5 reactions than expected and females reacted with fewer level 3 and fewer level 4 & 5 reactions than expected. This difference, however, was not evident in either 1982 ( $\chi^2 = 0.077$ ,  $df = 1$ ,  $p > 0.05$ ) or 1983 ( $\chi^2 = 1.315$ ,  $df = 4$ ,  $p > 0.05$ ). During the chick stage there were no significant differences found in either 1983 ( $\chi^2 = 5.201$ ,  $df = 3$ ,

**FIGURE 9.11**

Percentage of interactions, of different intensities of reaction, of male and female territory holders towards intruders, during different stages of reproduction for the three years of the study. (Data in Appendix 29)

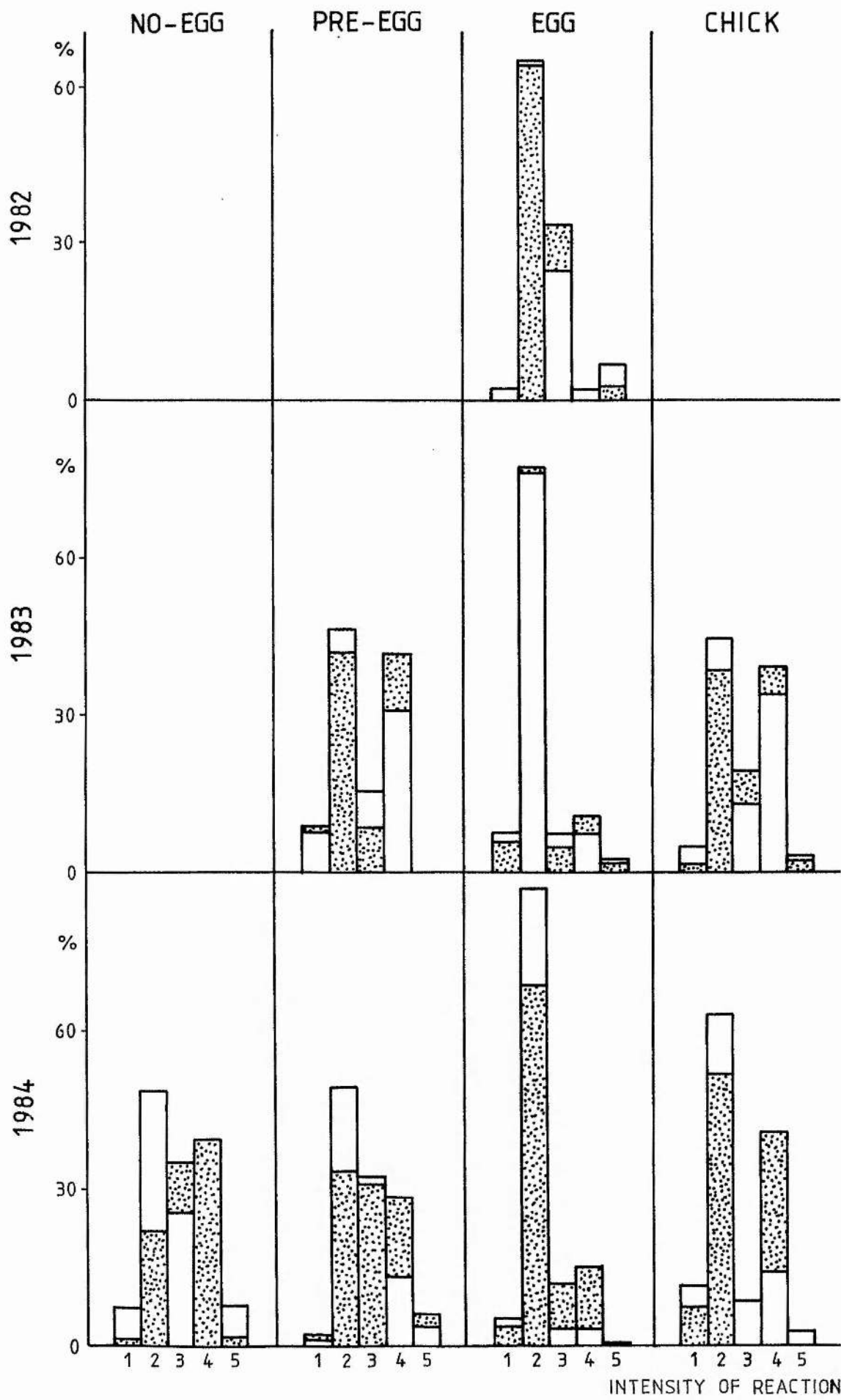


Male territory holders



Female territory holders

FIG 9.11



$p > 0.05$ ) or 1984 ( $\chi^2 = 1.574$ ,  $df = 1$ ,  $p > 0.05$ ). Thus, no-egg males and males during the egg stage of 1984, but not 1982 and 1983, were more aggressive towards intruders than the females were. During the pre-egg and chickstages and the egg stage of 1982 and 1983, however, males and females were equally aggressive towards intruders.

Chi-square tests of the frequencies observed for no-egg and pre-egg gulls, for each of the sexes, showed that no-egg and pre-egg females do not differ in their reactions ( $\chi^2 = 0.455$ ,  $df = 2$ ,  $p > 0.05$ ) while there is a tendency for no-egg males to be more aggressive than pre-egg males ( $\chi^2 = 10.236$ ,  $df = 3$ ,  $p < 0.05$ ). Chi-square tests of the frequencies observed during the egg and chick stages of 1983 for each of the sexes showed that males reacted with more level 1 & 2, fewer level 3 and fewer level 4 & 5 reactions than expected during the egg stage, while during the chick stage they react with fewer level 1 & 2, more level 3 and more level 4 & 5 reactions than expected ( $\chi^2 = 46.639$ ,  $df = 2$ ,  $p < 0.001$ ). The picture for females is similar with more level 2 and fewer level 4 & 5 reactions than expected during the egg stage and fewer level 2 and more level 4 & 5 reactions than expected during the chick stage ( $\chi^2 = 28.119$ ,  $df = 3$ ,  $p < 0.001$ ). Tests on the frequencies observed in all three stages (pre-egg, egg and chick) of 1984 showed that pre-egg-stage males reacted with fewer level 1 & 2, more level 3 and more level 4 & 5 reactions than expected while during the egg stage they reacted with more level 1 & 2, fewer level 3 and fewer level 4 & 5 reactions than expected ( $\chi^2 = 59.307$ ,  $df = 4$ ,  $p < 0.001$ ). Similarly, females reacted with fewer level 1 & 2 and more level 3, 4 & 5 reactions than expected during the pre-egg stage and with fewer level 3, 4 & 5 reactions than expected during the egg stage ( $\chi^2 = 40.343$ ,  $df = 2$ ,  $p < 0.001$ ).

So, to summarise, no-egg males had a tendency to be more aggressive towards intruders than pre-egg males. Both males and females were more aggressive during the pre-egg stage than they were during the egg stage and both were less aggressive during the egg stage than they were during the chick stage.

#### 9.3.6.4 Differences in Reaction of Gulls During the Egg and Chick Stages Between Those Brooding and Those Not Brooding - 1983 and 1984.

Appendix 30 and Figure 9.12 show the frequencies of the different levels of reactions observed during the egg and chick stages when the gulls were incubating and brooding and when they were not incubating and not brooding. Chi-square tests were done on the frequencies observed for brooding and non-brooding gulls for each of the stages and for each of the two years (1983 and 1984).

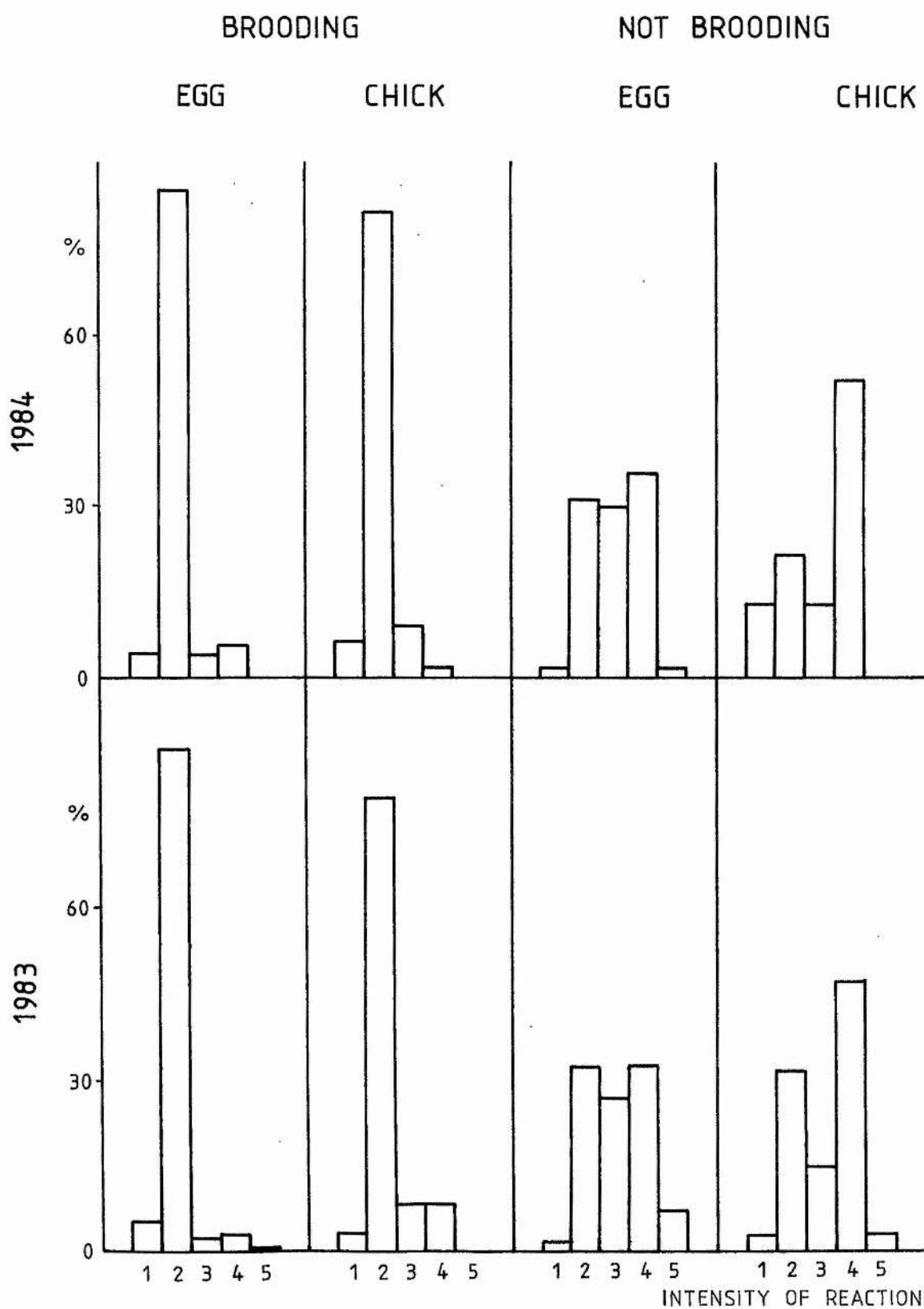
During the egg stage of 1983, incubating gulls reacted with more level 1 & 2, fewer level 3 and fewer level 4 & 5 reactions than expected while non-incubating gulls reacted with fewer level 1 & 2, more level 3 and more level 4 & 5 reactions than expected ( $\chi^2=100.543$ ,  $df=2$ ,  $p<0.001$ ). During 1984 incubating gulls reacted with fewer level 3 and level 4 & 5 reactions than expected while non-incubating gulls reacted with fewer level 2 and more level 3 and level 4 & 5 reactions than expected ( $\chi^2=115.342$ ,  $df=2$ ,  $p<0.001$ ). During the chick stage of 1983 brooding gulls reacted with more level 2 and fewer level 4 reactions than expected and non-brooding gulls reacted with fewer level 2 reactions than expected ( $\chi^2=45.065$ ,  $df=4$ ,  $p<0.001$ ). During 1984, brooding gulls reacted with fewer level 3,4 & 5 reactions than expected while non-brooding gulls reacted with fewer level 1 & 2 and more level 3,4 & 5 reactions than expected ( $\chi^2=20.918$ ,  $df=1$ ,  $p<0.001$ ).

Therefore, the black-headed gulls reacted less aggressively to intruders on their territories when they were incubating eggs or brooding chicks than they did when they were not.

FIGURE 9.12

Percentage of interactions, of different intensities of reaction, of territory holders during the egg and chick stages of 1983 and 1984, when the territory holders were brooding and not brooding. (Data in Appendix 30)

FIG 9.12





## 9.4 Summary and Discussion

### 9.4.1 Summary of Results.

No-egg and pre-egg territory holders reacted more aggressively towards intruders than egg and chick stage gulls, and egg stage gulls reacted less aggressively to intruders than chick stage gulls. Also, no-egg gulls reacted more aggressively towards intruders than pre-egg gulls, particularly towards strangers. (Sections 9.3.6.1 and 9.3.6.2.)

Neighbouring gulls were allowed to get closer to territory holders' nests before being reacted to than strangers, immatures and other species for no-egg and egg stage gulls, and closer than strangers only for pre-egg gulls. During the chick stage neighbours and strangers were allowed closer than other species, and immatures were reacted to at a greater distance than strangers, but there were few data for this stage. (Section 9.3.5.)

No-egg gulls reacted more aggressively towards strangers than neighbours, immatures and other species, and pre-egg gulls reacted to neighbours less aggressively than strangers, immatures and other species. During the egg stage there was no difference in the intensity of reactions towards neighbours and strangers, but in 1984 immatures were reacted to more aggressively than the other intruder types. During the chick stage in 1982 neighbours were reacted to less aggressively than strangers but in 1983 the difference was not significant. (Section 9.3.6.2.)

No-egg, pre-egg and 1984 egg-stage male territory holders were involved in significantly more interactions than females. However, they were involved in similar numbers of interactions relative to the amount of time they spent on the territory in all stages of reproduction in 1983 and 1984. (Section 9.3.2.) When both gulls were on the territory together, male gulls were involved in more interactions than the females for no-egg, pre-egg and egg stage gulls (insufficient data for chick stage). Also, pre-

egg females were involved in a larger proportion of the total number of interactions than no-egg females. (Section 9.3.3.)

Female territory holders allowed intruders to get closer to the nest before reacting to them than male territory holders in the no-egg group and egg stage. Pre-egg and chick stage gulls showed no difference between the sexes, however, although there were not many data available for analysis of chick stage interactions. (Section 9.3.5.) Male territory holders reacted towards intruders more aggressively than female territory holders in the no-egg group and during the egg stage of 1984 only. There was no significant difference between pre-egg and chick stage males and females nor between egg stage males and females in the other two years. Both males and females were more aggressive during the pre-egg stage and the chick stage than they were during the egg stage, and no-egg males were found to be more aggressive towards intruders than pre-egg males while females did not differ. (Section 9.3.6.3.)

There were many more male/male interactions observed than any other combination of the sexes for no-egg, pre-egg and egg stage gulls (insufficient data for the chick stage), and during the egg stage there were more female-territory-holder/male-intruder reactions seen than there were for no-egg and pre-egg groups. (Section 9.3.4.)

During both the egg and chick stages, incubating and brooding gulls reacted much less aggressively towards intruders than non-incubating and non-brooding gulls. (Section 9.3.6.4.) Incubating gulls allowed neighbours to get closer to the nest before reacting to them than strangers, immatures and other species. They also reacted to other species at a greater distance from the nest than any other type of intruder. Non-incubating gulls on the other hand reacted to neighbours at a greater distance from the nest than all other intruders during the egg stage. Non-incubating gulls reacted towards neighbours, strangers and immatures at a greater distance from the nest than incubating gulls but they allowed other species to get closer to the nest before reacting to them than incubating gulls. (Section 9.3.5.)

#### 9.4.2 Discussion

No-egg gulls differed from pre-egg gulls in several ways in their reactions towards intruders on their territories. The main difference between them was the much greater role played by the no-egg males in the defence of the territory, its resources (eg nesting material) and its mate. The no-egg females played a very small role in defence but it is not known which is the cause and which the effect ie. whether the males had to play a greater role because the females did not chase off intruders or whether the females had to play a smaller role because the males were so active in defence. However, the results suggest that the difference lies largely with the behaviour of the males because although no-egg and pre-egg females show no difference in their intensity of reaction towards intruders, no-egg males are much more aggressive towards intruders than pre-egg males. The fact that no-egg males also appeared more restless and went to and from the territory more often than pre-egg males, while females do not differ, suggests that the failure of the no-egg gulls to establish their territory and go on to lay eggs may have something to do with the behaviour of the male gulls, or at least with some incompatibility between males and females that causes the males to behave differently to the pre-egg males which remained and subsequently produced eggs.

The black-headed gulls were more aggressive towards intruders on their territory during the pre-egg-laying stage than they were when they had eggs or chicks in the nest. One might expect them to be more aggressive when they had eggs or more especially chicks to protect and thus had more to lose in terms of reproductive investment. However, it would seem that much more aggression is required in order to establish and keep a breeding territory than is needed to protect the eggs and chicks from intruders. Burger (1980a) observed that before egg-laying began, herring gulls chased away intruders at greater distances than necessary for successful courtship and mating and she suggested that this was done to establish a territory large enough for subsequent reproductive activities. She also observed an enlargement of the defended territory when any neighbouring territory was temporarily deserted, as did Emlen (1956) in the ring-billed gull. This behaviour was also seen in the black-headed gulls and it

is thought that it is advantageous in deterring other gulls from establishing a territory between neighbours.

Although the intensity of the aggressive behaviour of the two sexes towards intruders did not differ during the pre-egg-laying stage, males were involved in far more interactions than females at this time. This was also reported in black-headed gulls by Tinbergen (1956) and in a variety of colonial sea birds (Burger 1981b, 1981c; Pierotti 1981). Tinbergen (1956) and Burger (1981b) also reported, as was observed in this study, that males were mainly involved in aggression against other males. In fact, Burger found that 90% of the interactions seen prior to egg-laying were male/male interactions. Here nearly 70% of the interactions seen, where the sexes of the two gulls were known, involved aggression between male territory holders and male intruders.

Prior to egg-laying, males invest a great deal of time and energy defending the territory while females invest very little. Thus it seems possible that male aggression may be related to the protection of the females from insemination by other males. Attempts at forced copulations by strange males are fairly common, though they are vigorously resisted by the females concerned, and the possibility of mate guarding has been suggested in many species (Tinbergen 1956; MacRoberts 1973; Birkhead 1979; Burger 1981c). Burger (1981b) found that more attacks were seen by male gannets (*Sula bassana*) when their mates were also on the territory, and the males were more aggressive when their mates were present while the females were not. The large percentage of male/male interactions observed appears also to indicate that male intruders were seen as a great threat to male territory holders during this stage. As the male gulls appear to play the major role in the choice of the territory and in nest building, it could be argued that males are more aggressive because they are simply establishing and defending territories. Burger (1981b), however, reported that when gannet pairs lose their eggs and chicks and prepare to re-lay, the males again become very aggressive just when the females are being inseminated but when they already have the boundaries of their territory well established.

During the pre-egg stage neighbours were allowed closer to the nest than strangers and were also reacted to less aggressively (as in Moynihan 1955). Thus strange gulls, which may have been looking for somewhere to establish their own territory, were seen as a greater threat to an established pair of gulls than a neighbour which already had a territory of its own nearby. There were also more interactions seen with strangers than expected during the pre-egg stage. This probably occurred because many strange gulls were landing in the nesting areas looking for suitable nesting sites or materials. Immatures and other species were also reacted to more aggressively than neighbours. As an unknown entity they were probably treated as a greater threat than neighbouring birds which were known to the territory holders, but as it was unlikely that either group would be in competition with them for part of their territory (although immatures were infrequently seen attempting and sometimes succeeding in breeding) they would not be expected to be as great a threat as strangers were.

During an aggressive interaction a retreat from the territory would incur a greater loss for a territory holder than an intruder would gain by winning (Maynard-Smith & Parker 1976). The owner of a territory may have invested a lot of time and energy settling boundaries with neighbours and building a nest etc, and it would have to reinvest all over again in a new territory if it were displaced. Therefore, a large asymmetry is created which favours the territory holder and this raises the question as to why some intruders risk escalating the aggression of territory holders by remaining on the territory. In such cases it may be that the intruder is attempting to take over only a small portion on the edge of a territory and thus it may have more to gain than the territory holder has to lose. If an intruder can defeat several territory holders individually in such a fashion, it may obtain a territory for itself amongst them.

During the egg stage both male and female gulls were less aggressive towards intruders than they were during the pre-egg stage. Males and females were involved in a similar number of interactions relative to the time they spent on the territory. However, there were differences in their behaviour during this stage. In Chapter 8 it was found that males tended to be present on the territory more often than the time they spent incubating and so they were sometimes present when the females were incubating the

eggs, while the females were present less often when the males were incubating. During these periods, when the female was on the nest, the male chased away virtually all the intruders on the territory, leaving the female to incubate the eggs. For this reason males were found to react to intruders at a greater distance from the nest than females and in one of the three years males were more aggressive towards intruders than females. The females, however, only ever left the nest to chase off intruders that got very close to them. Female Western gulls (Pierotti 1981) allowed intruders to cross the territory or stand about on it without responding and only defended the territorial boundaries after the eggs had hatched.

During the egg stage of 1982 territory holders were less aggressive towards intruders than they were during the other two years. In 1982 the nests were much closer together than in 1983 and 1984 and it may be that this result occurred because of the greater density of nesting in this year. A reaction involving any movement towards an intruder in a dense nesting area may be enough to cause it to leave, whereas in the 2 years when the density of nesting was much less, territory holders may have had to resort to the more aggressive acts to chase intruders off. Also, in Section 9.3.1 it was shown that because of the dense nesting conditions there were more interactions with neighbouring gulls than with strangers and in Section 9.3.6.2 it was shown that neighbours tend to be reacted to less aggressively than strangers. Fewer interactions were seen with strangers during the egg stage than expected compared to the pre-egg stage. Fewer gulls will be looking for nesting sites during the egg stage and in Chapter 7 it was recorded that at about the start of egg-laying unoccupied gulls began to collect on communal non-nesting areas of the colony rather than in the breeding areas.

Incubating gulls were much less aggressive in their reactions towards intruders, and usually only left their eggs when they were alone to chase away intruders that got very close to the nest. During this period one gull of a pair was always present on the territory, and its reproductive investment (the eggs) was best protected by it remaining seated on the nest. However, the gulls still needed to maintain their territory at a size necessary for mobile chicks, and to prevent intruders from establishing territories where they would be a threat to their offspring. Thus, although the gulls were less aggressive when



sitting on eggs, because they remained on them rather than leaving them to chase intruders away, they still reacted to an intruder's presence with squawks at the same distance from the nest as they did during the pre-egg and chick stages.

Although strangers were still reacted to at a greater distance from the nest than neighbours, as they posed a greater threat to the territory holder, both intruder types were reacted to with the same intensity of aggression because the territory holders remained on the nest to protect the eggs. Immatures were reacted to more aggressively than any other intruder type suggesting that they were seen as a greater threat to the incubating gulls. However, the reason for this is not obvious.

It would appear that during incubation the males still take the major role of territory defence, as they did during the pre-egg stage, and the females only do their share of the incubating and defend the immediate area around the nest.

During the chick stage both the males and the females were less aggressive towards intruders than they were during the pre-egg stage but more aggressive than they were during the incubation stage (Ytreberg 1956; Hunt & Hunt 1976; Burger 1980a, 1981c; Knight & Temple 1986b). Males and females were involved in a similar number of interactions and did not differ in their aggressive behaviour towards intruders. Unlike the previous two stages both males and females played an equal role in the defence of the territory and the protection of the chicks.

During this stage intruders were ignored more in 1982 than in 1983. The data collected during 1982 was from gulls with chicks during only their first week of life and in 1983 data were available from gulls with chicks of all ages. Thus it is likely that this result reflects the tendency of gulls to brood very young chicks more often than older chicks. Parents would be much less likely to ignore an intruder if their chicks were walking about freely on the territory than they would if they were safely protected under them in the nest.

Neighbours and strangers were reacted to equally aggressively in 1983 (insufficient data in 1982) because although strangers may have posed a greater threat to the maintainance of the territory, both types of gulls posed a threat to the chicks. Any chicks straying from their territory or left undefended on their territory were in danger of being attacked by other gulls. As some chicks died as a result of such attacks, the threat at this stage was a very real one.

Burger (1981c) suggested that the seasonal changes she observed in aggressive behaviour reflected differences in the objects being defended and differential parental investment. Trivers (1972) suggested that since females invest more in the eggs than males do then the females should invest more in the defence of the eggs and the chicks. Clearly, this does not appear to be the case here nor with several seabird species studied (Montevocchi & Porter 1980). During the pre-egg stage it was the males that invested most time and energy in the defence of the territory, its mate and in the building of the nest, and although the females invested a lot of their resources in the production of the eggs the males invested most time and energy in defence during the egg stage. Gannet males have been reported to lose more weight during the pre-egg-laying period of territorial defence than the females lose while producing eggs (Burger 1981b). Thus, the males simply invest their energy differently. Although they contribute little to the actual production of the eggs, without their presence in establishing and maintaining the territory, successful reproduction would not be possible as the female only plays an equal part in defence after the chicks have hatched.



## CHAPTER 10 - GROWTH AND FEEDING OF THE CHICKS

### 10.1 Introduction

The adequate feeding of chicks by their parents is a very important factor in their survival, both during the breeding season and after they have fledged, and chicks with high growth rates have been shown to have higher survival rates than slow growing chicks (herring gull - Kadlec et al 1969, Hunt 1972; Western gull - Hunt & Hunt 1975).

The provision of food for the young depends on a rather complex system of interactions between the young, the adults and the food in the environment, and the time and energy devoted to foraging may be limited if other activities will result in the production of more offspring; for example, the parents must avoid risks such as predation, exposure of the young and physical exhaustion that will reduce their total reproductive output.

In this chapter the aim is to investigate several aspects of black-headed gull feeding behaviour which may throw some light on how the two sexes of parent differ in their behaviour, what effect different brood sizes have on the parents' feeding behaviour and how the parents' behaviour towards the chicks changes as the chicks grow older.

## 10.2 Methods

All instances of chick feeding seen on the territories of the gulls being kept under detailed observation were recorded. A group of five nests was kept under observation at any one time, and three such groups were observed throughout the season. The following information was collected:

- 1) Territory number
- 2) Time of day
- 3) Identity of parent
- 4) Whether or not the chicks begged and how often
- 5) Whether or not the chicks were fed when they begged
- 6) The time between the chicks starting to beg and the parent regurgitating food
- 7) The number of times that the parent regurgitated during the feed
- 8) The number of times that the parent picked up food and held it for the chicks

This information was recorded by voice onto a cassette tape and then transcribed onto check sheets at the end of each day to enable each feed to be recorded in as much detail as possible. All the chicks on the study area that could be found during each day of their first week of life were weighed to obtain measures of growth (see Section 3.7).

The collection of data on the feeding of chicks proved to be unexpectedly difficult. In two of the three years of the study, the entrance of the fox into the colony early in the chick stage brought the investigations to an abrupt halt as most of the chicks being observed were killed. But even in the remaining year there were difficulties. One of the problems was visibility. The parents frequently regurgitated with their backs to the hide so obscuring many of the details of the feed. Also, the vegetation around the nests grew very quickly during the later months of the breeding season and, although it was trimmed regularly to improve visibility, it still obscured some of the feeds. Another problem was the loss of broods under study, either through death or because they moved away from their territories, some to other parts of the colony and some to another part of the study area where

they were not visible from the hide. When this happened, another nearby nest was added to the group, but this resulted in the study comprising small amounts of data on a lot of different broods, while very few broods were observed throughout the whole of the feeding period. Therefore, it was necessary to pool the data for all the nests together to do the analysis.

### 10.3 Results

#### 10.3.1 Growth of the chicks

Chicks were easily found for weighing during their first two days of life as they usually remained in or near the nest at this age. Thereafter, however, they became increasingly difficult to find and so sufficient data were collected only to calculate the weight gain of most chicks between the day they were hatched and three days later. This information was used to calculate the mean weight increase for chicks from different sized broods and to examine any differences between first, second and third hatched chicks.

Appendix 31 and Figure 10.1 show the mean weight gain during the first three days of life of chicks from single-chick broods, first and second hatched chicks from 2-chick broods and first, second and third hatched chicks from 3-chick broods. Analysis of variance of all the data shows that there are significant differences between the means ( $F=4.901$ ,  $df=5,53$ ,  $p<0.01$ ) and a Newman-Keuls test shows that the mean weight gain of third hatched chicks is significantly lower than all the other five groups of chicks.

#### 10.3.2 Feeding of the chicks

Feeding of the chicks was usually initiated by the begging of one or more of the chicks, frequently when an absent parent returned to the territory. With young chicks this usually took place in the nest but older chicks would follow the parent all over the territory while begging. The parent frequently turned away from these older chicks, as if trying to avoid their pecking begs, but when they were ready to regurgitate they would move towards the nest and regurgitate onto it or occasionally very close to it. Graves et al (1984) reported that herring gull parents frequently regurgitate at some distance from the

FIGURE 10.1

Mean weight gain and standard error of chicks, from different sized broods, during their first three days of life. (Data in Appendix 31)

FIGURE 10.2

Mean number and standard error of feeds given per hour to different sized broods. (Data in Appendix 32)

FIGURE 10.3

Mean number and standard error of feeds given per hour per chick to different sized broods. (Data in Appendix 33)

FIGURE 10.4

Percentage of feeds given to different sized broods by male and female parents. (Data in Appendix 35)

FIG 10.1

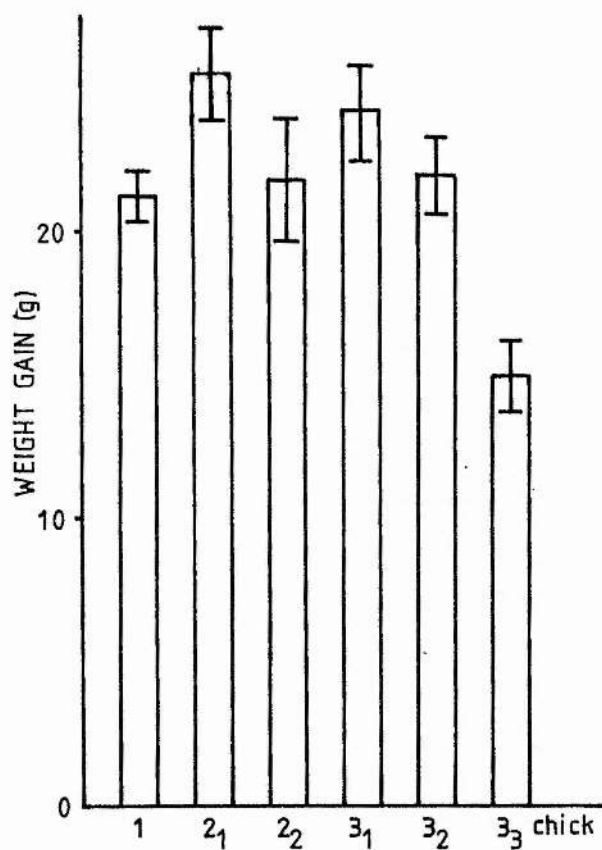


FIG 10.2

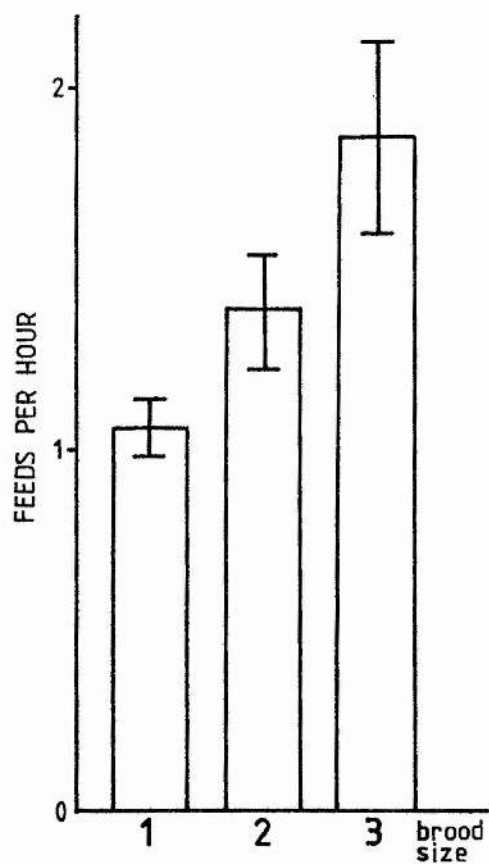


FIG 10.4

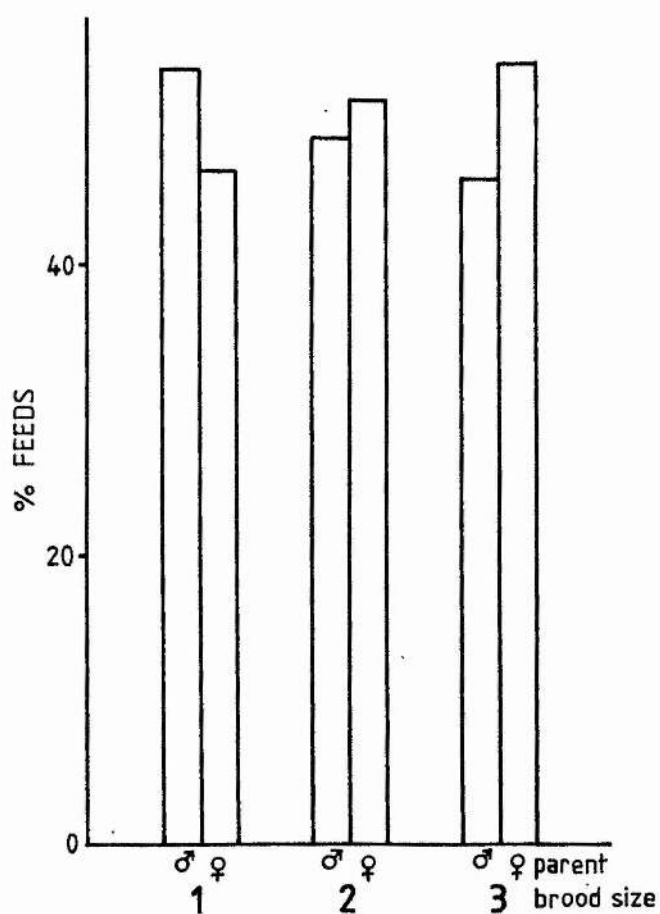
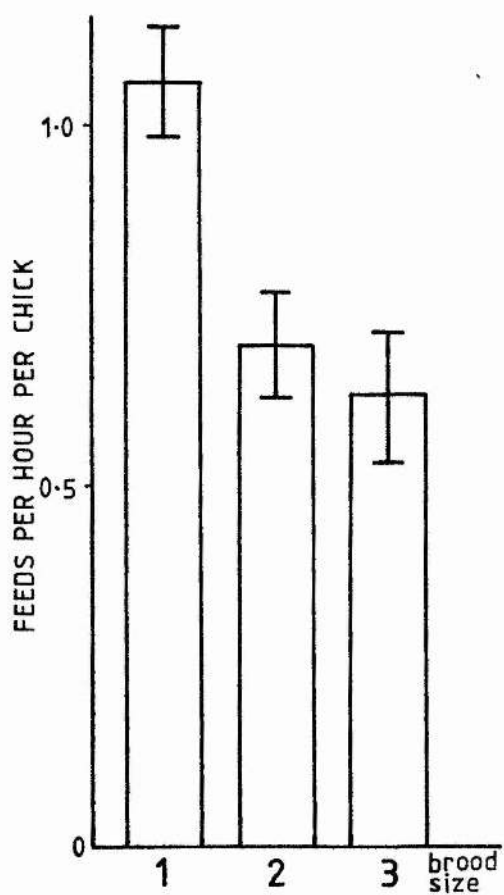


FIG 10.3



nest. However, black-headed gull parents were never seen to do this, but always regurgitated on or very near the nest. When the chicks started eating, the parent frequently picked up pieces of food and held them in its bill for the chicks to take, especially if the chicks were young. If the food was quickly eaten and begging resumed, then the parent regurgitated more food, occasionally doing this several times. If there was food left after a feed or, more usually, if the chicks were slow to eat the food, it was often re-eaten by the parent. If the second parent was also present it too would sometimes help itself to some of the food and it was also, on occasions, seen holding food, regurgitated by the first parent, for the chicks. A feed ended either when the chicks had eaten the food and no longer begged for more, or when the parent left the territory or moved out of the begging chicks' reach.

At the end of each day's observations the mean number of feeds seen per hour of observation for each territory was calculated. This was then used to look at the difference between the number of feeds per hour given to different sized broods of chicks. Appendix 32 and Figure 10.2 show the means and standard errors for the three different brood sizes and analysis of variance shows that the means do differ significantly ( $F=6.158$ ,  $df=2,195$ ,  $p<0.01$ ). There is an increase in the mean number of feeds given per hour with increasing brood size, and in fact there is a significant positive correlation between the mean number of feeds given per hour and the size of the brood ( $r=0.251$ ,  $df=196$ ,  $p<0.02$ ). However, from the values it is clear that the number of feeds does not increase in proportion to the number of chicks in the nest. The mean number of feeds per hour per chick was calculated, and is shown in Appendix 33 and Figure 10.3. It is clear that more feeds per hour per chick were given to single chicks than were given to 2-chick and 3-chick broods ( $F=6.195$ ,  $df=2,195$ ,  $p<0.05$ ).

Appendix 34 shows that male and female parents each gave approximately 50% of all the feeds observed. The numbers of feeds given to different sized broods by males and females are shown in Appendix 35 and Figure 10.4 and here too males and females give a similar number of feeds ( $\chi^2=1.038$ ,  $df=2$ ,  $p>0.5$ ).

On many occasions chicks begged from a parent but did not get fed by it. Appendix 36 and Figure 10.5 show the number of times this occurred, as a percentage of the total number of occasions that the chicks did beg, for the three different brood sizes. Although there appears from the graph to be some variation between groups, an analysis of frequencies showed that this is not significant ( $\chi^2=5.267$ ,  $df=2$ ,  $p>0.05$ ). The same data was then divided into groups according to the age of the oldest chick in the nest. Data were collected from chicks of one to 30 days of age, so four five-day divisions were made for aged one to 20 day old chicks and one 10-day group for 21-30 day old chicks as there were less data collected from older chicks. Appendix 37 and Figure 10.6 show these results and chi-square analysis revealed that 1-5 day old chicks were refused food significantly less often than expected and that 11-15 day old chicks were refused food significantly more often than expected ( $\chi^2=15.071$ ,  $df=4$ ,  $p<0.01$ ).

Chicks were also fed on occasions when they did not beg. The numbers of occasions this occurred and the percentage of the total number of feeds given are shown for different brood sizes in Appendix 38 and Figure 10.7. Although there appears to be an increase in the percentage of feeds given without begging with increasing brood size, a chi-square test shows that there is no significant difference ( $\chi^2=0.848$ ,  $df=2$ ,  $p>0.5$ ).

Appendix 39 and Figure 10.8 show the percentage of feeds given to different aged chicks without begging. From the graph it can be seen that 60% of feeds to 1 day old chicks were given without begging. This decreased to 35% for 2-day old chicks and to 20% for 9-day old chicks. The number of feeds observed for each individual age, however, are small and chi-square analysis carried out on the data when pooled into 2-day age intervals shows that there is no significant difference between the frequencies observed ( $\chi^2=8.810$ ,  $df=4$ ,  $p>0.05$ ).

The mean time between the onset of begging by the chicks and the regurgitation of food by the parents for different sized broods is shown in Appendix 40 and Figure 10.9. Analysis of variance shows that there is no significant difference between the means ( $F=2.918$ ,  $df=2,216$ ,  $p>0.05$ ).



FIGURE 10.5

Percentage of times chicks from different sized broods have begged but not been fed. (Data in Appendix 36)

FIGURE 10.6

Percentage of times chicks from different age groups have begged but not been fed. (Data in Appendix 37)

FIGURE 10.7

Percentage of times chicks from different sized broods have been fed without begging. (Data in Appendix 38)

FIGURE 10.8

Percentage of times different aged chicks have been fed without begging. (Data in Appendix 39)

FIG 10.5

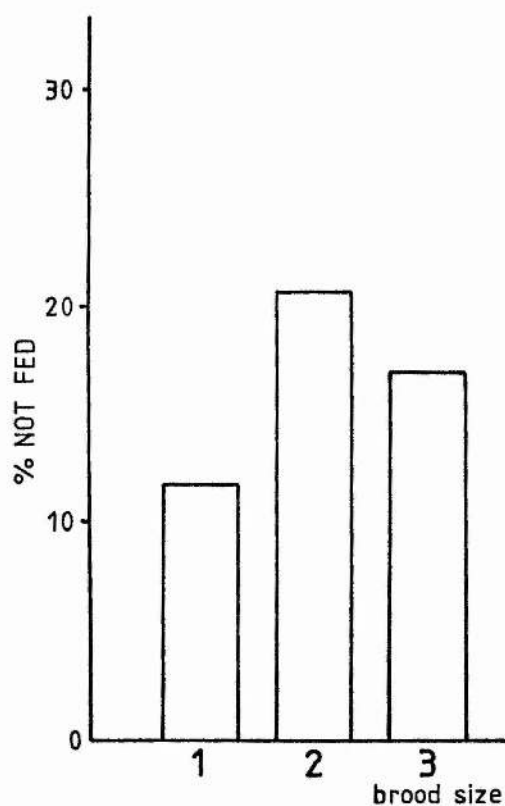


FIG 10.6

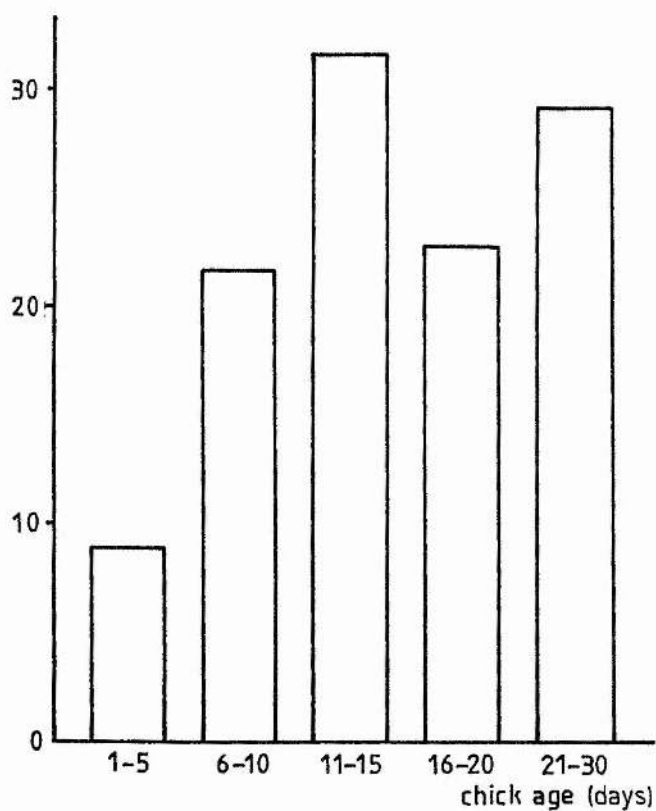


FIG 10.7

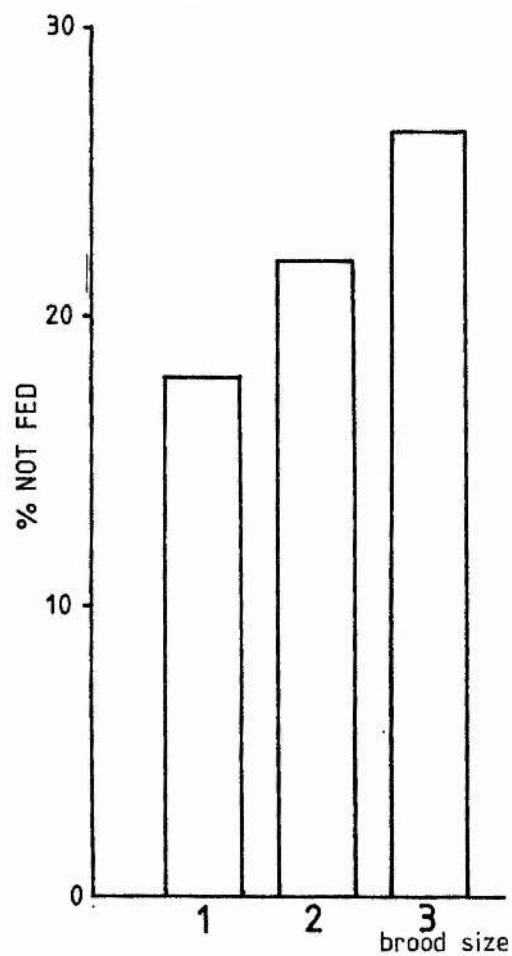


FIG 10.8

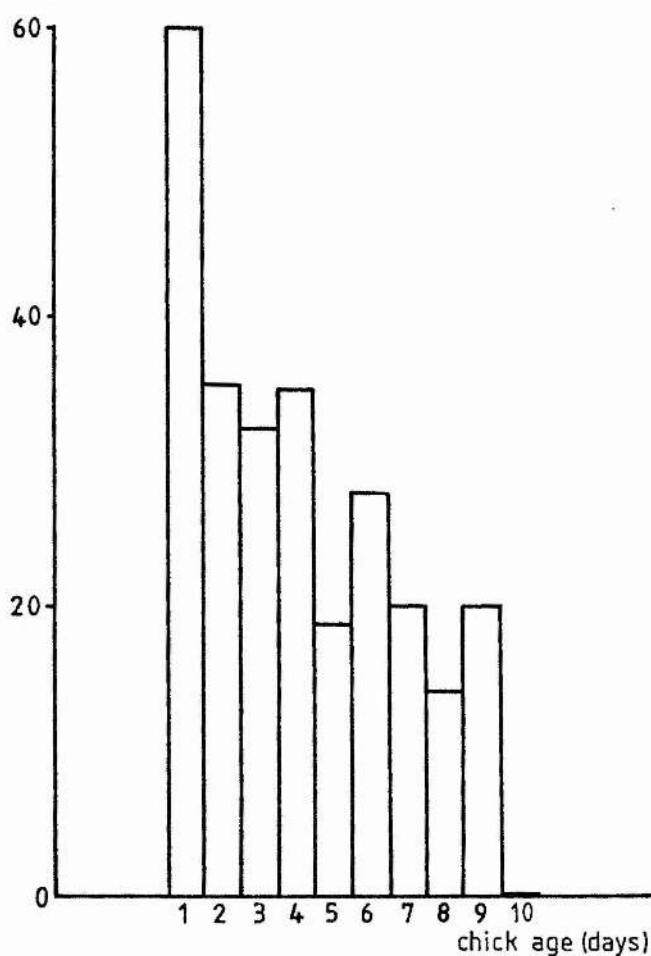


FIGURE 10.9

Mean time elapsed and standard error between the chicks begging and the parent regurgitating, for chicks from different sized broods. (Data in Appendix 40)

FIGURE 10.10

Mean time elapsed and standard error between the chicks begging and the parent regurgitating, for different age groups of chicks. (Data in Appendix 41)

FIG 10.9

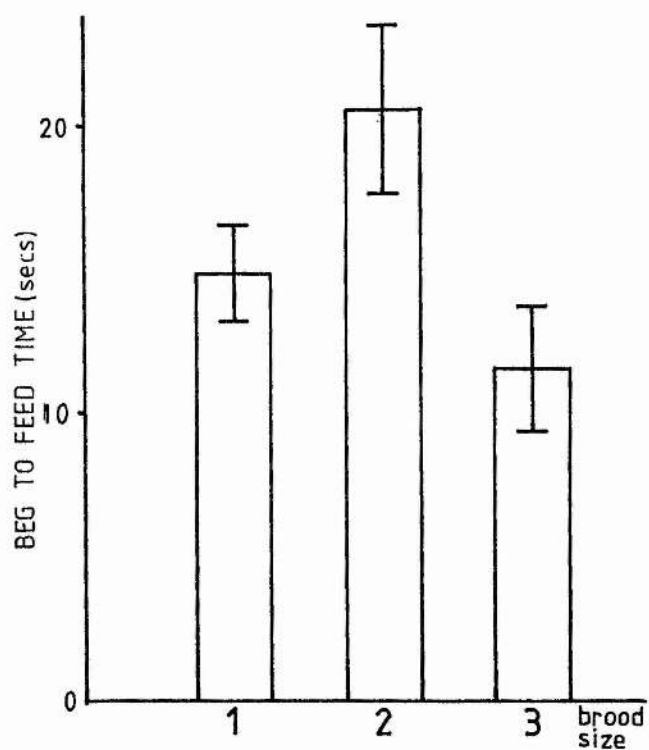
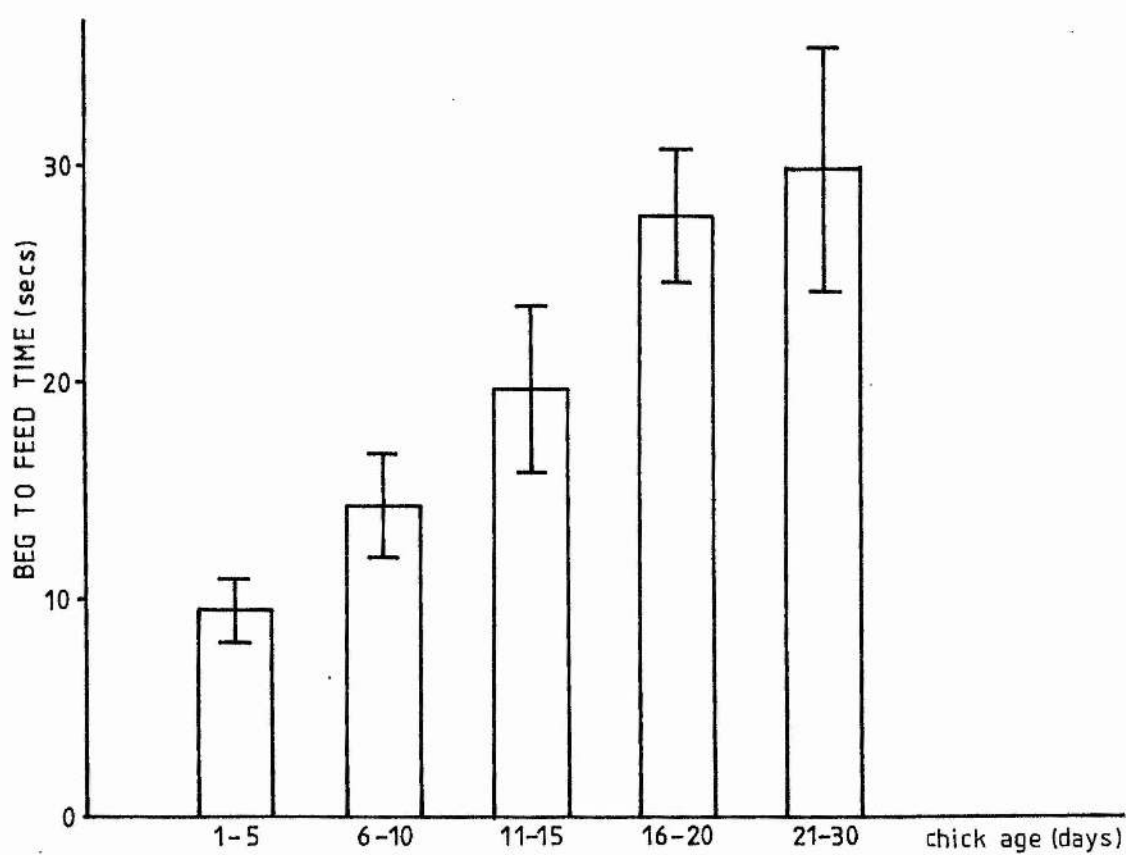


FIG 10.10



Appendix 41 and Figure 10.10 show the mean beg-to-feed times observed for increasing age groups of chicks. The graph shows clearly that the mean beg-to-feed time increased as the age of the chick increases. In fact there is a positive correlation between the beg-to-feed time and the age of the chicks ( $r = 0.412$ ,  $df = 214$ ,  $p < 0.001$ ).

Appendix 42 and Figure 10.11 show the mean beg-to-feed time for males and females with different brood sizes and analysis of variance shows that males and females do not differ in their behaviour ( $F = 2.730$ ,  $df = 1,159$ ,  $p > 0.05$ ). The mean beg-to-feed time of males and females with different aged chicks is shown in Appendix 43 and Figure 10.12. The data were split into four groups, the first two groups comprising 5-day age ranges and the second two of 10-day age ranges. Analysis of variance showed that there was a difference between the sexes ( $F = 4.631$ ,  $df = 1,157$ ,  $p < 0.05$ ) and between the different age groups of chicks ( $F = 7.157$ ,  $df = 3,157$ ,  $p < 0.01$ ). However there was no interaction between the sex of the parent and the age of the chicks ( $F = 0.195$ ,  $df = 3,157$ ,  $p > 0.05$ ) and a Newman-Keuls test did not reveal any difference between the means for males and females feeding the same aged chicks.

The mean number of regurgitations and food-holdings given to different sized broods of chicks are shown in Appendices 44 and 45 and in Figures 10.13 and 10.14. There is no difference between the number of either given to different brood sizes (regurgitate -  $F = 1.197$ ,  $df = 2,242$ ,  $p > 0.05$ ; food-hold -  $F = 0.503$ ,  $df = 2,242$ ,  $p > 0.05$ ).

In Appendices 46 and 47 and Figures 10.15 and 10.16 the mean number of regurgitations and food-holdings per feed given to different aged chicks are shown. Although there is no significant difference in the number of regurgitations given to different aged chicks ( $F = 2.927$ ,  $df = 3,241$ ,  $p > 0.05$ ) there is clearly a decrease in the number of times parents hold food for the chicks as the chicks' ages increase. In fact there is a negative correlation between the number of times parents hold food for the chicks and the age of the chicks ( $r = -0.350$ ,  $df = 240$ ,  $p < 0.001$ ).

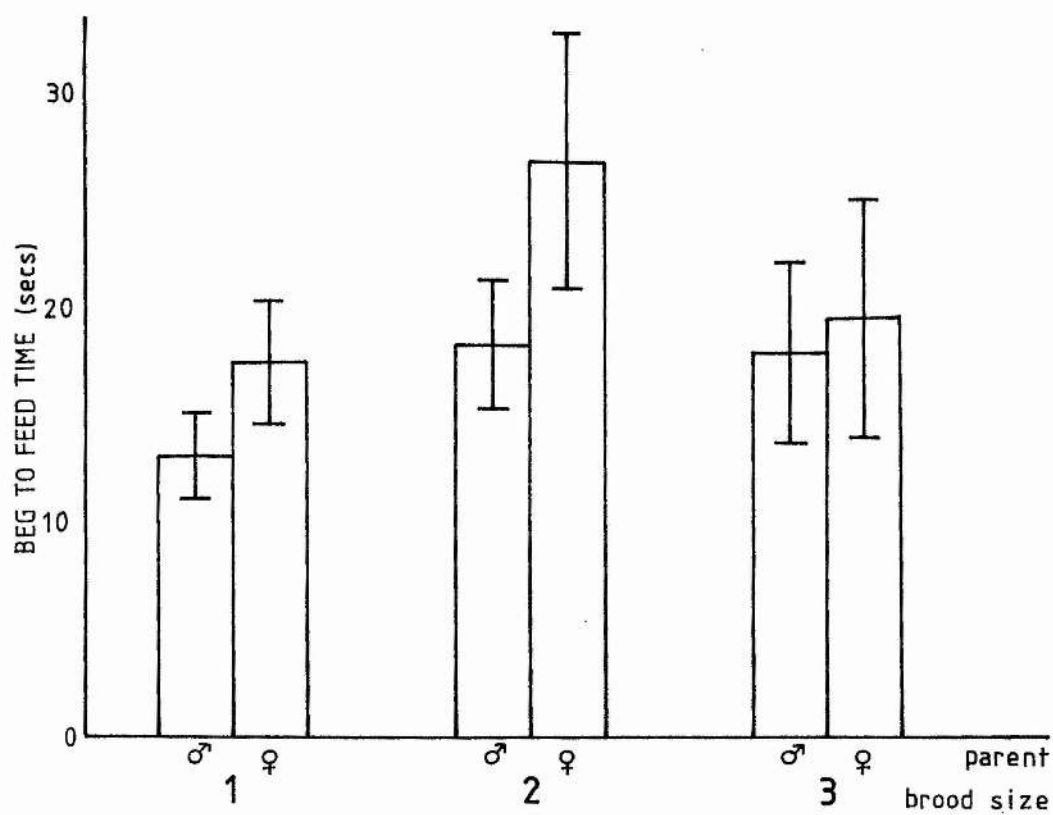
FIGURE 10.11

Mean time elapsed and standard error between the chicks begging and male and female parents regurgitating, for chicks from different sized broods. (Data in Appendix 42)

FIGURE 10.12

Mean time elapsed and standard error between the chicks begging and male and female parents regurgitating, for different age groups of chicks. (Data in Appendix 43)

**FIG 10.11**



**FIG 10.12**

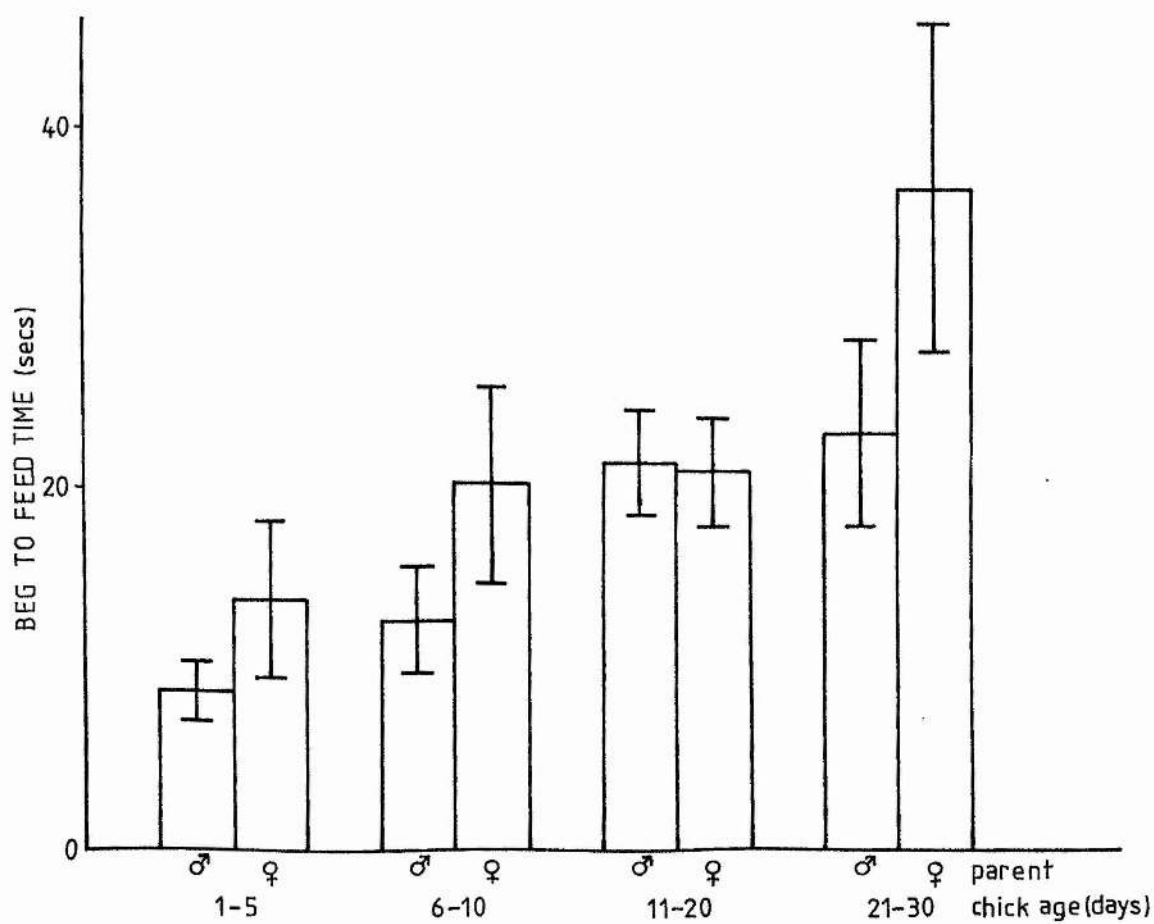


FIGURE 10.13

Mean number and standard error of times the parent regurgitated per feed for chicks from different sized broods. (Data in Appendix 44)

FIGURE 10.14

Mean number and standard error of times the parent held food per feed for chicks from different sized broods. (Data in Appendix 45)

FIGURE 10.15

Mean number and standard error of times the parent regurgitated per feed for different age groups of chicks. (Data in Appendix 46)

FIGURE 10.16

Mean number and standard error of times the parent held food per feed for different age groups of chicks. (Data in Appendix 47)



FIG 10.13

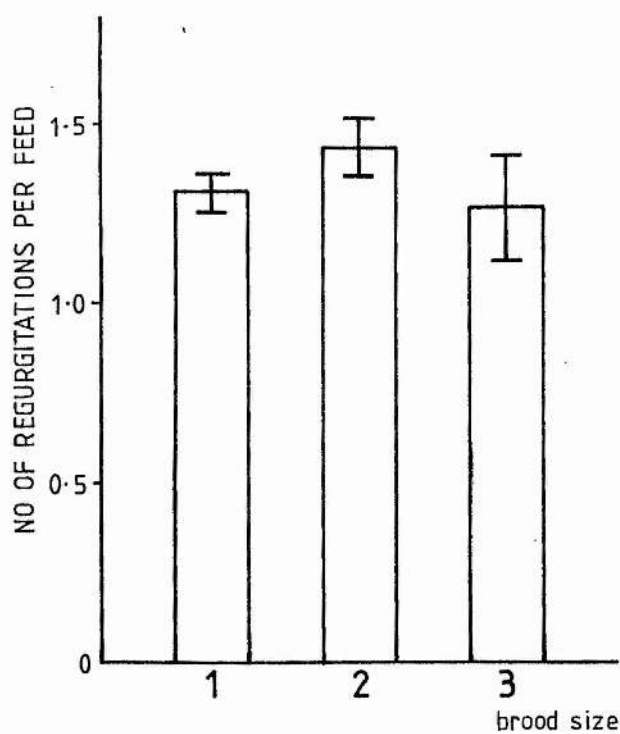


FIG 10.15

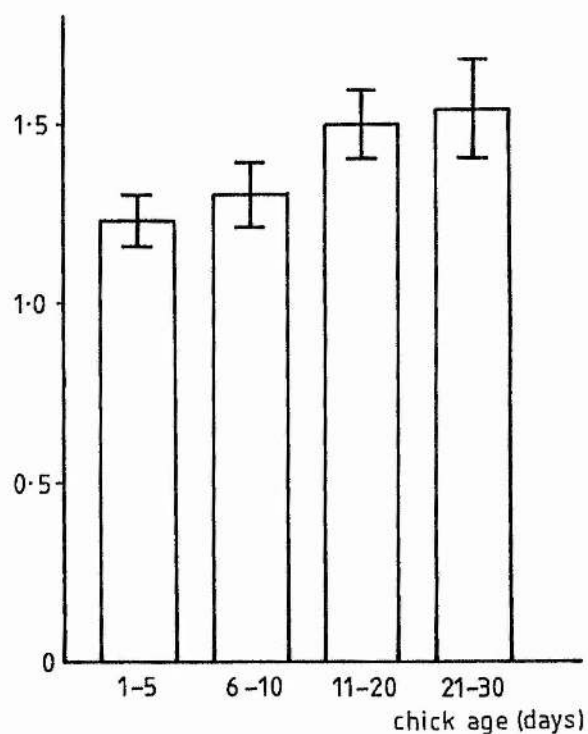


FIG 10.14

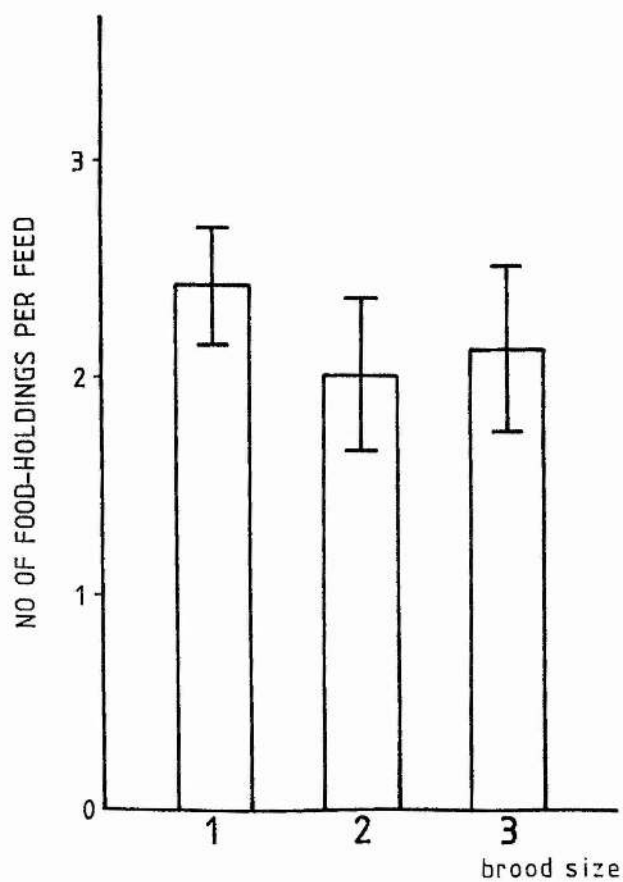
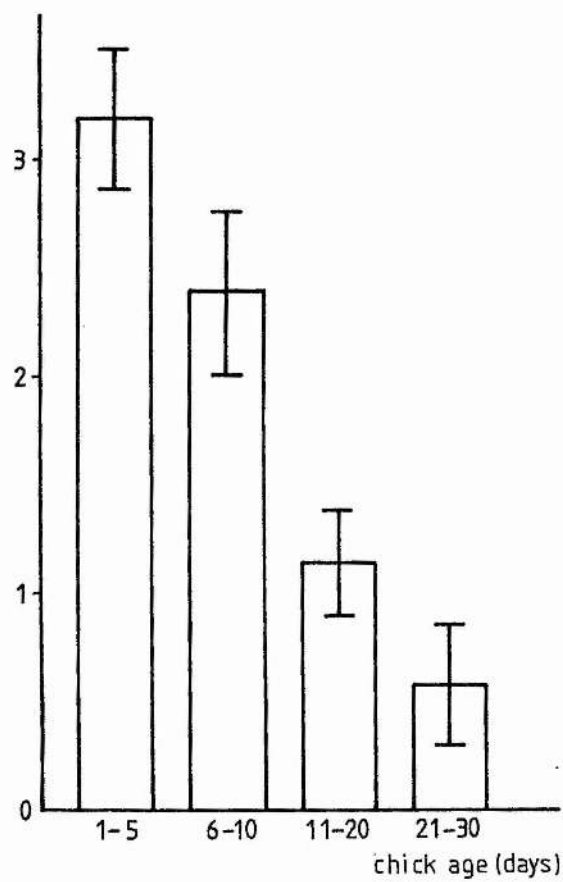


FIG 10.16



Appendices 48 and 49 and Figures 10.17 and 10.18 show the mean numbers of regurgitations and food-holdings given by males and female parents. In both cases there is no significant difference between the sexes (regurgitate -  $F=3.650$ ,  $df=1,188$ ,  $p>0.05$ ; food-hold -  $F=0.754$ ,  $df=1,188$ ,  $p>0.05$ ).

The mean numbers of regurgitations and food-holdings per feed given by males and females with different sized broods are shown in Appendices 50 and 51 and Figures 10.19 and 10.20). Here again there is no difference between the sexes (regurgitate -  $F=3.782$ ,  $df=1,186$ ,  $p>0.05$ ; food-hold -  $F=0.677$ ,  $df=1,186$ ,  $p>0.05$ ).

In Appendices 52 and 53 and Figures 10.21 and 10.22 the mean numbers of regurgitations and food-holdings per feed given by males and females with different aged chicks are shown and yet again there was no difference found between the sexes (regurgitate -  $F=3.665$ ,  $df=1,182$ ,  $p>0.05$ ; food-hold -  $F=1.420$ ,  $df=1,182$ ,  $p>0.05$ ) and no sex/age interaction (regurgitate -  $F=0.255$ ,  $df=3,182$ ,  $p>0.05$ ; food-hold -  $F=1.850$ ,  $df=3,182$ ,  $p>0.05$ ), but only between the number of food-holdings for different aged chicks (regurgitate -  $F=2.232$ ,  $df=3,182$ ,  $p>0.05$ ; food-hold -  $F=10.699$ ,  $df=3,182$ ,  $p<0.01$ ).

FIGURE 10.17

Mean number and standard error of times male and female parents regurgitated per feed. (Data in Appendix 48)

FIGURE 10.18

Mean number and standard error of times male and female parents held food per feed. (Data in Appendix 49)

FIGURE 10.19

Mean number and standard error of times male and female parents regurgitated per feed, for chicks from different sized broods. (Data in Appendix 50)

FIGURE 10.20

Mean number and standard error of times male and female parents held food per feed, for chicks from different sized broods. (Data in Appendix 51)

FIG 10.17

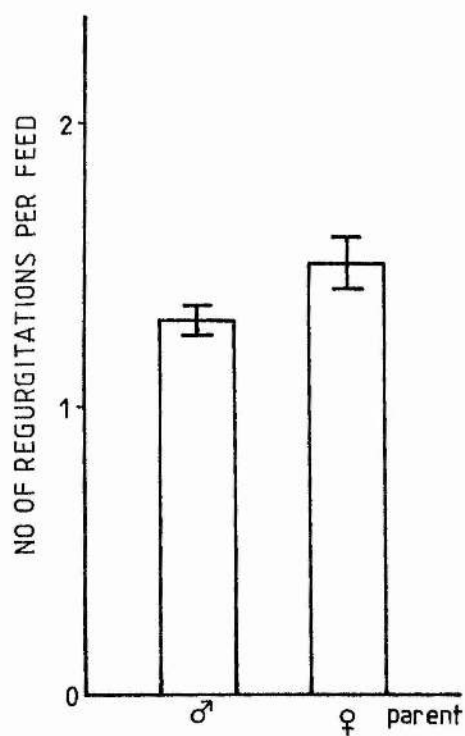


FIG 10.19

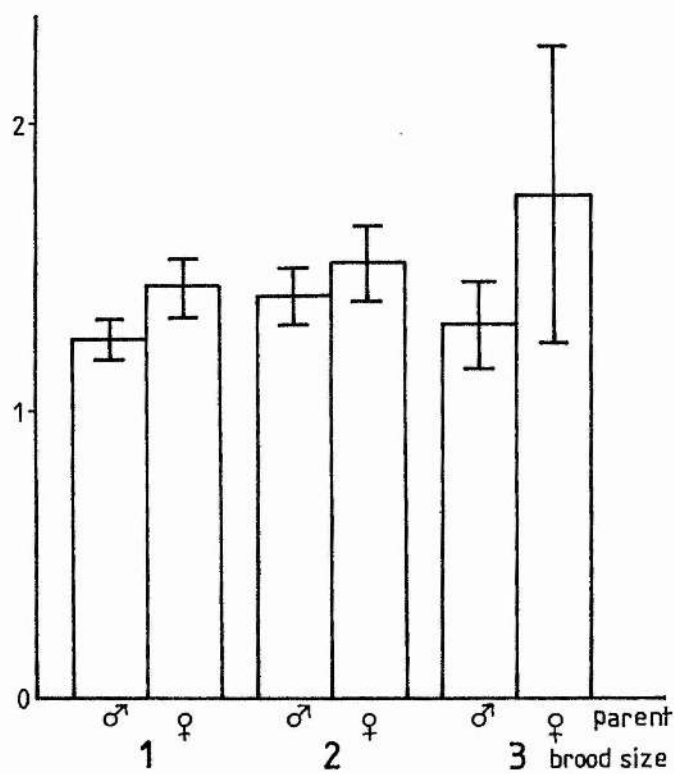


FIG 10.18

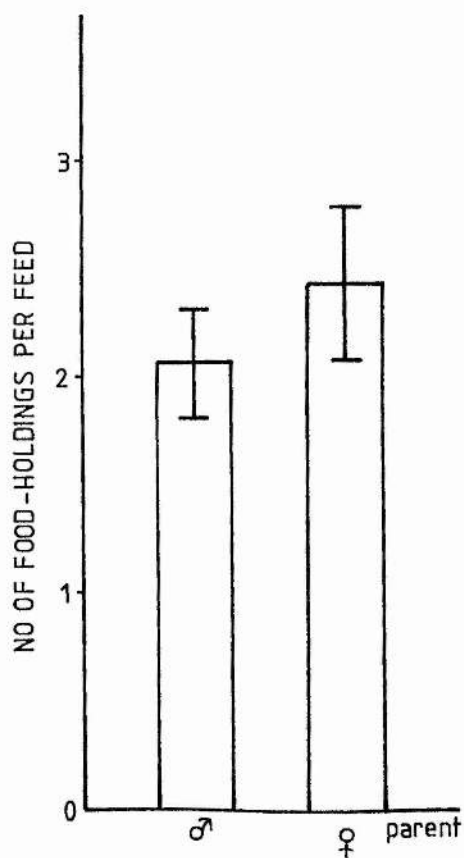


FIG 10.20

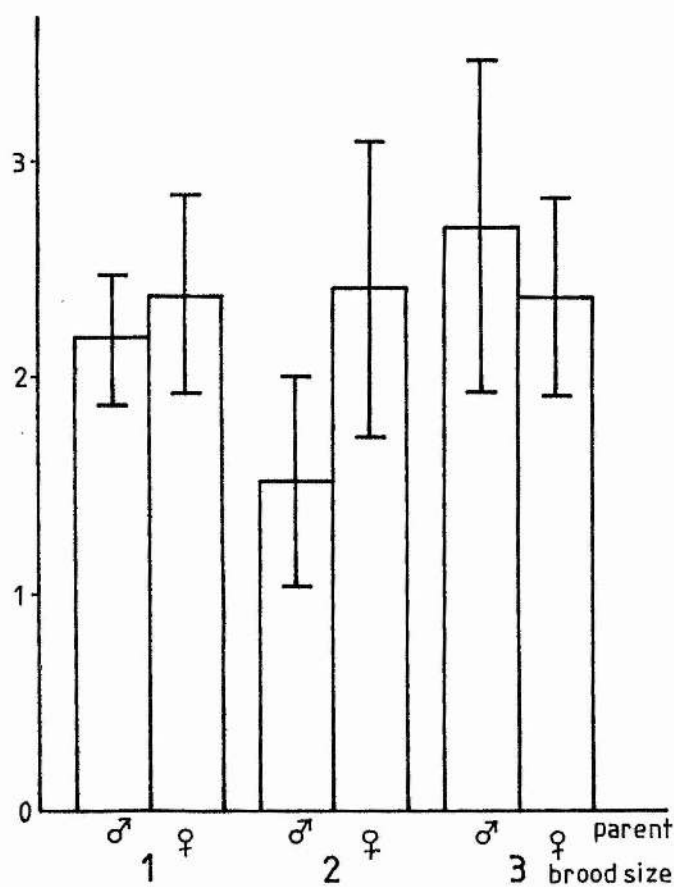


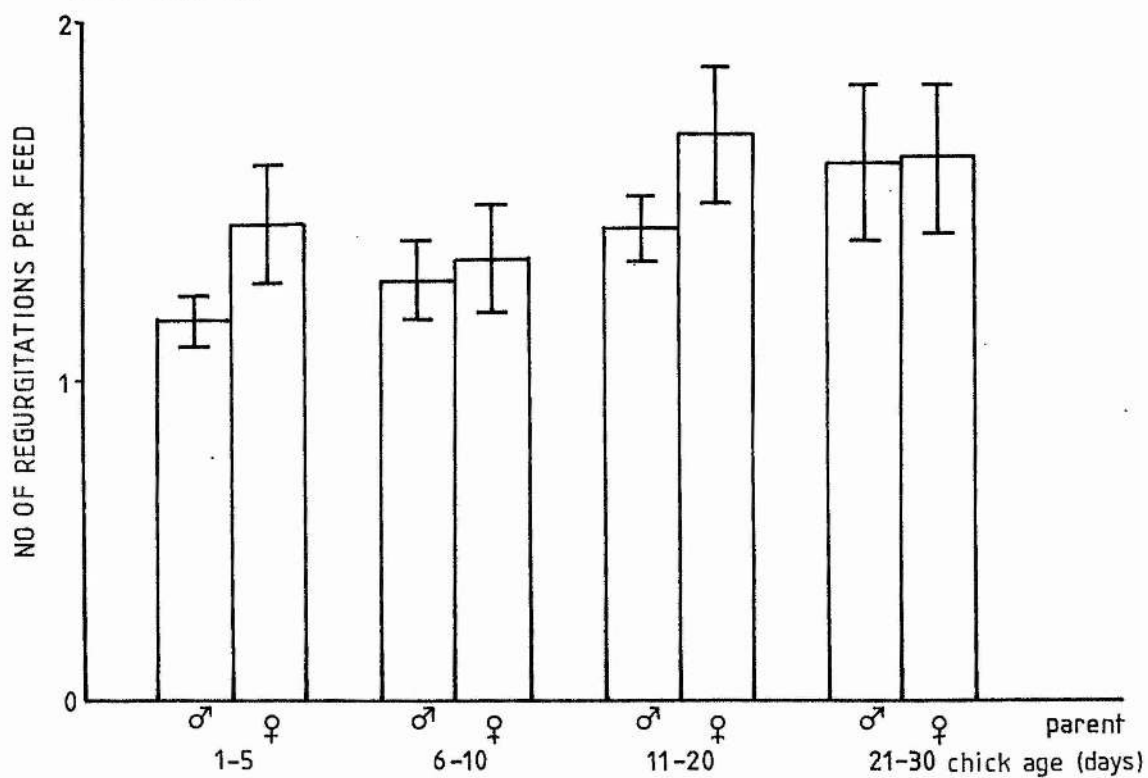
FIGURE 10.21

Mean number and standard error of times male and female parents regurgitated per feed, for different aged groups of chicks. (Data in Appendix 52)

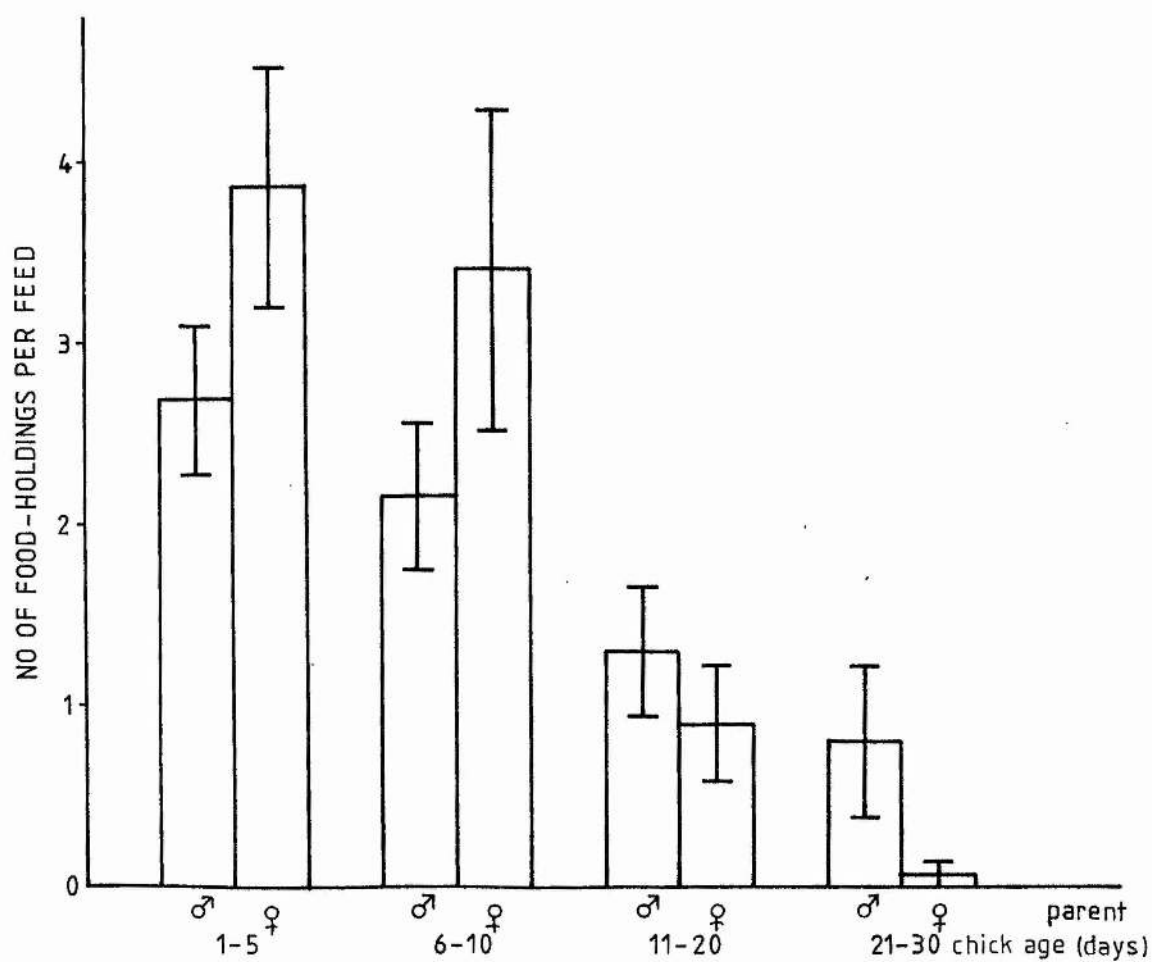
FIGURE 10.22

Mean number and standard error of times male and female parents held food per feed, for different aged groups of chicks. (Data in Appendix 53)

**FIG 10.21**



**FIG 10.22**



#### 10.4 Discussion

In all the aspects of feeding behaviour examined in this chapter male and female parents were found to play an equal role in the feeding of the chicks regardless of the size of the brood or the age of the chicks. In most of the other aspects of breeding behaviour so far investigated eg. time spent on the territory, time spent brooding and aggression towards intruders, there have been differences found in behaviour between the two sexes. However, as far as the feeding of the chicks is concerned, both sexes of parent appear to invest equally. Burger (1981a) found that this was also the case overall in herring gulls.

The only difference found in the feeding of different brood sizes was the number of feeds given to them by their parents. The number of feeds given per hour was found to increase with increasing brood size, though not proportionally so. Two and three-chick broods received fewer feeds per hour per chick than single chicks received. This does not take into account the amount of food regurgitated at each feed and it should not be assumed that similar amounts were regurgitated each time. Moreau (1947) found that in nine species of birds, the more young there were in the nest the more frequent were the parents visits, but, as was also the case here, this was not in proportion to the number of young (also Robertson & Biermann 1979). He therefore concluded that on average a solitary nestling was getting more food than a member of a pair or a 3-chick brood. Royama (1966) found that there was a clear inverse relationship between the total weight of food brought per chick per day and the size of the brood in great tits. He suggested that this arose because the heat loss is greater in small broods than in larger broods and so the total food requirement by a brood does not vary directly in proportion to its size.

There were several changes observed in feeding behaviour as the chicks grew older. Very young chicks were often fed when they did not beg, but this happened less frequently as the chicks aged and was never seen with chicks over nine days of age. Similarly, 1-5 day old chicks were refused food when they begged much less frequently than older chicks while 11-15 day old chicks were refused food when they

begged most frequently. The time elapsed between the first begging actions of the chicks towards a parent and the point at which that parent regurgitated food was found to increase with the age of the chicks i.e. young chicks did not have to beg for so long before being fed as older chicks did. After regurgitating food for their chicks the parents often picked pieces up again and held them for the chicks to take. The frequency of this behaviour was found to be highest with the youngest chicks and decreased as the chicks grew older.

All these results indicate that when their chicks were young the parents were eager and willing to feed them. During the first nine days they were often offered food without begging for it and when they did beg they were given food within 10-15 seconds of begging (on average) and were rarely refused food. The parents also helped the chicks in their feeding by frequently holding pieces of the regurgitated food in their bills for them to take. However, as the chicks grew older the parents appeared to be more reluctant to feed them. The chicks were never fed without begging and when they did beg they had to do so for an average of about 30 seconds before being fed. For 30% of the time they did not get fed at all when they begged and the parents rarely held food in their bills for the chicks to take.

Increased parental care presumably increases the survival prospects of the young while potentially decreasing the long-term survival of the parents and therefore their ability to invest in future offspring. Therefore, Trivers (1972, 1974) and Parker & MacNair (1978) suggested that parents are in conflict with their offspring over how much parental care the offspring should have. In general, parent-offspring conflict is expected to increase during the period of parental care and this certainly appears to be the case here, with the amount of parental care that the offspring are wanting becoming more than the parents are prepared to give in the pre-fledging period. Henzi et al (in prep.) discovered that refusal to feed chicks in herring gulls peaked just before fledging which would be predicted by a parent-offspring conflict theory.

In Chapter 7 it was found that there was a tendency for third laid eggs to fail to hatch more often than first or second laid eggs from 3-egg clutches and that third hatched chicks had a higher mortality rate



than first or second hatched chicks from 3-chick broods. And, the results here show that third hatched chicks put on less weight during their first three days of life than first or second hatched chicks and than chicks from 1-chick and 2-chick broods.

Langham (1972) found that the success of a third common tern chick varied from 2/3 to 1/8 the success of a first chick over three years, and Kadlec et al (1969) reported that herring-gull chicks which ultimately died grew more slowly from the start, implying that they were not as well fed as the surviving chicks.

The parents of many bird species begin incubation before laying is complete, producing an asynchronously hatched brood (Clark & Wilson 1981). This creates a sibling feeding hierarchy because of the differences in age and size between siblings, and so food is consistently distributed to the older chicks first. These chicks then grow faster and have higher survival rates (O'Connor 1978). The weight differences within the broods are commonly assumed to be the outcome of a parental strategy of selectively starving one or more offspring so as to enhance the survival of the remaining chicks. One might expect that parents should oppose unequal accumulation of resources if it reduces their reproductive output by endangering the survival of some young (Trivers 1974), however, under certain circumstances they might benefit by encouraging the selective starvation of one or more young if that would improve sufficiently the survival prospects of those remaining.

Although there are several hypotheses to explain the strategy of asynchronously hatched broods (see Section 7.4.2), most researchers believe that it acts to reduce the number of offspring to that which can be reared given the level of food available (Lack 1947, 1954, 1966, 1968; Ricklefs 1965; Howe 1976, 1978; O'Connor 1978) and the chicks that subsequently died would be those that the parents had invested least in so avoiding jeopardising the survival of the other brood members (Langham 1972; Hahn 1981).

Some workers do not believe that starvation is a major factor in gull chick mortality (Harris 1964; Kadlec et al 1969; Parsons 1971; Hunt and Hunt 1976), and Hunt & McLoon (1975) found that chicks that failed to obtain food were more active and wandered near territory boundaries where they were attacked by neighbouring adults more frequently than chicks that had obtained food. Graves et al (1984), however, showed that the placing of food supplements beside the nests of herring gulls during their first five days of parenthood produced increased weight gains and a higher fledging success, particularly in third hatched chicks. Also, in control nests, they observed that underweight third chicks died for no other reason than their low weight.

Fujioka (1985) showed that in experimentally synchronized broods of cattle egrets the frequency of begging by chicks, the frequency of parental nest-visits with food and the food mass eaten by chicks were greater than in asynchronously hatched broods during the first half of the nesting period. Thus, an increase in parental efforts increased the growth and survival rates for these synchronously hatched broods and suggests that the parents of asynchronously hatched broods were not putting as much effort into providing food as they might have done. In seabird species that normally rear only one chick, parental feeding rates have been increased by experimental 'twinning' (Harris 1966; Nelson 1966; Perrins et al 1973; Schifferli 1978). However, Nelson (1964) observed that in gannets during the later stages of growth, twins began to strain the food-gathering powers of the adults and Graves et al (1984) came to the conclusion that fledging three herring gull chicks rather than one or two greatly increased the parents reproductive effort. Thus it appears that parents are normally conservative in parental efforts in a given breeding season, avoiding overwork which might reduce their future survival and breeding success.

Graves et al (1984) discovered that third hatched chicks showed the greatest increase in fledging success when food supplements were placed by the nests when they were only 1-3 days of age, showing that weight gains during this stage were crucial to the chicks' survival. They therefore interpreted the function of a third egg or chick as insurance against the loss of another egg or of an older sibling in the first days after hatching, and not as an additional offspring that could be fed if food became plentiful.

The majority of chick deaths have been found to occur in the first few days of life (Parsons 1971; Langham 1972; Graves et al 1984; Fujioka 1985) at a time when the food requirements of the brood as a whole are relatively low, and certainly, it was observed at Red Myre that while some parents were providing insufficient food for young 3-chick broods, others were returning with enough food to feed two fully grown chicks. In Chapter 6 the number of gulls counted on the water in the colony gradually increased after peak hatching for about two weeks suggesting that gulls that were not on the territories were spending time in other parts of the colony when they would have been expected to be away foraging for food. Therefore, it would seem unlikely that the lower weight gain of the third chicks was reflecting an inability of the parents to provide enough food for a 3-chick brood, but rather that the parents were deliberately providing less food initially because they were more likely to be able to raise a brood of two chicks without potentially decreasing their own future survival and thus contribution to the gene pool.

## CHAPTER 11 - SUMMARY

### PREDATION

Two of the three years of this project were drier and sunnier than all the other years in the 13-year period from 1973 to 1985. These conditions enabled mammalian predators to gain access to the breeding areas and resulted in almost total breeding failure of the colony in 1982 and greatly reduced breeding success in 1984.

Colonial breeding is obviously an advantage to black-headed gulls in guarding against losses to avian predators, such as crows, which were the main predator in a 'normal' year at Red Myre. When the numbers of breeding pairs in the colony was greatly reduced by fox predation in 1984, the small number of breeding gulls remaining was not sufficient to continue to deter the crows from entering the colony.

### TIMING OF BREEDING

Synchronisation of breeding was evident at Red Myre, both in the changing activities of the gulls in the colony as a whole, and in the pattern of laying and hatching dates of the eggs on the study area.

Largely because of the predation, there were few records breeding success in this study, and although there appeared to be a tendency for early breeders to suffer the least egg and chick mortality and late breeders to suffer the most, this was not significant.

In 1982 the only gulls that were successful in raising chicks to fledging were those that had started breeding early in the season, and whose chicks were old enough to swim to safety into the water when

the fox was in the colony. Therefore, it is interesting that in the following year the majority of the eggs on the study area were laid earlier in the season. Unfortunately there was no way of knowing how many of the gulls breeding on the study area in 1983 were the same as those that had bred there in 1982.

#### EGG LAYING AND EGG AND CHICK MORTALITY

Black-headed gulls are commonly reported to lay three eggs. However, the majority of the gulls at Red Myre laid three eggs in only one of the study years, 1983. It is possible that infrequent visits in 1982 and a thin egg shell problem in 1984 could have contributed to this result. However, even in 1983, only 40% of the clutches contained three eggs.

Most of the egg losses in 1983 were due to predation, natural breakage and eggs falling out of the nest. A small number also failed to hatch properly. In this year 57% of the eggs laid successfully hatched.

Chicks were seen moving away from the study area on several occasions, and the conclusion was drawn that many of these moves were caused by my regular disturbance of the gulls on the study area. It is also likely that chick mortality was higher than it would have been in an undisturbed colony, because some of the chicks that got lost after a disturbance were either injured by other adult gulls or died of exposure when they could not find their way back. Some stray chicks, however, did survive when they got lost, either by being found by their parents or by being adopted by other breeding gulls.

#### HATCHING ASYNCHRONY

An examination of egg and chick mortality levels revealed a tendency for third laid eggs and third hatched chicks to have a higher mortality rate than first or second laid eggs and hatched chicks.

## CHANGES IN BEHAVIOUR THROUGH THE BREEDING CYCLE

Not all the gulls that established territories on the study area at the beginning of the breeding season remained there to lay eggs. An examination of the allocation of time on the territory and the aggressive behaviour of the two groups of gulls (the no-egg gulls that did not remain to lay eggs and the pre-egg gulls that did subsequently lay eggs) revealed that no-egg gulls left their territories unattended much more often and the no-egg males were more restless and more aggressive than pre-egg males.

The behaviour of breeding black-headed gulls undergoes several changes throughout the breeding season as their reproductive circumstances change. During the pre-egg laying stage both gulls spent more of their time on the territory together than they did during the incubation and chick stages. The territory was left unattended only 7% of the time during the pre-egg stage, but it was virtually never left unattended once the eggs had been laid and incubation commenced. During the chick stage, both gulls spent less and less time on the territory and less and less time together as the chicks grew.

Breeding gulls were most aggressive towards intruders on their territory during the pre-egg stage, and least aggressive when they had eggs in the nest because they remained on the nest, where they were best able to protect the eggs, rather than leaving the eggs to chase them away.

The gulls' reactions towards different types of intruders also changed throughout time. Neighbours with established territories were reacted to less aggressively and allowed closer to the nest during the pre-egg and egg stages than strangers, which were likely to be on the lookout for a territory. However, during the chick stage there was no discrimination between neighbours and strangers.

Several changes in parental feeding behaviour were observed as the chicks grew older. The number of times that chicks were fed when they did not beg decreased as they aged, as did the average number of times the parents held food for them during a feed. The time elapsed between the chicks begging and

the parent regurgitating increased as the chicks grew, and older chicks were also refused food altogether more often. All these changes point to a decrease in the parents' eagerness to feed their chicks with time.

### SEX DIFFERENCES

Right up to the time that the eggs hatch, the male gulls were responsible for the majority of nest/territory defence, and, in one year at least, they were responsible for the majority of the care of the eggs. When the chicks had hatched, however, the two sexes took an equal share in the defence of the brood and the territory, although the females may have spent more time in the presence of the chicks. The feeding of the chicks was also shared equally by the two sexes and there was no difference found between the sexes in any aspects of parental feeding behaviour studied.

### BROOD SIZE

The number of feeds given per hour to different sized broods increased with brood size. However the number of feeds given per hour per chick to 2-chick and 3-chick broods was smaller than the number given to single chicks. This suggests that the larger broods were receiving less food per chick than single chick broods, but this is not a certainty as no measure was made of the amount of food given at each feed.



## REFERENCES

- Anderson, D. W. & Keith, J. O. 1980. The human influence on seabird nesting success: Conservation implications. *Biol. Conserv.*, **18**, 65-80.
- Andersson, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. *Ibis*, **118**, 208-217.
- Andersson, M. & Wiklund, C. G. 1978. Clumping versus spacing out: experiments on nest predation in Fieldfares (*Turdus pilaris*). *Anim. Behav.*, **26**, 1207-1212.
- Andersson, M., Wiklund, C. G. & Rundgren, H. 1980. Parental defence of offspring: A model and an example. *Anim. Behav.*, **28**, 536-542.
- Bancroft, G. T. 1985. The influence of total nest failures and partial losses on the evolution of asynchronous hatching. *Am. Nat.*, **126**, 495-504.
- Bedard, J. & Meunier, M. 1983. Parental care in the savannah sparrow *Passerculus sandwichensis*. *Can. J. Zool.*, **61**, 2836-2843.
- Beer, C. G. 1961. Incubation and nest-building behaviour of black-headed gulls: I. Incubation behaviour in the incubation period. *Behaviour*, **18**, 62-106.
- Beer, C. G. 1962. Incubation and nest-building behaviour of black-headed gulls: II. Incubation behaviour in the laying period. *Behaviour*, **19**, 283-304.
- Beer, C. G. 1963a. Incubation and nest-building behaviour of black-headed gulls: III. The pre-laying period. *Behaviour*, **21**, 13-77.
- Beer, C. G. 1963b. Incubation and nest-building behaviour of black-headed gulls: IV. Nest building in the laying and incubation periods. *Behaviour*, **21**, 155-176.
- Beer, C. G. 1965. Clutch size and incubation behaviour in black-billed gulls (*Larus bulleri*). *Auk*, **82**, 1-18.
- Beer, C. G. 1966. Incubation and nest-building behaviour of black-headed gulls: V. The post-hatching period. *Behaviour*, **26**, 189-214.
- Beer, C. G. 1969. Laughing gull chicks: Recognition of their parents' voices. *Science*, **166**, 1030-1032.
- Beer, C. G. 1970a. On the responses of laughing gull chicks (*Larus atricilla*) to the calls of adults. I. Recognition of the voices of the parents. *Anim. Behav.*, **18**, 652-660.
- Beer, C. G. 1970b. On the responses of laughing gull chicks (*Larus atricilla*) to the calls of adults. II. Age changes and responses to different types of call. *Anim. Behav.*, **18**, 661-677.
- Beer, C. G. 1979. Vocal communication between laughing gull (*Larus atricilla*) parents and chicks. *Behaviour*, **70**, 118-146.
- Birkhead, T. R. 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *J. Anim. Ecol.*, **46**, 751-764.
- Birkhead, T. R. 1979. Mate guarding in the magpie *Pica pica*. *Anim. Behav.*, **27**, 866-874.
- Blancher, P. J. & Robertson, R. J. 1982. Kingbird aggression: Does it deter predation? *Anim. Behav.*, **30**, 929-930.
- Brown, R. G. B. 1967. Breeding success and population growth in a colony of herring and lesser black-backed gulls, *Larus argentatus* and *Larus fuscus*. *Ibis*, **109**, 502-515.
- Bryant, D. M. 1975. Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis*, **117**, 180-216.
- Bryant, D. M. 1978. Establishment of weight hierarchies in the broods of house martins *Delichon urbica*. *Ibis*, **120**, 16-26.
- Burger, J. 1974. Breeding adaptations of Franklin's gull (*Larus pipixan*) to a marsh habitat. *Anim. Behav.*, **22**, 521-567.
- Burger, J. 1979a. Colony size: A test for breeding synchrony in herring gull (*Larus argentatus*) colonies. *Auk*, **96**, 694-703.
- Burger, J. 1980a. Territory size differences in relation to reproductive stage and type of intruder in herring gulls (*Larus argentatus*). *Auk*, **97**, 733-741.
- Burger, J. 1981a. Becoming independent in herring gulls (*Larus argentatus*): Parent-young conflict. *Am. Nat.*, **117**, 444-456.
- Burger, J. 1981b. Sexual differences in parental activities of breeding black skimmers. *Am. Nat.*, **117**.
- Burger, J. 1981c. Aggressive behaviour of black skimmers (*Rynchops niger*). *Behaviour*, **76**, 207-222.
- Butler, R. G. & Trivelpiece, W. 1981. Nest spacing, reproductive success and behaviour of the great black-backed gull (*Larus marinus*). *Auk*, **98**, 99-107.
- Clark, A. B. & Wilson, D. S. 1981. Avian breeding adaptations: Hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.*, **56**, 253-277.
- Clark, A. B. & Wilson, D. S. 1985. The onset of incubation in birds. *Am. Nat.*, **125**, 603-611.
- Coulson, J. C. 1963. Egg size and shape in the kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. *Proc. Zool. Soc.*, **140**, 211-227.
- Coulson, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake *Rissa tridactyla*. *J. Anim. Ecol.*, **33**, 269-279.
- Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature*, **217**, 478-479.
- Coulson, J. C. & White, E. 1956. A study of colonies of the kittiwake *Rissa tridactyla* L. *Ibis*, **98**, 63-79.



- Coulson, J. C. & White, E. 1958. The effect of age on the breeding biology of the kittiwake *Rissa tridactyla*. *Ibis*, **100**, 40-51.
- Coulson, J. C. & White, E. 1960. The effect of age and density of breeding birds on the timing of breeding birds on the timing of breeding of the kittiwake *Rissa tridactyla*. *Ibis*, **102**, 71-86.
- Coulson, J. C. & Wooller, R. D. 1984. Incubation under natural conditions in the kittiwake gull *Rissa tridactyla*. *Anim. Behav.*, **32**, 1204-1215.
- Cramp, S. & Simmons, K. E. L. (Eds.) 1983. The birds of the Western Palearctic Vol III. Oxford: Oxford University Press.
- Cullen, E. 1957. Adaptations in the kittiwake to cliff nesting. *Ibis*, **99**, 275-303.
- Darling, F. F. 1938. Bird flocks and the breeding cycle. Cambridge: Cambridge University Press.
- Dawkins, R. 1976. The selfish gene. Oxford: Oxford University Press.
- Dawkins, R. & Impeken, M. 1969. The "peck/no peck decision-maker" in the black-headed gull chick. *Anim. Behav.*, **17**, 243-251.
- Davies, S. & Carrick, R. 1962. On the ability of crested terns, *Sterna bergii*, to recognise their own chicks. *Aust. J. Zool.*, **10**, 171-177.
- Davis, J. W. F. & Dunn, E. K. 1976. Intraspecific predation and colonial breeding in the lesser black-backed gull *Larus fuscus*. *Ibis*, **118**, 65-72.
- Drent, R. H. 1967. Functional aspects of the incubation in the herring gull (*Larus argentatus* Pont.). *Behav. Suppl.*, **17**.
- Drury, W. H. & Smith, W. J. 1968. Defense of feeding areas by adult herring gulls and intrusion by young. *Evolution*, **22**, 193-207.
- Dunn, E. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.*, **46**, 634-652.
- Dunnett, G. M. 1955. The breeding of the starling *Sturnus vulgaris* in relation to its food supply. *Ibis*, **97**, 619-662.
- Ellison, L. N. & Cleary, L. 1978. Effects of human disturbance on the breeding of double-crested cormorants. *Auk*, **95**, 510-517.
- Emlen, J. T. Jr. 1956. Juvenile mortality in a ring-billed gull colony. *Wils. Bull.*, **68**, No 3.
- Emlen, S. T. & Demong, N. J. 1975. Adaptive significance of synchronized breeding in a colonial bird: A new hypothesis. *Science*, **188**, 1029-1031.
- Evans, R. M. 1970. Imprinting and mobility in young ring-billed gulls (*Larus delawarensis*). *Anim. Behav. Monogr.*, **3**, 193-248.
- Feare, C. J. 1976. The breeding of the sooty tern (*Sterna fuscata*) in the Seychelles and the effects of experimental removal of its eggs. *J. Zool.*, **179**, 317-360.
- Fetterolf, P. M. 1984. Aggression, nesting synchrony and reproductive fitness in ring-billed gulls (*Larus delawarensis*). *Anim. Behav.*, **32**, 1004-1010.
- Findlay, C. S. & Cooke, F. 1982. Synchrony in the lesser snow goose (*Anser caerulescens caerulescens*). II. The adaptive significance of reproductive synchrony. *Evolution*, **36**, 786-799.
- Fogden, M. P. L. 1964. The reproductive behaviour and taxonomy of Hemprich's gull *Larus hemprichi*. *Ibis*, **106**, 299-320.
- Fretwell, S. D. 1969. The adjustments of birthrate to mortality in birds. *Ibis*, **111**, 624-627.
- Fretwell, S. D. 1972. Populations in a seasonal environment. New Jersey: Princeton University Press.
- Fujioka, M. 1985. Food delivery and sibling competition in experimentally even-aged broods of the cattle egret. *Behav. Ecol. Sociobiol.*, **17**, 67-74.
- Gibb, J. 1950. The breeding biology of the great blue titmice. *Ibis*, **92**, 507-539.
- Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. In: Behaviour of marine animals (Eds. Burger, J., Olla, B. & Winn, H.) Vol 4. Marine birds. Plenum Press, New York.
- Goodbody, I. M. 1955. The breeding of the black-headed gull. *Bird Study*, **2**, 192-199.
- Goransson, G., Karlsson, J., Nilsson, S. G. & Ulfstrand, S. 1975. Predation on birds' nests in relation to anti-predator aggression and nest density: An experimental study. *Oikos*, **26**, 117-120.
- Gotmark, F. 1982. Coloniality in five *Larus* gulls: A comparative study. *Ornis. Scand.*, **13**, 211-224.
- Gotmark, F. & Andersson, M. 1984. Colonial breeding reduces nest predation in the common gull (*Larus canus*). *Anim. Behav.*, **32**, 485-492.
- Gowaty, P. A. 1981. Aggression of breeding Eastern bluebirds (*Sialia sialis*) toward their mates and models of intra and interspecific intruders. *Anim. Behav.*, **29**, 1013-1023.
- Graves, J. A. & Whiten, A. 1980. Adoption of strange chicks by herring gulls *Larus argentatus*. *Z. Tierpsychol.*, **54**, 267-278.
- Graves, J. A., Whiten, A. & Henzi, P. 1984. Why does the herring gull lay three eggs? *Anim. Behav.*, **32**, 798-805.
- Hahn, D. C. 1981. Asynchronous hatching in the laughing gull *Larus atricilla* cutting losses and reducing rivalry. *Anim. Behav.*, **29**, 421-427.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour II. *J. Theor. Biol.*, **7**, 17-52.
- Hand, J. L. 1980. Human disturbance in Western gull *Larus occidentalis* Livers colonies and possible amplification of intraspecific predation. *Biol. Conserv.*, **18**, 59-63.

- Harris, M. P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus*, *Larus fuscus* and *Larus marinus*. *Ibis*, 106, 432-456.
- Harris, M. P. 1966. Breeding biology of the manx shearwater *Puffinus puffinus*. *Ibis*, 108, 17-33.
- Harris, M. P. 1970. Rates and causes of increases of some British gull populations. *Bird Study*, 17, 325-335.
- Hayman, P. & Burton, P. 1976. The birdlife of Britain. Mitchell Beazley Publishers Ltd.
- Henzi, P., Graves, J.A., & Whiten, A. (in prep.) Reaction of resident adult herring gulls to intruders at the nest during the breeding season.
- Holcombe, L. C. 1969a. Breeding biology of the American goldfinch in Ohio. *Bird Banding*, 40, 23-44.
- Holcombe, L. C. 1969b. Age-specific mortality of American goldfinch nestlings. *Auk*, 86, 760-761.
- Holley, A. J. F. 1971. Some aspects of rearing the young in *Larus* gulls at Stert Island - An interim report. *Brist. Ornith.*, 3, 100-117.
- Holley, A. J. F. 1981. Naturally arising adoption in the herring gull. *Anim. Behav.*, 29, 302-303.
- Hoogland, J. L. & Sherman, P. W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.*, 46 33-58.
- Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). *Ecology*, 49, 682-694.
- Howe, H. F. 1976. Egg size, hatching asynchrony, sex and brood reduction in the common grackle. *Ecology*, 57, 1195-1207.
- Howe, H. F. 1978. Initial investment, clutch size and brood reduction in the common grackle (*Quiscalus quisculus* L.). *Ecology*, 59, 1109-1122.
- Hunt, G. L. Jr. 1972. Influence of food distribution and human disturbance on the reproductive success of herring gulls. *Ecology*, 53, 1051-1061.
- Hunt, G. L. Jr. & Hunt, M. W. 1975. Aspects of the reproductive ecology of the Western gull *Larus occidentalis*: The importance of nest spacing. *Auk*, 92, 270-279.
- Hunt, G. L. Jr. & Hunt, M. W. 1976. Gull chick survival: The significance of growth rates, timing of breeding and territory size. *Ecology*, 57, 62-75.
- Hunt, G. L. Jr. & McLoon, S. C. 1975. Activity patterns of gull chicks in relation to feeding by parents: Their potential significance for density-dependent mortality. *Auk*, 92, 523-527.
- Hussell, D. T. R. 1972. Factors affecting clutch size in Arctic passerines. *Ecol. Monogr.*, 42, 317-364.
- Hutson, C. D. 1977. Agnostic display and spacing in the black-headed gull *Larus ridibundus*. *Anim. Behav.*, 25, 765-773.
- Huxley, J. S. & Fisher, J. 1940. Hostility reactions in black-headed gulls. *Proc. Zool. Soc. London*, 110, 1-10.
- Impeken, M. 1969. Motivationally controlled stimulus preference in chicks of the black-headed gull (*Larus ridibundus* L.). *Anim. Behav.*, 17, 252-270.
- Ingram, C. 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. *Auk*, 76, 218-277.
- Kadlec, J. A. & Drury, W. H. 1968. Structure of the New England herring gull population. *Ecology*, 49, 644-676.
- Kadlec, J. A., Drury, W. H. & Onion, D. K. 1969. Growth and mortality of herring gull chicks. *Bird Banding*, 40, 222-233.
- King, K. A., Meeker, D. L. & Swineford, D. M. 1980. White-faced ibis (*Plegadis chihi*) populations and pollutants in Texas, U. S. A., 1969-1976. *Southwest Nat.*, 25, 225-240.
- Kirkman, F. B. 1937. Bird behaviour (black-headed gull). T. Nelson & Sons, Ltd., London.
- Klaas, E. E., Wiemeyer, S. N., Ohlendorf, H. M. & Swineford, D. M. 1978. Organochlorine residues, eggshell thickness, and nest success in barn owls from the Chesapeake Bay. *Estuaries*, 1, 46-53.
- Knight, R. L. & Temple, S. A. 1986a. Methodological problems in studies of avian nest defence. *Anim. Behav.*, 34, 561-566.
- Knight, R. L. & Temple, S. A. 1986b. Nest defence in the American goldfinch. *Anim. Behav.*, 34, 887-897.
- Krebs, J. R. 1971. Territory and breeding density in the great tit, *Parus major* L. *Ecology*, 52, 2-22.
- Kruuk, H. 1964. Predator and anti-predator behaviour of the black-headed gull (*Larus ridibundus* L.). *Behav. Suppl.*, 11, 129p.
- Kruuk, H. 1972. Surplus killing by carnivores. *J. Zool.*, 166, 233-244.
- Kruuk, H., Paillette, M. & Stamm, R. 1962. How do black-headed gulls distinguish between eggs and egg-shells? *Brit. Birds*, 55, 120-129.
- Lack, D. 1947. The significance of clutch size. *Ibis*, 89, 302-352.
- Lack, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford.
- Lack, D. 1966. Population studies of birds. Clarendon, Oxford.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lack, D. & Lack, E. 1951. The breeding biology of the swift *Apus apus*. *Ibis*, 93, 501-546.
- Langham, N. P. E. 1972. Chick survival in terns (*Sterna* spp.) in particular reference to the common tern. *J. Anim. Ecol.*, 41, 385-395.
- Loman, J. & Goransson, G. 1978. Egg shell dumps and crow (*Corvus cornix*) predation on simulated birds' nests. *Oikos*, 30, 461-466.

- MacRoberts, M. H. 1973. Extra-marital courting in lesser black-backed and herring gulls. *Z. Tierpsychol.*, 32, 62-74.
- Manley, G. H. 1960. The swoop and soar performance of the black-headed gull *Larus ridibundus*. *Ardea*, 48, 37-51.
- Maynard-Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.*, 25, 1-9.
- Maynard-Smith, J. & Parker, G. A. 1976. The logic of asymmetric contests. *Anim. Behav.*, 24, 159-175.
- Meyburg, B. 1974. Sibling aggression and mortality among sibling eagles. *Ibis*, 116, 224-228.
- Miller, D. E. & Emlen, J. T. 1975. Individual chick recognition and family integrity in the ring-billed gull. *Behaviour*, 52, 125-144.
- Mock, D. W. & Parker, G. A. 1986. Advantages and disadvantages of egret and heron brood reduction. *Evolution*, 40, 459-470.
- Mock, D. W. & Plodger, B. T. 1987. Parental manipulation of optimal hatch asynchrony in cattle egrets: An experimental study. *Anim. Behav.*, 35, 150-160.
- Montevicchi, W. A. & Porter, J. 1980. Parental investment in Northern gannet and other seabirds. In: Behaviour of marine animals (Eds. Burger, J., Olla, B. & Winn, H.) Vol 4. Marine birds. Plenum, New York.
- Moreau, R. 1947. Relations between number in brood, feeding rate and nestling period in nine species of birds in Tanganyika Territory. *J. Anim. Ecol.*, 16, 205-209.
- Moynihan, M. 1953. Some displacement activities of the black-headed gull. *Behaviour*, 5, 58-80.
- Moynihan, M. 1955. Some aspects of reproductive behaviour in black-headed gulls (*Larus ridibundus*) and related species. *Behav. Suppl.*, 4.
- Nelson, J. B. 1964. Factors influencing clutch-size and chick growth in the North Atlantic gannet *Sula bassana*. *Ibis*, 106, 63-77.
- Nelson, J. B. 1966. Breeding biology of the gannet *Sula bassana*. *Ibis*, 108, 584-626.
- Nelson, J. B. 1978. The Sulidae. Oxford: Oxford University Press.
- Newton, I. & Bogan, J. 1974. Relationships between organo-chlorine residues, eggshell thinning and hatching success in British sparrowhawks. *Nature*, 249, 582-3.
- Newton, I. & Bogan, J. 1978. The role of different organo-chlorine compounds in the breeding of sparrowhawks. *J. Appl. Ecol.*, 15, 105-116.
- Newton, I., Marquis, M. & Moss, D. 1980. Habitat, female age, organochlorine compounds and breeding of European sparrowhawks, (*Accipiter nisus*). *J. Appl. Ecol.*, 16, 777-794.
- Nisbet, I. C. T. 1973. Courtship feeding, egg size and breeding success in common terns. *Nature*, 241, 141-142.
- Nisbet, I. C. T. 1975. Selective effects of predation in a tern colony. *Condor*, 77, 221-226.
- Nisbet, I. C. T. & Drury, W. H. 1972. Post-fledging survival in herring gulls in relation to brood-size and date of hatching. *Bird Banding*, 43, 161-240.
- O'Connor, R. J. 1978. Brood reduction in birds: Selection for fratricide, infanticide and suicide? *Anim. Behav.*, 26, 79-96.
- Olsen, P. & Olsen, J. 1979. Eggshell thinning in the peregrine, *Falco peregrinus* (Aves, Falconidae), in Australia. *Aust. Wildl. Res.*, 6, 217-226.
- Panov, E. N., Zykova, L. Yu., Kostina, G. N. & Andrusenko, N. N. 1980. The mortality of nestlings caused by social causes and cannibalism in colonies of the great black-backed gull *Larus ichthyaetus*. 1. Scale and causes of juvenile mortality. *Zool. Zh.*, 59, 1694-1705.
- Parker, R. E. 1980. Introductory statistics for biology. The Camelot Press Ltd, Southampton.
- Parker, G. A. & MacNair, M. R. 1978. Models of parent-offspring conflict. 1. Monogamy. *Anim. Behav.*, 26, 97-110.
- Parsons, J. 1970. Relationship between egg-size and post-hatch chick mortality in the herring gull *Larus argentatus*. *Nature*, 228, 1221-1222.
- Parsons, J. 1971. Cannibalism in herring gulls. *Brit. Birds*, 64, 528-537.
- Parsons, J. 1972. Egg size, laying date and incubation period in the herring gull. *Ibis*, 114, 536-541.
- Parsons, J. 1975. Seasonal variation in the breeding success of the herring gull: An experimental approach to pre-fledging success. *J. Anim. Ecol.*, 44, 553-573.
- Parsons, J. 1976. Nest density and breeding success in the herring gull *Larus argentatus*. *Ibis*, 118, 537-546.
- Parsons, J., Chabrzyk, G. & Duncan, N. 1975. Effects of hatching date on post-fledging survival in the herring gull. *J. Anim. Ecol.*, 45, 667-675.
- Patterson, I. J. 1965. Timing and spacing of broods in the black-headed gull (*Larus ridibundus* L.). *Ibis*, 107, 433-460.
- Paynter, R. A. Jr. 1949. Clutch size and egg and chick mortality of Kent Island herring gulls. *Ecology*, 30, 146-166.
- Perrins, C. M. 1965. Population fluctuations and clutch size in the great tit *Parus major*. *J. Anim. Ecol.*, 34, 601-648.
- Perrins, C. M. 1966. Survival of young manx shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. *Ibis*, 108, 132-135.
- Perrins, C. M. 1970. The timing of birds breeding seasons. *Ibis*, 112, 242-255.



- Perrins, C. M., Harris, M. P. & Britton, C. K. 1973. Survival of manx shearwaters *Puffinus puffinus*. *Ibis*, 115, 535-548.
- Perrins, C. M. & Moss, D. 1974. Survival of young great tits in relation to age of female parent. *Ibis*, 116, 220-224.
- Pierotti, R. 1981. Male and female parental roles in the Western gull under different environmental conditions. *Auk*, 98, 532-549.
- Pourtois, A. 1977. Nesting of the black-headed gull *Larus ridibundus*. *Aves*, 14, 146.
- Ricklefs, R. E. 1965. Brood reduction in the curve-billed thrasher. *Condor*, 67, 505-510.
- Ricklefs, R. E. 1969. An analysis of nestling mortality in birds. Washington D C: Smithsonian Institution Press.
- Robertson, R. J. & Biermann, G. C. 1979. Parental investment strategies determined by expected benefits. *Z. Tierpsychol*, 50, 124-128.
- Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling great tits *Parus major*. *Ibis*, 108, 313-347.
- Schifferli, L. 1978. Experimental modification of brood size among house sparrows *Passer domesticus*. *Ibis*, 120, 365-369.
- Smith, J. N. M. 1974. The food searching behaviour of two European thrushes. II. The adaptiveness of the search patterns. *Behaviour*, 49, 1-61.
- Sturkie, P. D. 1965. Avian physiology. New York.
- Stinson, C. H. 1979. On the selective advantage of fratricide in raptors. *Evol.*, 33, 1219-1225.
- Tinbergen, N. 1952. On the significance of territory in the herring gull. *Ibis*, 94, 158-159.
- Tinbergen, N. 1956. On the function of territory in gulls. *Ibis*, 98, 401-411.
- Tinbergen, N., Broekhuysen, G. J., Feekes, F., Houghton, J. C. W., Kruuk, H. & Szulc, E. 1962a. Eggshell removal by the black-headed gull *Larus ridibundus* L.. *Behaviour*, 19, 74-118.
- Tinbergen, N., Kruuk, H., Paillette, M. & Stamm, R. 1962b. How do black-headed gulls distinguish between eggs and egg-shells? *Brit. Birds*, 55, 120-129.
- Tinbergen, N., Impeken, M. & Frank, D. 1967. An experiment on spacing-out as a defence against predation. *Behaviour*, 28, 307-321.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: Sexual selection and descent of man. Campbell, B. Ed. Alpine, Chicago.
- Trivers, R. L. 1974. Parent-offspring conflict. *Amer. Zool.*, 14, 249-261.
- Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the sandwich tern (*Sterna s. Sandvicensis* Lath.). *Behav. Suppl.*, 20, 1-93.
- Verbeek, N. A. M. 1982. Egg predation by Northwestern crows: Its association with human and bald eagle activity. *Auk*, 99, 347-352.
- Vermeer, K. 1970. Breeding biology of California and ring-billed gulls: A study of ecological adaptation to the island habitat. *Can. Wildl. Serv. Rep. Ser.*, 12, 52p.
- Weidmann, U. 1956. Observations and experiments on egg-laying in the black-headed gull (*Larus ridibundus*). *Anim. Behav.*, 4, 150-161.
- Weidmann, U. 1961. The stimuli eliciting begging in gulls and terns. *Anim. Behav.*, 9, 115-116.
- Weidmann, R. & Weidmann, U. 1958. An analysis of the stimulus situation releasing food-begging in the black-headed gull. *Anim. Behav.*, 6, 114.
- Whiten, A. & Barton, R. A. 1988. Demise of the checklist: Using off-the-shelf miniature hand-held computers for remote fieldwork applications. *Trends Ecol. Evol.*, 3, 146-148.
- Wiklund, C. G. & Andersson, M. 1980. Nest predation selects for colonial breeding among fieldfares *Turdus pilaris*. *Ibis*, 122, 363-366.
- Ytreberg, N-J. 1956. Contributions to the breeding biology of the black-headed gull (*Larus ridibundus* L.) in Norway. Nest, eggs and incubation. *Nytt. Mag Zool.*, 4, 5-106.
- Ytreberg, N-J. 1960. Some observations on egg-laying in the black-headed gull (*Larus ridibundus* L.) and the common gull (*Larus canus* L.). *Nytt. Mag. Zool.*, 9, 5-15.
- Zykova, L. Yu. & Panov, E. N. 1983. The influence of numbers and density of nesting colonies on reproductive success in the herring gull *Larus argentatus*. *Zool. Zh.*, 62, 1533-1540.

APPENDIX 1 TOTAL RAINFALL AND HOURS OF BRIGHT SUNSHINE FOR EACH MONTH  
OF THE THREE STUDY YEARS

	<u>RAINFALL (mm)</u>			<u>BRIGHT SUNSHINE (hrs)</u>		
	1982	1983	1984	1982	1983	1984
JAN	100	75	127	25.4	45.6	45.9
FEB	37	19	43	57.7	65.2	58.0
MAR	62	51	115	143.5	103.5	76.3
APR	26	56	9	170.1	115.5	178.2
MAY	36	80	33	230.6	91.1	230.9
JUN	49	69	51	108.0	173.4	197.4
JUL	40	13	34	223.2	182.6	226.9
AUG	46	35	13	156.9	171.4	169.0
SEP	93	85	86	122.1	110.4	105.6
OCT	122	51	93	66.0	88.0	87.4
NOV	99	18	159	52.5	64.2	26.1
DEC	89	87	59	25.7	22.3	29.4

APPENDIX 2 TOTAL RAINFALL AND HOURS OF BRIGHT SUNSHINE FOR TWO GROUPS  
OF MONTHS FROM 1973 TO 1985

	<u>RAINFALL (mm)</u>		<u>BRIGHT SUNSHINE (hrs)</u>	
	FEB-MAY	APR-JUL	FEB-MAY	APR-JUL
1973		198		615.5
1974	182	160	505.9	764.7
1975	119	158	541.1	770.8
1976	218	156	411.4	681.2
1977	271	166	517.9	747.1
1978	276	228	493.0	686.6
1979	232	215	474.6	668.9
1980	210	211	524.5	725.6
1981	213	179	496.0	726.9
1982	161	151	601.9	731.9
1983	206	210	375.4	562.6
1984	200	127	543.5	833.5
1985	214	292	459.4	594.8
MEAN	208.5	188.5	495.4	700.8
SD	42.8	43.4	60.6	76.5

APPENDIX 3 MEAN NUMBER OF GULLS ON THE STUDY AREA ON DIFFERENT DAYS  
THROUGHOUT THE BREEDING SEASON

1982

DAY OF YEAR	TOTAL NO OF GULLS		GULLS ON NESTS		OTHER GULLS		NO OF OBS.
	NO	SD	NO	SD	NO	SD	
102	0.0		0.0		0.0		1
105	29.7	3.5	2.3	0.9	27.4	3.1	16
109	47.4	3.1	2.3	0.6	45.1	2.8	10
111	43.3	5.2	7.3	3.7	36.0	2.4	3
113	41.0	6.2	6.3	1.0	34.7	6.1	7
116	73.0	4.6	14.3	4.3	58.7	3.1	7
117	64.7	6.4	11.3	4.3	53.3	4.8	9
118	62.0		15.0		47.0		1
119	71.4	2.1	15.4	3.1	56.0	1.3	5
120	79.0	3.6	22.2	0.9	56.8	4.3	6
121	71.0	1.6	22.0	2.6	49.0	0.6	4
123	82.7	4.5	27.8	1.8	54.8	0.2	6
124	94.8	3.4	33.4	2.5	61.4	1.4	10
126	101.4	5.9	50.9	2.4	50.6	6.8	7
128	83.0	2.9	50.0	1.4	33.0	4.3	3
130	75.0	2.4	48.7	1.2	26.3	1.2	3
131	60.0	1.9	47.2	1.5	12.8	1.3	4
132	61.3	2.5	44.7	1.7	16.7	2.1	3
133	57.8	3.7	49.2	2.0	8.7	3.0	6
134	58.5	1.7	46.5	2.2	12.0	1.3	6
135	50.0		44.0		6.0		1
138	62.3	2.5	50.7	1.9	11.6	1.4	7
139	48.6	2.1	43.9	1.6	4.7	1.2	7
140	52.0	2.2	47.1	1.4	4.9	1.2	7
144	55.8	3.8	48.5	2.1	7.2	1.9	4
145	53.0		47.0		5.0		1
146	51.0		45.0		6.0		1
147	48.0	1.0	43.5	0.5	4.5	1.5	2
148	45.0		41.0		4.0		1
151	42.0		33.0		9.0		1
154	4.0		1.0		3.0		1
158	2.0		0.0		1.0		1
162	0.0		0.0		0.0		1

APPENDIX 4 MEAN NUMBER OF GULLS ON THE STUDY AREA ON DIFFERENT DAYS  
THROUGHOUT THE BREEDING SEASON

1983 - STUDY AREA A

DAY OF YEAR	TOTAL NO OF GULLS		GULLS ON NESTS		OTHER GULLS		NO OF OBS.
	NO	SD	NO	SD	NO	SD	
99	0.0		0.0		0.0		1
102	14.3	2.9	0.0	0.0	14.3	2.9	3
111	15.0	2.0	0.5	0.5	14.5	2.5	2
114	23.2	1.6	3.2	1.0	20.0	1.4	5
116	24.7	3.7	4.3	0.7	20.3	3.9	6
117	19.6	3.6	2.6	1.2	17.0	3.1	7
118	26.4	2.0	6.4	1.0	20.0	1.9	5
120	31.7	2.1	8.3	1.2	23.3	3.1	3
121	24.0	5.7	7.7	1.6	16.3	5.2	6
124	27.3	3.4	12.7	2.7	14.7	3.1	6
125	32.5	2.5	10.0	1.0	22.5	1.5	2
129	27.7	1.9	19.2	1.1	8.5	2.1	6
130	27.3	1.7	20.7	0.5	6.7	1.4	6
131	27.4	2.1	20.8	0.8	6.6	1.9	5
134	26.3	1.3	21.2	0.7	5.2	1.1	6
135	28.0	2.0	22.5	0.5	5.5	1.5	2
137	24.2	1.5	22.0	0.0	2.2	1.5	5
138	24.5	0.5	21.8	0.4	2.7	0.4	4
139	23.4	0.8	21.0	0.0	2.4	0.8	5
141	25.6	1.9	20.8	0.4	4.8	1.7	5
144	22.7	1.5	20.0	0.0	2.7	1.5	7
145	24.7	2.0	20.4	0.5	4.3	1.7	7
146	23.6	1.6	18.8	0.8	4.8	1.2	5
148	25.2	0.8	20.2	0.8	5.0	1.2	4
150	25.5	1.5	17.5	0.5	8.0	1.9	4
151	25.0	1.8	16.8	1.2	8.2	1.3	5
152	28.2	0.4	17.4	1.0	10.8	1.0	5
154	23.2	0.8	14.2	2.4	9.0	2.9	4
155	21.0	0.8	11.0	0.0	10.0	0.8	3
157	20.0		3.0		17.0		1
158	18.4	1.0	6.8	1.8	11.6	1.4	5
159	19.2	1.9	4.2	1.6	15.0	1.4	5
162	17.4	2.7	3.2	1.2	14.2	2.1	5
163	20.0	2.5	3.0	0.0	17.0	2.5	4
165	17.4	1.9	2.6	1.4	14.8	1.7	5
167	20.4	1.4	1.9	0.8	18.6	1.5	7
169	20.0	4.0	2.5	1.5	17.0	5.0	2
170	19.2	0.8	4.4	0.8	14.8	1.2	5
172	18.8	1.1	2.5	1.1	16.2	1.1	4
173	18.8	4.3	2.8	1.1	16.0	4.7	4
174	15.7	3.1	2.0	1.6	13.7	1.7	3
180	15.8	4.9	1.2	1.0	14.6	4.3	5
181	16.2	1.9	3.0	1.4	13.2	2.0	5
185	12.0	0.8	0.0	0.0	12.0	0.8	3
186	15.7	2.4	1.7	0.5	13.3	1.2	3
192	13.5	2.2	1.5	1.3	12.0	2.9	6
193	12.0	0.0	1.5	0.5	10.5	0.5	2
194	3.0		0.0		3.0		1
195	0.0	0.0	0.0	0.0	0.0	0.0	3



APPENDIX 5 MEAN NUMBER OF GULLS ON THE STUDY AREA ON DIFFERENT DAYS  
THROUGHOUT THE BREEDING SEASON

1983 - STUDY AREA B

DAY OF YEAR	TOTAL NO OF GULLS		GULLS ON NESTS		OTHER GULLS		NO OF OBS.
	No	SD	No	SD	No	SD	
129	23.7	2.1	16.5	1.5	7.2	2.7	6
130	25.0	1.9	17.5	1.4	7.5	2.3	6
131	25.4	1.5	18.2	0.8	7.2	1.2	5
134	26.2	2.4	19.3	0.9	6.8	1.8	6
135	26.0	3.0	20.0	0.0	6.0	3.0	2
137	24.0	0.6	21.0	0.6	3.0	0.9	5
138	25.8	1.5	21.0	0.0	4.8	1.5	4
139	23.8	1.2	20.2	0.4	3.6	1.2	5
141	26.2	1.3	21.4	0.5	4.8	1.2	5
144	23.4	1.4	18.3	1.9	5.1	2.2	7
145	23.4	1.2	19.6	1.3	3.9	1.5	7
146	23.2	1.9	17.6	1.0	5.6	1.6	5
148	24.0	2.1	18.8	0.4	5.2	1.8	4
150	22.5	0.5	14.2	0.8	8.2	0.8	4
151	23.4	1.0	15.4	2.3	8.0	2.3	5
152	22.2	1.5	16.0	1.8	6.2	0.4	5
154	20.8	0.4	15.8	1.8	5.0	1.6	4
155	20.3	0.5	9.0	1.4	11.3	1.2	3
157	22.0		5.0		17.0		1
158	19.2	1.2	7.6	2.4	11.6	1.5	5
159	17.8	1.2	8.2	1.3	9.6	1.4	5
162	20.4	1.5	7.0	1.4	13.4	2.6	5
163	19.5	1.5	4.8	0.4	14.8	1.3	4
165	16.0	2.1	6.6	2.4	9.4	2.4	5
167	15.9	1.2	3.7	0.9	12.1	1.6	7
169	12.0	2.0	3.5	0.5	8.5	2.5	2
170	13.4	2.1	2.2	1.0	11.2	1.2	5
172	13.8	2.9	2.0	1.0	11.8	1.9	4
173	13.5	1.5	1.0	0.7	12.5	1.8	4
174	14.0	2.2	1.3	0.5	12.7	1.7	3
180	13.4	2.3	1.6	1.4	11.8	2.3	5
181	12.2	1.5	2.4	0.8	9.8	1.5	5
185	9.7	0.9	1.3	0.5	8.3	1.2	3
186	10.7	2.4	2.3	0.9	8.3	2.1	3
192	11.2	3.3	2.5	2.2	8.7	3.4	6
193	11.0	1.0	1.5	0.5	9.5	0.5	2
194	2.0		1.0		1.0		1
195	0.0	0.0	0.0	0.0	0.0	0.0	3

APPENDIX 6 MEAN NUMBER OF GULLS ON THE WATER AND ON COMMUNAL AREAS ON  
DIFFERENT DAYS THROUGHOUT THE BREEDING SEASON

1983

DAY OF YEAR	NO OF GULLS ON WATER		NO OF GULLS ON COMMUNAL GROUND		NO OF OBS
	NO	SD	NO	SD	
99	0.0				1
102	92.5	0.5			2
111	113.5	4.5			2
114	102.6	18.6			5
116	93.6	5.8			5
117	55.8	6.0			4
118	64.0	5.2			5
120	70.0	15.8			3
121	58.0	6.2			5
124	46.0	10.2			5
125	38.5	6.5			2
129	32.0	5.0	16.8	9.0	5
130	38.0	10.0	17.6	7.3	5
131	33.5	10.7	27.0	5.6	4
134	28.4	9.3	39.2	10.2	5
135	19.5	15.5	72.5	6.5	2
137	39.3	2.5	48.7	4.8	3
138	20.3	4.5	37.3	7.4	3
139	19.6	10.3	25.4	10.6	5
141	21.8	2.6	71.0	16.4	4
144	26.2	11.0	48.3	9.6	6
145	29.1	7.1	57.7	21.0	7
146	25.3	4.6	24.7	6.9	3
148	23.2	4.0	30.0	3.7	4
150	15.5	4.7	28.0	5.4	4
151	16.2	3.3	42.3	6.8	4
152	14.8	2.5	34.4	2.6	5
154	22.3	4.3	35.8	16.6	4
155	17.3	4.1	18.7	1.2	3
157	49.0		42.0		1
158	11.8	5.9	22.5	1.7	4
159	24.0	8.3	16.0	7.1	5
162	28.6	10.8	34.6	6.5	5
163	39.0	6.7	13.3	1.2	3
165	24.5	2.3	24.0	1.2	4
167	38.3	2.7	12.2	4.5	6
169	27.0		17.0		1
170	38.0	10.9	45.2	12.1	5
172	65.7	5.6	28.7	12.0	3
173	22.0	5.0	38.0	2.0	2
174	56.5	0.5	44.0	5.0	2
180	43.0	9.8	34.0	5.7	3
181	30.2	9.4	32.2	4.8	4
185	22.3	6.2	21.0	3.6	3
186	25.5	9.5	27.0	12.0	2
192	20.8	9.1	21.0	3.5	4
193	24.0	4.0	27.5	2.5	2
194	8.0		13.0		1
195	4.3	2.5	7.7	2.9	3
198	5.0		6.0		1
199	5.5	3.6	3.2	1.1	4
203	6.0	4.1	5.0	2.4	3
209	4.0	1.0	2.0	1.0	2
211	3.0		1.0		1
215	1.0		0.0		1
222	0.0	0.0	0.0	0.0	3

APPENDIX 7 MEAN NUMBER OF GULLS ON THE STUDY AREA ON DIFFERENT DAYS  
THROUGHOUT THE BREEDING SEASON

1984 - STUDY AREA A

DAY OF YEAR	TOTAL NO OF GULLS		GULLS ON NESTS		OTHER GULLS		NO OF OBS.
	NO	SD	NO	SD	NO	SD	
86	0.0	0.0	0.0	0.0	0.0	0.0	2
88	9.3	5.2	0.0	0.0	9.3	5.2	9
90	10.8	3.6	0.1	0.3	10.6	3.5	8
94	8.4	2.2	0.1	0.3	8.3	2.2	9
96	10.5	2.5	0.0	0.0	10.5	2.5	4
100	21.0	3.3	1.7	1.2	19.3	2.8	6
102	21.7	6.3	1.7	1.2	20.0	5.1	3
108	23.4	5.8	2.0	2.1	21.4	5.7	7
109	38.4	3.2	4.3	1.7	34.1	3.1	7
110	20.0	4.0	5.0	2.3	16.7	12.6	5
113	31.5	7.5	4.5	2.5	27.0	5.0	2
114	37.2	3.1	9.4	2.4	27.8	3.8	5
116	46.0	3.6	12.0	1.4	34.0	4.6	3
117	42.8	4.2	10.2	2.2	32.5	3.3	4
118	35.8	3.3	12.5	1.7	23.2	3.6	4
121	31.2	1.8	15.0	2.4	16.2	3.2	5
123	36.2	3.5	20.7	2.3	15.5	4.4	6
124	31.3	2.6	20.7	1.3	10.7	1.7	3
126	35.2	4.0	22.0	2.4	13.2	5.9	4
128	29.4	3.2	23.4	2.4	6.0	2.0	5
130	29.0	1.2	23.0	1.4	6.0	1.9	6
131	29.8	3.5	22.5	2.5	7.2	1.5	4
132	29.6	2.0	22.7	1.8	6.9	3.0	7
135	26.0	1.0	23.5	0.5	2.5	0.5	2
136	26.0	1.1	23.4	1.2	2.6	1.8	7
137	30.1	11.1	21.3	0.5	5.0	2.2	3
138	23.4	0.8	22.2	0.8	1.2	0.8	5
139	23.8	1.3	20.8	0.4	3.2	1.7	5
140	24.5	1.7	21.5	0.9	3.0	2.0	4
142	17.0	1.4	16.2	1.2	0.8	0.8	5
144	13.7	1.2	12.0	0.8	1.7	0.9	3
146	11.6	0.8	10.0	0.0	1.6	0.8	5
148	7.8	0.8	6.0	0.0	1.8	0.8	4
149	7.2	0.8	4.8	1.0	2.4	1.0	5
150	5.8	0.4	5.7	0.4	0.0	0.0	4
151	7.4	2.0	6.0	1.3	1.4	0.8	5
152	5.2	0.4	4.2	0.8	1.0	0.9	5
156	0.3	0.5	0.0	0.0	0.3	0.5	3
157	0.0	0.0	0.0	0.0	0.0	0.0	3

APPENDIX 8 MEAN NUMBERS OF GULLS ON THE STUDY AREA ON DIFFERENT DAYS  
THROUGHOUT THE BREEDING SEASON

1984 - STUDY AREA B

DAY OF YEAR	TOTAL NO OF GULLS		GULLS ON NESTS		OTHER GULLS		NO OF OBS.
	NO	SD	NO	SD	NO	SD	
86	0.0	0.0	0.0	0.0	0.0	0.0	2
88	18.4	3.3	0.0	0.0	18.4	3.3	9
90	20.6	2.4	0.4	0.5	20.2	2.2	8
94	28.2	6.0	0.3	0.7	27.9	5.9	9
96	28.0	4.5	2.2	1.9	25.9	2.9	4
100	41.5	6.1	1.0	0.6	40.5	6.4	6
102	37.0	4.6	2.3	2.0	34.7	3.9	3
108	37.0	5.1	4.4	2.3	32.6	6.2	7
109	44.7	2.4	5.1	2.1	39.6	3.2	7
110	42.4	4.7	7.0	2.6	34.6	3.4	5
113	38.5	5.5	8.5	5.5	30.0	0.0	2
114	40.2	4.5	8.0	1.7	32.2	5.7	5
116	49.5	2.9	14.5	3.6	35.0	5.3	4
117	44.8	2.6	16.2	2.3	28.5	4.7	4
118	40.5	3.2	17.0	3.2	23.5	3.9	4
121	38.6	2.1	19.8	3.3	18.8	4.3	5
123	38.8	2.2	22.0	2.4	16.8	3.2	6
124	32.7	0.5	25.3	1.2	7.3	1.2	3
126	34.2	1.3	22.5	1.7	11.7	1.5	4
128	34.4	1.5	26.0	1.1	8.4	2.2	5
130	33.8	3.2	25.0	1.6	8.8	4.7	6
131	36.5	1.7	27.5	2.1	9.0	3.2	4
132	34.4	2.2	26.7	1.5	7.7	1.6	7
135	31.5	1.5	23.0	2.0	8.5	3.5	2
136	28.6	2.4	24.6	1.3	4.0	2.3	7
137	28.7	0.5	23.0	1.4	5.7	1.2	3
138	28.6	2.0	22.2	2.3	6.4	3.1	5
139	29.6	2.2	23.8	1.5	5.8	1.8	5
140	29.2	3.1	22.8	2.2	6.5	1.7	4
142	25.8	1.2	21.8	0.8	4.0	0.9	5
144	19.3	3.3	14.0	0.8	5.3	2.6	3
146	18.4	2.2	10.8	1.5	7.6	3.4	5
148	15.0	2.0	5.8	0.4	9.2	2.3	4
149	11.2	1.2	6.4	0.5	4.8	1.0	5
150	11.5	0.5	5.5	0.9	6.0	0.7	4
151	6.8	2.3	2.8	0.8	4.0	2.1	5
152	6.8	2.3	2.4	0.5	4.4	2.3	5
156	7.7	3.9	0.7	0.5	7.7	3.9	3
157	3.3	0.5	1.0	0.0	2.3	0.5	3
159	5.8	2.0	1.8	1.2	4.0	2.1	5
160	8.2	1.6	2.6	1.0	5.6	1.0	5
162	5.5	1.7	1.2	0.4	4.2	1.3	4
164	2.0	0.0	0.0	0.0	2.0	0.0	3
165	1.5	0.5	0.0	0.0	1.5	0.5	2
167	2.5	0.5	0.0	0.0	2.5	0.5	2
170	6.0	1.6	0.8	0.8	5.2	1.3	4
172	3.2	1.5	0.5	0.5	2.8	1.3	4
174	4.8	1.5	0.5	0.5	4.2	1.8	4
178	6.0		1.0		5.0		1
180	0.0		0.0		0.0		1
185	0.0		0.0		0.0		1

APPENDIX 9 MEAN NUMBER OF GULLS ON THE WATER AND ON COMMUNAL AREAS ON  
DIFFERENT DAYS THROUGHOUT THE BREEDING SEASON

1984

DAY OF YEAR	NO OF GULLS ON WATER		NO OF GULLS ON COMMUNAL GROUND		NO OF OBS
	NO	SD	NO	SD	
86	0.0	0.0	0.0	0.0	2
88	200.5	38.8	3.0	1.7	8
90	140.0	12.7	0.6	0.9	8
94	195.5	45.1	1.9	1.7	9
96	222.0	26.3	9.0	4.9	3
100	337.3	56.2	12.7	1.8	6
102	279.7	36.0	10.7	0.5	3
108	174.9	35.3	10.6	6.0	7
109	210.6	17.2	15.4	3.3	7
110	184.8	18.6	27.8	0.3	4
113	245.0		16.0		1
114	166.4	24.7	43.0	10.3	5
116	138.0	6.0	62.3	20.8	2
117	152.5	45.4	50.8	19.9	4
118	106.5	14.6	66.5	20.0	4
121	127.2	21.8	8.8	6.7	5
123	83.0	20.1	27.7	18.5	6
124	46.7	1.7	69.3	13.5	3
126	44.2	5.0	15.8	13.6	4
128	30.4	4.5	25.0	14.8	5
130	30.8	9.9	32.0	21.3	6
131	28.0	7.0	22.8	3.1	4
132	32.0	10.9	34.3	19.9	7
135	27.0		7.0		1
136	23.0	9.8	8.7	7.1	7
137	28.3	1.2	32.3	18.4	3
138	28.4	7.4	30.8	12.8	5
139	21.2	2.7	34.0	12.7	5
140	24.5	9.6	23.5	9.3	4
142	8.4	4.8	36.6	5.3	5
144	12.3	3.3	7.7	2.6	3
146	18.2	4.7	18.6	7.3	5
148	8.5	3.5	4.0	2.1	4
149	10.2	4.0	4.2	2.0	5
150	12.0	7.0	5.5	2.1	4
151	18.6	5.2	5.6	3.7	5
152	14.6	5.6	4.6	1.9	5
156	28.3	17.3	16.3	7.6	3
157	29.3	12.0	16.3	3.3	3
159	26.7	8.3	14.5	6.3	6
160	25.0	6.0	18.8	6.7	5
162	43.7	11.8	16.7	1.7	3
164	28.3	9.0	37.0	9.4	3
165	27.5	3.5	5.0	2.0	2
167	32.0	16.0	14.5	8.5	2
170	44.7	17.0	33.3	9.4	3
172	27.7	5.2	29.7	3.7	3
174	87.0	30.0	78.0	7.4	3
178	26.0		45.0		1
180	49.0		20.0		1
185	0.0		0.0		1

APPENDIX 10 NUMBERS OF EGGS LAID ON EACH DAY THROUGHOUT THE LAYING PERIOD

<u>DATES EGGS LAID</u>		<u>NUMBER OF EGGS</u>	
		1983	1984
APRIL	20		5.3
	21		4.3
	22		13.3
	23		9.3
	24		9.3
	25	1	9.3
	26	4	8.3
	27	8	7.5
	28	7	11.4
	29	5	14.4 PEAK
	30	12	9.4
		7	13.5
MAY	1	12.3 PEAK	13.5
	2	7.3	10
	3	9.3	7.8
	4	9	6.8
	5	6.7	6.2
	6	4.7	4.2
	7	5.7	2
	8	4	3
	9	4	2
	10	1	5
	11	9	2.5
	12	1.5	2.5
	13	2.5	3
	14	1.7	3
	15	1.7	5
	16	1.7	
	17	1	1
	18	2	
	19		
	20		
	21		
	22		3 FOX
	23		
	24		
	25	2	1
	26		
	27		
	28		4
	29		
	30	1	
JUNE	31	0.5	
	1	0.5	
	2	0.5	
	3	1.5	
	8	1	

APPENDIX 11    NUMBERS OF CHICKS HATCHED ON EACH DAY THROUGHOUT THE  
HATCHING PERIOD

DATES CHICKS HATCHED		NUMBER OF CHICKS		
		1982	1983	1984
MAY	14			1
	15			
	16			9 PEAK
	17			5
	18			5
	19			5
	20	3		3
	21	1	1	6 FOX
	22	1	7	3
	23	2	4	6
	24	3	3	1
	25	3	13 PEAK	
	26	9	6	
	27	5	3	1
	28	7	3	
	29	6	5	2
	30	10	2	1
	31	11 PEAK/FOX	3	
JUNE	1	6	3	
	2	6	5	
	3	2	3	
	4	1	3	
	5	3	3	
	6		3	
	7			
	8		2	
	9			
	10	1		
	11			
	12			
	13			
	14		1	
	15			
	16			
	17			
	18			
	19		2	

APPENDIX 12 HATCHING AND FLEDGING SUCCESSES FOR DIFFERENT CLUTCH AND  
BROOD SIZES

1983

NO OF EGGS	NESTS	TOTAL EGGS	HATCHED		(MIN)		FLEDGED		(MAX)	
			No	%	No	%	No	%	No	%
1	15	15	6	40.0	3	20.0			5	33.0
2	21	42	24	57.1	11	26.2			22	52.4
3	25	75	45	60.0	21	28.0			39	52.0
4	1	4	2	50.0	1	25.0			1	25.0

NO OF CHICKS	NESTS	TOTAL CHICKS	(MIN)		FLEDGED		(MAX)	
			No	%	No	%	No	%
1	16	16	7	43.7	14	87.5		
2	20	40	20	50.0	36	90.0		
3	7	21	9	42.9	17	80.9		



APPENDIX 13    NUMBERS OF DIFFERENT CLUTCH AND BROOD SIZES LAID AND  
HATCHED AT DIFFERENT TIMES OF THE SEASON

(a)

<u>EGGS</u>	1		2		3		4		x
	No	%	No	%	No	%	No	%	
1983									
EARLY	6	30.00	3	15.00	11	55.00			2.25
MID	3	13.64	12	54.55	7	31.82			2.18
LATE	6	30.00	6	30.00	7	35.00	1	5.00	2.15
1984									
EARLY	7	24.14	9	31.03	13	44.83			2.21
MID	10	25.64	15	38.46	14	35.90			2.10
LATE	7	25.00	14	50.00	7	25.00			2.00

(b)

<u>CHICKS</u>	1		2		3		x
	No	%	No	%	No	%	
1983							
EARLY	5	31.25	8	50.00	3	18.75	1.88
MID	7	41.18	9	52.94	1	5.88	1.65
LATE	4	40.00	3	30.00	3	30.00	1.90
1984							
EARLY	7	41.18	6	35.29	4	23.53	1.82
MID	11	91.67	1	8.33			1.08
LATE	2	66.67	1	33.33			

APPENDIX 14 HATCHING AND FLEDGING SUCCESS OF EGGS LAID AT DIFFERENT  
TIMES OF THE SEASON

	EGGS LAID	CHICKS HATCHED		CHICKS FLEDGED			
				(MIN)		(MAX)	
		No	%	No	%	No	%
1983							
EARLY	45	30	66.7	13	28.9	26	57.8
MID	48	28	58.3	16	33.3	25	52.1
LATE	43	19	44.2	7	16.3	16	37.2

	EGGS LAID	CHICKS HATCHED		CHICKS FLEDGED	
		No	%	No	%
1984					
EARLY	64	31	48.4	5	7.8
MID	82	13	15.9	1	1.2
LATE	56	4	7.1	1	1.8

APPENDIX 15 FATE OF EGGS AND CHICKS FROM THREE EGG CLUTCHES AND THREE CHICK BROODS

<u>1983 3-EGG NESTS</u>	1st EGG		2nd EGG		3rd EGG	
	No	%	No	%	No	%
HATCHED	18	66.67	18	69.23	14	53.85
DIED HATCHING OR FAILED TO HATCH	1	3.70	1	3.85	8	30.77
LOST BEFORE HATCHING DATE	8	29.63	7	26.92	4	15.38

<u>1983 3-CHICK NESTS</u>	1st CHICK		2nd CHICK		3rd CHICK	
	No	%	No	%	No	%
FLEDGED	5	62.50	4	50.00	1	12.50
FOUND DEAD	0	0.00	1	12.50	4	50.00
DISAPPEARED	3	37.50	3	37.50	3	37.50

APPENDIX 16 % TIME PARENTS SPENT ON THE TERRITORY AT DIFFERENT TIMES OF THE SEASON

1983		% TIME SPENT ON TERRITORY				PERIODS	PER HR	NO OF OBS
		MALE	FEMALE	BOTH	NONE	MALE	FEMALE	
NO-EGG	%	29.33	53.93	8.00	24.73	2.40	2.04	5
	SE	18.12	17.01	4.55	11.78	0.68	1.04	
PRE-EGG	%	57.29	58.33	21.19	5.58	2.02	1.81	13
	SE	10.49	8.73	6.47	2.49	0.39	0.41	
EGG	%	58.47	54.49	13.15	0.16	1.16	1.12	144
	SE	3.30	3.24	1.93	0.12	0.11	0.09	
CHICK	%	48.97	44.21	10.65	17.48	1.52	1.45	137
	SE	2.78	2.78	1.51	2.41	0.12	0.11	
1984								
NO-EGG	%	56.53	49.08	26.27	19.97	1.85	0.99	57
	SE	3.80	4.67	3.20	3.60	0.20	0.09	
PRE-EGG	%	67.36	57.67	35.96	7.07	1.37	1.15	39
	SE	4.63	4.22	3.63	2.35	0.13	0.10	
EGG	%	60.61	50.88	12.08	0.59	0.84	0.62	141
	SE	2.55	2.74	1.60	0.42	0.06	0.04	
CHICK	%	45.79	60.96	12.77	6.03	0.93	0.84	21
	SE	4.14	4.47	3.62	3.24	0.20	0.09	

APPENDIX 17 TIME PARENTS WITH DIFFERENT AGE GROUPS OF CHICKS SPENT ON THE TERRITORY

1983		% TIME SPENT ON TERRITORY				PERIODS	PER HR	NO OF OBS
CHICK AGE		MALE	FEMALE	BOTH	NONE	MALE	FEMALE	
WEEK 1	%	59.43	51.39	15.57	4.75	1.48	1.41	48
	SE	4.63	4.57	2.95	2.26	0.17	0.18	
WEEK 2	%	52.34	48.23	12.32	11.74	1.49	1.78	45
	SE	4.20	4.69	2.80	2.79	0.17	0.23	
WEEK 3	%	39.40	33.24	4.60	31.96	1.87	1.19	34
	SE	5.49	5.49	1.84	6.04	0.30	0.19	
WEEK 4	%	16.09	28.91	0.13	55.13	0.61	1.10	10
	SE	8.78	10.64	0.13	10.63	0.28	0.35	

APPENDIX 18 TIME PARENTS SPENT INCUBATING AND BROODING

1984		% TIME SPENT BROODING			PERIODS PER HR		NO OF OBS
		MALE	FEMALE	NONE	MALE	FEMALE	
EGG	Z	53.69	45.03	1.05	0.53	0.48	137
	SE	2.59	2.55	0.40	0.03	0.03	
CHICK	Z	34.27	46.98	18.79	0.73	0.82	20
	SE	4.42	3.97	5.36	0.11	0.10	

APPENDIX 19 COMPARISON OF THE TIME PARENTS SPENT ON THE TERRITORY AND THE TIME THEY SPENT INCUBATING AND BROODING

1984			EGG		CHICK	
			MALE	FEMALE	MALE	FEMALE
TIME	TIME	Z	60.61	50.88	45.79	60.96
	PRESENT	SE	2.55	2.74	4.11	4.47
	TIME	Z	53.69	45.03	34.27	46.98
	BROODING	SE	2.59	2.55	4.42	3.97
PERIODS PER HR.	TIME	Z	0.84	0.62	0.93	0.84
	PRESENT	SE	0.06	0.04	0.20	0.09
	TIME	Z	0.53	0.48	0.73	0.82
	BROODING	SE	0.03	0.03	0.11	0.10

APPENDIX 20    NUMBERS OF INTERACTIONS BETWEEN TERRITORY HOLDERS AND  
DIFFERENT TYPES OF INTRUDERS AT DIFFERENT TIMES OF THE  
SEASON

	NEIGHBOUR		STRANGER		IMMATURE		OTHER SPECIES	
	No	%	No	%	No	%	No	%
1982								
EGG	106	63.86	53	31.93	1	0.60	6	3.61
CHICK	40	43.96	36	39.56	11	12.09	4	4.40
1983								
NO-EGG	1	20.00	4	80.00	0	0.00	0	0.00
PRE-EGG	9	18.00	37	74.00	1	2.00	3	6.00
EGG	59	21.69	177	65.07	11	4.04	25	9.19
CHICK	46	13.22	256	73.56	9	2.59	28	8.05
1984								
NO-EGG	50	21.55	130	56.03	22	9.48	30	12.93
PRE-EGG	37	16.97	132	60.55	25	11.47	24	11.01
EGG	43	11.26	164	42.93	60	15.77	115	30.10
CHICK	5	7.69	32	49.23	6	9.23	22	33.85

APPENDIX 21 NUMBERS OF INTERACTIONS INVOLVING MALE AND FEMALE TERRITORY  
HOLDERS AT DIFFERENT TIMES OF THE SEASON

		MALES		FEMALES	
		No	%	No	%
1982	EGG	71	66.98	35	33.02
1983	NO-EGG	2	100.00	0	0.00
	PRE-EGG	24	64.86	13	35.14
	EGG	100	52.36	91	47.64
	CHICK	144	54.55	120	45.45
1984	NO-EGG	203	83.20	41	16.80
	PRE-EGG	152	73.79	54	26.21
	EGG	219	61.69	136	38.31
	CHICK	28	44.44	35	55.56

APPENDIX 22 NUMBERS OF INTERACTIONS INVOLVING MALE AND FEMALE TERRITORY  
HOLDERS AT DIFFERENT TIMES OF THE SEASON WHEN BOTH GULLS  
ARE PRESENT ON THE TERRITORY

1984	MALES		FEMALES	
	No	%	No	%
NO-EGG	105	97.22	3	2.78
PRE-EGG	65	78.31	18	21.69
EGG	44	78.57	12	21.43
CHICK	7	58.33	5	41.67

APPENDIX 23      NUMBERS OF INTERACTIONS BETWEEN DIFFERENT SEXES OF  
INTRUDERS AND TERRITORY HOLDERS

1984	TERRITORY	INTRUDER			
	HOLDER	MALE		FEMALE	
		No	%	No	%
NO-EGG	MALE	59	72.84	15	18.52
	FEMALE	7	8.64	0	0.00
PRE-EGG	MALE	40	67.80	12	20.34
	FEMALE	5	8.47	2	3.39
EGG	MALE	39	52.00	12	16.00
	FEMALE	19	25.33	5	6.67
CHICK	MALE	1	6.67	2	13.33
	FEMALE	8	53.33	4	26.67



APPENDIX 24 MEAN DISTANCE OF DIFFERENT TYPES OF INTRUDER FROM THE NEST  
WHEN REACTED TO AT DIFFERENT TIMES OF THE SEASON

1984	TERRITORY HOLDER	MEAN DISTANCE (ft)	STANDARD ERROR	NO OF OBS
NO-EGG	NEIGHBOUR	1.72	0.16	50
	STRANGER	2.52	0.13	130
	IMMATURE	2.59	0.20	22
	OTHER SPECIES	2.50	0.17	30
PRE-EGG	NEIGHBOUR	1.84	0.13	37
	STRANGER	2.33	0.09	132
	IMMATURE	2.48	0.29	25
	OTHER SPECIES	2.38	0.18	24
EGG	NEIGHBOUR	1.81	0.18	43
	STRANGER	2.38	0.07	164
	IMMATURE	2.63	0.18	60
	OTHER SPECIES	2.59	0.09	115
CHICK	NEIGHBOUR	1.80	0.20	5
	STRANGER	2.03	0.15	32
	IMMATURE	2.83	0.31	6
	OTHER SPECIES	2.50	0.20	22

APPENDIX 25 MEAN DISTANCE OF DIFFERENT TYPES OF INTRUDER FROM THE NEST  
WHEN REACTED TO AT DIFFERENT TIMES OF THE SEASON

(a) TERRITORY HOLDER INCUBATING OR BROODING

1984

	TERRITORY HOLDER	MEAN DISTANCE (ft)	STANDARD ERROR	NO OF OBS
EGG	NEIGHBOUR	1.43	0.13	30
	STRANGER	2.29	0.06	140
	IMMATURE	2.17	0.10	47
	OTHER SPECIES	2.65	0.09	102
CHICK	NEIGHBOUR	1.75	0.25	4
	STRANGER	1.88	0.19	17
	IMMATURE	2.50	0.29	4
	OTHER SPECIES	2.39	0.24	18

(b) TERRITORY HOLDER NOT INCUBATING OR BROODING

EGG	NEIGHBOUR	3.70	0.48	20
	STRANGER	2.85	0.22	26
	IMMATURE	2.83	0.31	6
	OTHER SPECIES	2.15	0.32	13
CHICK	NEIGHBOUR	2.00		1
	STRANGER	2.73	0.41	15
	IMMATURE	3.50	0.50	2
	OTHER SPECIES	2.60	0.55	5

APPENDIX 26 MEAN DISTANCE OF INTRUDERS FROM THE NEST WHEN REACTED TO BY  
DIFFERENT SEXES OF TERRITORY HOLDERS AT DIFFERENT TIMES OF  
THE SEASON

1984	TERRITORY HOLDER	MEAN DISTANCE (ft)	STANDARD ERROR	NO OF OBS
NO-EGG	MALE	2.42	0.10	188
	FEMALE	1.95	0.16	39
PRE-EGG	MALE	2.31	0.09	151
	FEMALE	2.28	0.15	53
EGG	MALE	2.55	0.08	217
	FEMALE	2.22	0.07	35
CHICK	MALE	2.39	0.15	28
	FEMALE	2.26	0.21	35

APPENDIX 27 NUMBERS OF DIFFERENT INTENSITIES OF REACTIONS RECORDED AT  
DIFFERENT TIMES OF THE SEASON

			INTENSITY OF REACTION TOWARDS INTRUDER				
			1	2	3	4	5
1982	EGG	No	3	113	42	3	5
		%	1.81	68.07	25.30	1.81	3.01
	CHICK	No	11	39	11	25	4
		%	12.22	43.33	12.22	27.78	4.44
1983	PRE-EGG	No	3	25	5	17	0
		%	6.00	50.00	10.00	34.00	0.00
	EGG	No	13	207	21	25	6
		%	4.78	76.10	7.72	9.19	2.21
	CHICK	No	8	112	45	104	7
		%	2.90	40.58	16.30	37.68	2.54
1984	NO-EGG	No	6	62	76	79	7
		%	2.61	26.96	33.04	34.35	3.04
	PRE-EGG	No	5	84	64	52	11
		%	2.31	38.89	29.63	24.07	5.09
	EGG	No	16	290	32	40	1
		%	4.22	76.52	8.44	10.55	0.26
	CHICK	No	6	38	3	16	1
		%	9.38	59.37	4.69	25.00	1.56

APPENDIX 28    NUMBERS OF DIFFERENT INTENSITIES OF REACTIONS RECORDED  
TOWARDS DIFFERENT TYPES OF INTRUDERS AT DIFFERENT TIMES  
OF THE SEASON

<u>1982</u>		INTENSITY OF REACTION TOWARDS INTRUDER				
		1	2	3	4	5
<u>EGG</u>						
NEIGHBOUR	No	2	74	27	0	3
	%	1.89	69.81	25.47	0.00	2.83
STRANGER	No	1	33	15	2	2
	%	1.89	62.26	28.30	3.77	3.77
IMMATURE	No	0	1	0	0	0
	%	0.00	100.00	0.00	0.00	0.00
OTHER SP.	No	0	5	0	1	0
	%	0.00	83.33	0.00	16.67	0.00
<u>CHICK</u>						
NEIGHBOUR	No	8	21	2	6	2
	%	20.51	53.85	5.13	15.39	5.13
STRANGER	No	3	11	5	16	1
	%	8.33	30.56	13.89	44.44	2.78
IMMATURE	No	0	5	3	2	1
	%	0.00	45.45	27.27	18.18	9.09
OTHER SP.	No	0	2	1	1	0
	%	0.00	50.00	25.00	25.00	0.00
<u>1983</u>						
<u>PRE-EGG</u>						
NEIGHBOUR	No	2	5	2	0	0
	%	22.22	55.56	22.22	0.00	0.00
STRANGER	No	1	17	3	16	0
	%	2.70	45.95	8.11	43.24	0.00
IMMATURE	No	0	1	0	0	0
	%	0.00	100.00	0.00	0.00	0.00
OTHER SP.	No	0	2	0	1	0
	%	0.00	66.67	0.00	33.33	0.00
<u>EGG</u>						
NEIGHBOUR	No	7	39	4	5	4
	%	11.86	66.10	6.78	8.48	6.78
STRANGER	No	5	135	15	20	2
	%	2.82	76.27	8.48	11.30	1.13
IMMATURE	No	0	10	1	0	0
	%	0.00	90.91	9.09	0.00	0.00
OTHER SP.	No	1	23	1	0	0
	%	4.00	92.00	4.00	0.00	0.00

APPENDIX 28 (continued)

		INTENSITY OF REACTION TOWARDS INTRUDER				
<u>CHICK</u>		1	2	3	4	5
NEIGHBOUR	No	0	20	4	17	0
	%	0.00	48.78	9.76	41.46	0.00
STRANGER	No	5	72	41	81	3
	%	2.48	35.64	20.30	40.10	1.48
IMMATURE	No	0	3	0	2	0
	%	0.00	60.00	0.00	40.00	0.00
OTHER SP.	No	3	17	0	4	4
	%	10.71	60.71	0.00	14.29	14.29
<u>1984</u>						
<u>NO-EGG</u>						
NEIGHBOUR	No	1	19	12	15	1
	%	2.08	39.58	25.00	31.25	2.08
STRANGER	No	0	25	51	49	5
	%	0.00	19.23	39.23	37.69	3.85
IMMATURE	No	0	9	5	7	1
	%	0.00	40.91	22.73	31.82	4.55
OTHER SP.	No	5	9	8	8	0
	%	16.67	30.00	26.67	26.67	0.00
<u>PRE-EGG</u>						
NEIGHBOUR	No	1	23	5	6	1
	%	2.78	63.89	13.89	16.67	2.78
STRANGER	No	1	43	46	31	10
	%	2.78	63.89	13.89	16.67	2.78
IMMATURE	No	1	8	6	10	0
	%	4.00	32.00	24.00	40.00	0.00
OTHER SP.	No	2	10	7	5	0
	%	8.33	41.67	29.17	20.83	0.00
<u>EGG</u>						
NEIGHBOUR	No	0	33	3	4	0
	%	0.00	82.5	7.50	10.00	0.00
STRANGER	No	1	128	16	19	0
	%	0.61	78.05	9.76	11.58	0.00
IMMATURE	No	0	40	8	11	1
	%	0.00	66.07	13.33	18.33	1.67
OTHER SP.	No	15	89	5	6	0
	%	13.04	77.39	4.35	5.22	0.00
<u>CHICK</u>						
NEIGHBOUR	No	0	5	0	0	0
	%	0.00	100.00	0.00	0.00	0.00
STRANGER	No	3	15	2	11	1
	%	9.38	46.88	6.25	34.37	3.12
IMMATURE	No	0	4	1	1	0
	%	0.00	66.66	16.67	16.67	0.00
OTHER SP.	No	3	14	0	4	0
	%	14.29	66.67	0.00	19.05	0.00

APPENDIX 29 NUMBERS OF DIFFERENT INTENSITIES OF REACTIONS RECORDED BY  
MALE AND FEMALE TERRITORY HOLDERS AT DIFFERENT TIMES OF  
THE SEASON

SEX OF TERR. HOLDER			INTENSITY OF REACTION TOWARDS INTRUDER				
			1	2	3	4	5
<u>1982</u>							
EGG	MALE	No	0	52	27	0	2
		%	0.00	64.20	33.33	0.00	2.47
	FEMALE	No	1	29	11	1	3
		%	2.22	64.44	24.44	2.22	6.67
<u>1983</u>							
PRE-EGG	MALE	No	2	10	2	10	0
		%	8.33	41.67	8.33	41.67	0.00
	FEMALE	No	1	6	2	4	0
		%	7.69	46.15	15.38	30.77	0.00
EGG	MALE	No	6	81	5	11	2
		%	5.71	77.14	4.76	10.48	1.91
	FEMALE	No	7	73	7	7	2
		%	7.292	76.04	7.292	7.292	2.08
CHICK	MALE	No	2	56	28	57	3
		%	1.37	38.36	19.18	39.04	2.06
	FEMALE	No	6	55	16	42	4
		%	4.88	44.72	13.01	34.15	3.25
<u>1984</u>							
NO-EGG	MALE	No	3	41	65	73	4
		%	1.61	22.04	34.95	39.25	2.15
	FEMALE	No	3	19	10	4	3
		%	7.69	48.72	25.64	10.26	7.69
PRE-EGG	MALE	No	3	49	46	42	9
		%	2.01	32.89	30.87	28.19	6.04
	FEMALE	No	1	26	17	7	2
		%	1.89	49.06	32.08	13.21	3.77
EGG	MALE	No	8	148	26	33	1
		%	3.70	68.52	12.04	15.28	0.46
	FEMALE	No	7	114	5	5	0
		%	5.34	87.02	3.82	3.82	0.00
CHICK	MALE	No	2	14	0	11	0
		%	7.41	51.85	0.00	40.74	0.00
	FEMALE	No	4	22	3	5	1
		%	11.43	62.86	8.57	14.29	2.86

APPENDIX 30 NUMBERS OF DIFFERENT INTENSITIES OF REACTIONS RECORDED BY  
BROODING AND NON-BROODING PARENTS DURING THE EGG AND CHICK  
STAGES

			INTENSITY OF REACTION TOWARDS INTRUDER				
SEX OF TERR. HOLDER			1	2	3	4	5
<u>1983</u>							
BROODING	EGG	No	12	189	6	7	2
		%	5.56	87.50	2.78	3.24	0.93
	CHICK	No	2	46	5	5	0
		%	3.45	79.31	8.62	8.62	0.00
NOT BROODING	EGG	No	1	18	15	18	4
		%	1.79	32.14	26.79	32.14	7.14
	CHICK	No	6	66	31	98	7
		%	2.89	31.73	14.90	47.12	3.36
<u>1984</u>							
BROODING	EGG	No	16	281	14	19	0
		%	4.85	85.15	4.24	5.76	0.00
	CHICK	No	3	36	0	4	1
		%	6.82	81.82	0.00	9.09	2.27
NOT BROODING	EGG	No	1	21	20	24	1
		%	1.49	31.34	29.85	35.82	1.49
	CHICK	No	3	5	3	12	0
		%	13.04	21.74	13.04	52.17	0.00



APPENDIX 31 MEAN WEIGHT GAIN OF CHICKS DURING THEIR FIRST THREE DAYS OF LIFE

CHICK	MEAN	STANDARD ERROR	NO OF OBS
1	21.60	0.76	15
2 <sub>1</sub>	25.80	1.60	10
2 <sub>2</sub>	22.09	2.01	11
3 <sub>1</sub>	24.50	1.69	8
3 <sub>2</sub>	22.25	1.33	8
3 <sub>3</sub>	15.29	1.13	7

APPENDIX 32 MEAN NO OF FEEDS GIVEN PER HOUR TO DIFFERENT SIZED BROODS

BROOD SIZE	MEAN	STANDARD ERROR	NO OF OBS
1	1.06	0.08	116
2	1.39	0.15	65
3	1.87	0.26	17

APPENDIX 33 MEAN NO OF FEEDS GIVEN PER HOUR PER CHICK TO DIFFERENT SIZED BROODS

BROOD SIZE	MEAN	STANDARD ERROR	NO OF OBS
1	1.06	0.08	116
2	0.69	0.07	65
3	0.62	0.09	17

APPENDIX 34 NO OF FEEDS GIVEN BY MALE AND FEMALE PARENTS

SEX OF PARENT	NO OF FEEDS NO %	
MALE	164	50.93
FEMALE	158	49.07

APPENDIX 35 NO OF FEEDS GIVEN BY DIFFERENT SEXES OF PARENTS TO  
DIFFERENT SIZED BROODS

SEX OF PARENT	1		BROOD SIZE 2		3	
	NO	%	NO	%	NO	%
MALE	93	53.45	54	48.65	17	45.95
FEMALE	81	46.55	57	51.35	20	54.05

APPENDIX 36 NO OF TIMES CHICKS FROM DIFFERENT SIZED BROODS WERE NOT FED  
WHEN THEY BEGGED

	1		BROOD SIZE 2		3	
	NO	%	NO	%	NO	%
NOT FED	28	11.97	36	20.57	11	16.92
FED	206	88.03	139	79.43	54	83.08

APPENDIX 37 ' NO OF TIMES CHICKS FROM DIFFERENT AGE GROUPS WERE NOT FED  
WHEN THEY BEGGED

AGE OF CHICKS	1-5		6-10		11-15		16-20		21-30	
	NO	%	NO	%	NO	%	NO	%	NO	%
NOT FED	12	8.76	21	21.65	18	31.58	10	22.73	14	29.17
FED	125	91.24	76	78.35	39	68.42	34	77.27	34	70.83

APPENDIX 38 NO OF TIMES CHICKS FROM DIFFERENT SIZED BROODS WERE FED WHEN THEY DID NOT BEG

NO OF CHICKS	1		2		3	
	NO	%	NO	%	NO	%
DID NOT BEG	20	17.86	16	21.92	9	26.47
BEGGED	112	82.14	73	78.08	34	73.53

APPENDIX 39 NO OF TIMES DIFFERENT AGED CHICKS WERE FED WHEN THEY DID NOT BEG

AGE OF CHICKS	NO BEGGING FEEDS		BEGGING FEEDS	
	NO	%	NO	%
1	6	60.00	4	40.00
2	6	35.29	9	64.71
3	10	32.26	21	67.74
4	7	35.00	13	65.00
5	3	18.75	13	81.25
6	5	27.78	13	72.22
7	2	20.00	8	80.00
8	1	14.29	6	85.71
9	1	20.00	4	80.00
10	0	0.00	7	100.00

APPENDIX 40 MEAN BEG TO FEED TIME FOR DIFFERENT SIZED BROODS

BROOD SIZE	MEAN	STANDARD ERROR	NO OF OBS
1	14.84	1.65	112
2	20.50	2.97	73
3	11.47	2.20	34

APPENDIX 41 MEAN BEG TO FEED TIME FOR DIFFERENT AGE GROUPS OF CHICKS

AGE OF CHICKS	MEAN	STANDARD ERROR	NO OF OBS
1-5	9.47	1.46	94
6-10	14.28	2.36	47
11-15	19.64	3.79	25
16-20	27.20	3.52	25
21-30	29.76	5.64	25

APPENDIX 42 MEAN BEG TO FEED TIME FOR DIFFERENT SIZED BROODS FED BY  
DIFFERENT SEXES OF PARENTS

BROOD SIZE	SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
1	MALE	12.98	2.00	53
	FEMALE	17.35	2.80	40
2	MALE	18.15	3.04	26
	FEMALE	26.64	5.95	28
3	MALE	17.90	4.15	10
	FEMALE	19.38	5.53	8

APPENDIX 43 MEAN BEG TO FEED TIME FOR DIFFERENT AGE GROUPS OF CHICKS  
FED BY DIFFERENT SEXES OF PARENTS

BROOD SIZE	SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
1-5	MALE	14.00	1.73	30
	FEMALE	8.80	4.26	27
6-10	MALE	12.71	3.03	24
	FEMALE	20.07	5.54	14
11-20	MALE	21.21	3.08	28
	FEMALE	21.00	2.88	20
21-30	MALE	23.00	5.16	8
	FEMALE	36.43	9.34	14

APPENDIX 44 MEAN NO OF TIMES FOOD WAS REGURGITATED PER FEED FOR  
DIFFERENT SIZED BROODS

BROOD SIZE	MEAN	STANDARD ERROR	NO OF OBS
1	1.31	0.05	137
2	1.44	0.08	75
3	1.27	0.14	33

APPENDIX 45 MEAN NO OF TIMES FOOD WAS HELD PER FEED FOR DIFFERENT SIZED  
BROODS

BROOD SIZE	MEAN	STANDARD ERROR	NO OF OBS
1	2.42	0.26	137
2	2.01	0.35	75
3	2.12	0.38	33

APPENDIX 46 MEAN NO OF TIMES FOOD WAS REGURGITATED PER FEED FOR  
DIFFERENT AGE GROUPS OF CHICKS

AGE OF CHICKS	MEAN	STANDARD ERROR	NO OF OBS
1-5	1.23	0.06	104
6-10	1.31	0.08	59
11-20	1.50	0.09	56
21-30	1.54	0.14	26

APPENDIX 47 MEAN NO OF TIMES FOOD WAS HELD PER FEED FOR DIFFERENT AGE GROUPS OF CHICKS

BROOD SIZE	MEAN	STANDARD ERROR	NO OF OBS
1-5	3.19	0.32	104
6-10	2.39	0.37	59
11-20	1.14	0.25	56
21-30	0.58	0.28	26

APPENDIX 48 MEAN NO OF TIMES FOOD WAS REGURGITATED PER FEED BY MALE AND FEMALE PARENTS

SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
MALE	1.31	0.05	104
FEMALE	1.50	0.09	86

APPENDIX 49 MEAN NO OF TIMES FOOD WAS HELD PER FEED BY MALE AND FEMALE PARENTS

SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
MALE	2.07	0.24	104
FEMALE	2.43	0.36	86

APPENDIX 50 MEAN NO OF TIMES FOOD WAS REGURGITATED PER FEED BY  
DIFFERENT SEXES OF PARENTS FOR DIFFERENT SIZED BROODS

BROOD SIZE	SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
1	MALE	1.25	0.07	63
	FEMALE	1.44	0.10	50
2	MALE	1.40	0.10	30
	FEMALE	1.52	0.14	31
3	MALE	1.30	0.15	10
	FEMALE	1.75	0.53	8

APPENDIX 51 MEAN NO OF TIMES FOOD WAS HELD PER FEED BY DIFFERENT SEXES  
OF PARENTS FOR DIFFERENT SIZED BROODS

BROOD SIZE	SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
1	MALE	2.18	0.30	63
	FEMALE	2.38	0.46	50
2	MALE	1.57	0.44	30
	FEMALE	2.42	0.69	31
3	MALE	2.70	0.78	10
	FEMALE	2.38	0.46	8



APPENDIX 52 MEAN NO OF TIMES FOOD WAS REGURGITATED PER FEED BY  
DIFFERENT SEXES OF PARENTS FOR DIFFERENT AGE GROUPS OF  
CHICKS

AGE OF CHICKS	SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
1-5	MALE	1.17	0.08	36
	FEMALE	1.43	0.17	30
6-10	MALE	1.28	0.11	29
	FEMALE	1.33	0.14	21
11-20	MALE	1.41	0.09	29
	FEMALE	1.68	0.19	22
21-30	MALE	1.60	0.22	10
	FEMALE	1.62	0.21	13

APPENDIX 53 MEAN NO OF TIMES FOOD WAS HELD PER FEED BY DIFFERENT SEXES  
OF PARENTS FOR DIFFERENT AGE GROUPS OF CHICKS

AGE OF CHICKS	SEX OF PARENT	MEAN	STANDARD ERROR	NO OF OBS
1-5	MALE	2.69	0.41	36
	FEMALE	3.87	0.68	30
6-10	MALE	2.17	0.40	29
	FEMALE	3.43	0.86	21
11-20	MALE	1.31	0.36	29
	FEMALE	0.91	0.32	22
21-30	MALE	0.80	0.42	10
	FEMALE	0.08	0.08	13