

THIRD-EGG NEGLECT IN THE HERRING GULL (LARUS ARGENTATUS)

by

SANDRA COLLEEN LEE

A thesis
presented to the University of Manitoba
in fulfillment of the
thesis requirement for the degree of
MASTER OF SCIENCE
in
DEPARTMENT OF ZOOLOGY

Winnipeg, Manitoba

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(LARUS ARGENTATUS)

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SANDRA COLLEEN LEE

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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MASTER OF SCIENCE

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ABSTRACT

The extent, timing, and consequences of third-egg neglect in the herring gull (Larus argentatus) were studied at a colony on Kent Island, in the Bay of Fundy, New Brunswick during the summers of 1986 and 1987.

Herring gulls lay 3 eggs (a-, b-, and c-) that hatch asynchronously. The amount of time the parents spent off the nest was low during incubation and pipping of the a-egg. After the a-chick hatched neglect increased, reaching a peak just before the c-chick hatched. This was evidenced by a decline in the mean, and an increase in the variability of pipped egg temperature as hatching progressed. There was also a decrease in duration of sitting spells by the parent, and percent complete settlings (a measure of how well the eggs are fit to the brood patch), and an increase in number of rising and resettling movements parents made/hour over the course of the hatching period. As a result, the c-egg was exposed to a more variable environment just prior to hatching (including temperature, movement of the egg, light, and also probably sound and gaseous conditions) than that experienced by the b-, and especially the a-egg during hatching.

Experimental manipulations in which c-eggs were hatched under more constant conditions than c-eggs are normally exposed to (similar to those during the hatch of the a-, or b-egg) showed the following: neglect normally experienced by c-eggs caused a significant increase in hatch synchrony and a subsequent increase in growth rates of c-chicks when compared with experimental, non-neglected c-chicks.

A high rate of survival of c-chicks and full broods occurred on Kent Island in the 1987 field season. This finding directly contradicts the conclusions reached by Graves et al. (1984) and Hebert and Barclay (1986) that the third chick functions primarily as insurance, rarely surviving unless one of its siblings fails to hatch or dies in the early post-hatch period.

The principal conclusions are that, while neglect of the c-egg is substantial during the last days before it hatches, this neglect does not significantly disadvantage the c-egg/chick in any way tested. Contrary to expectations published in the literature, neglect appears to reduce the competitive asymmetry within broods, and so may lower the probability that the c-chick will die before fledging as a result of the brood reduction process.

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Chapter I
GENERAL INTRODUCTION

The herring gull (Larus argentatus), like most gull species (Larinae), normally lays a clutch of three eggs. The third, or c-egg is smaller and hatches one to four days after its siblings (e.g. Paynter 1949, Paludan 1951, Parsons 1970, MacRoberts and MacRoberts 1972, Hebert and Barclay 1988). This c-chick commonly suffers disproportionately high mortality relative to its older siblings during the first week post-hatch (Paynter 1949, Paludan 1951, Kadlec et al. 1969, Parsons 1970, Haycock and Threlfall 1975, but see Harris 1964). Both the laying of a smaller third egg and hatch asynchrony brought about by initiation of incubation prior to completion of laying are known to be mechanisms by which parents facilitate brood reduction in this species (Parsons 1970, 1972, 1975, Graves et al. 1984, Hebert and Barclay 1986).

Recently, a third factor has been suggested as an additional mechanism that may lead to an increase in the competitive disadvantage of the c-chick and so facilitate brood reduction (Graves et al. 1984). Incubating herring gulls typically show a decline in attentiveness to eggs as hatch-

ing of the clutch proceeds (Drent 1970). This neglect of unhatched eggs has been postulated to lower hatchability and increase time to hatch of c-eggs (Paludan 1951, Beer 1962, 1966, Drent 1970, Haycock and Threlfall 1975). If neglected c-eggs hatch successfully but later than if not neglected, this would be expected to lead to an increase in competitive asymmetry within broods, and so hasten the brood reduction process.

However, the extent and timing of egg neglect by parents and its effects on the eggs/chicks that are subjected to it have not yet been documented. The first objective of this study was to establish the extent and timing of incubational irregularities and egg neglect during the hatching period in the herring gull, and to determine the importance, if any, of clutch size on the degree of neglect of the last-hatched egg. The second objective was to determine the effect of neglect on hatchability, hatch time, growth, and survival of the last-hatching chick during the early post-hatch period, in an effort to ascertain whether egg neglect plays a role in brood reduction in herring gulls. In addition, available data on survival of young from natural three-egg clutches were used to re-examine published conclusions of Graves et al. (1986) and Hebert and Barclay (1986) that the third chick rarely survives in this species, and functions primarily as insurance against loss of a- or b-eggs or chicks.

Chapter II

THIRD-EGG NEGLECT DURING HATCHING IN THE HERRING GULL

2.1 INTRODUCTION

Avian embryos are functionally poikilothermic organisms. They cannot maintain a constant body temperature, and rely on outside sources of heat for development to proceed. In most species, this heat is provided by direct contact with vascularized surfaces (abdomen or webs of feet) of the parent during incubation (Drent 1970).

Incubation attentiveness varies widely among species. Regular but short-term absences from the nest occur in many passerines (e.g. white-crowned sparrows Zonotrichia leucophrys, Zerba and Morton 1983; dusky flycatchers Empidonax oberholseri, Morton and Pereyra 1985) and Anatidae (e.g. mallards Anas platyrhynchos, McKinney 1952, Afton 1979). Longer-term neglect occurs in others, such as the Procellariiformes (e.g. fork-tailed storm-petrels Oceanodroma furcata, Boersma et al. 1980). In contrast, other species are characterized by parental attentiveness that has been shown to maintain a remarkably constant thermal environment in the nest throughout most of the incubation period, allowing

embryonic development to proceed with few or no delays (see Baldwin and Kendeigh 1932, Shilov 1973, and Webb 1987 for reviews).

In some species of birds the behaviour of the parent begins to change when the first egg pips, becoming more and more geared towards care of chicks, as opposed to incubating eggs, as hatch progresses (herring gulls, Drent 1970; black-headed gulls L. ridibundus, Beer 1961, Ytreberg 1956; lesser black-backed gulls L. fuscus, Paludan 1951; mallards, McKinney 1952; pied-billed grebes Podilymbus podiceps, Forbes and Ankney 1988; the black-tailed godwit Limosa limosa, Lind 1961 in Drent 1970; house wrens Troglodytes aedon, Kendeigh 1952; winter wrens T. troglodytes, Whitehouse and Armstrong 1953; the willow warbler Phylloscopus trochilus, Kuusisto 1941 in Drent 1970; the common raven Corvus corax, Gwinner 1965 in Drent 1970; and some calidrine sandpipers, Norton 1972). Attentiveness to the eggs wanes and patterns of incubation become increasingly irregular. Beer (1962), Drent (1970), Haycock and Threlfall (1975), Graves et al. (1984) and Forbes and Ankney (1988) have suggested that inefficient incubation and egg neglect during this transition period may affect the viability of last-hatching eggs of some gulls and water birds. Graves et al. (1984) further suggest that, in herring gulls, this egg neglect is a mechanism by which parents facilitate brood reduction. Failure to hatch and increased hatching asynchrony (with subsequent

competitive disadvantage or abandonment of late-hatching offspring) due to suboptimal incubation temperatures have been cited as probable consequences of disruption of incubation during this transition period (Paludan 1951, Beer 1962 1966, Drent 1970, and Haycock and Threlfall 1975).

Drent (1970) and Graves et al. (1984) use the word 'neglect' to describe irregular incubation of the last-hatching egg by herring gull parents, evidently assuming that such behaviour is detrimental to the embryo. However, only anecdotal evidence supports the hypothesis that the parental response has a negative impact. Until the consequences of this behaviour are known, the possibility that this so-called neglect is actually of a benign nature cannot be ruled out. For want of a better word, I have continued to use the term 'neglect' but define it simply as 'reduced or non-incubation', with no preconceptions of a positive or negative influence on the embryo.

Although the occurrence of a decline in the average nest temperature and constancy of incubation behaviour after the onset of hatching has been documented (Drent 1970, Kendeigh 1952, McKinney 1952, Whitehouse and Armstrong 1953, Ytreberg 1956), details of the actual amount and timing of this decline have not. The objective of this study was to document the extent and timing of incubational irregularities and egg neglect during the hatching period in the herring gull, and to assess the role, if any of clutch size on neglect of the last-hatched egg.

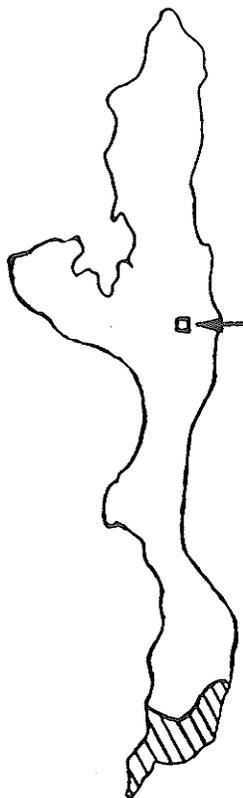
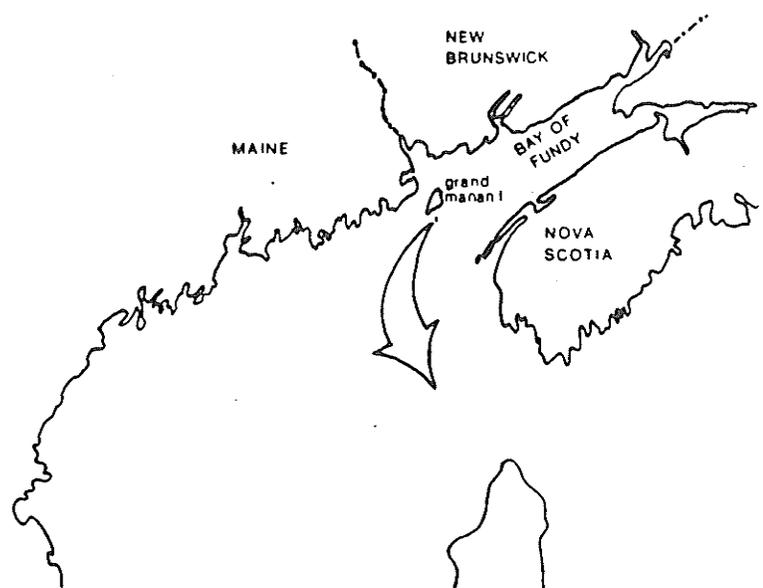
The herring gull was chosen as the study animal for this project for several reasons. This bird is very abundant along the coast and on large lakes and rivers in eastern North America (Robbins et al. 1966). It breeds in large, dense colonies, so large samples can be conveniently monitored within a small area (Strong 1914). Herring gulls typically lay three eggs that hatch asynchronously over a period of one to four days, during which time parental attentiveness deteriorates (Tinbergen 1953, Harris 1964, Drent 1970, Parsons 1970 and 1972, Haycock and Threlfall 1975). They also have the advantage of having been studied extensively so that a large literature base is available (see Baerends et al. 1970, Drent 1970 and ref. therein), including work done at the same colony as was used in this study (Hebert 1985 1987, Hebert and Barclay 1986 1988, Knudsen 1987). In particular, herring gull incubation behaviour, next to that of the domestic chicken, has been one of the most intensely studied of any avian species and so provides an excellent starting point for this study.

2.2 METHODS

Field work was carried out at a herring gull colony located on Kent Island (44° 35' N, 66° 45' W), the southern-most island of the Grand Manan archipelago, New Brunswick, in the mouth of the Bay of Fundy. Kent Island covers an area of about 75 ha, the southern half of which is treeless and provides nesting sites for a large proportion of the island's population of nesting herring gulls. The largest concentration of these birds is found on the two small hills and the intervening gully that make up approximately the southern-most 10% of the island. About 1000 of the nesting pairs had territories in this area during the breeding seasons of 1986 and 1987. It was this most concentrated part of the colony that was used as the study area for this project (see Fig. 1).

The major plant species on the study area were blue aster (Aster foliaceus), common ragweed (Ambrosia artemisiifolia), and red raspberry (Rubus idaeus) (McCain 1975). Other birds seen breeding on the study area included great black-backed gulls (Larus marinus), black guillemots (Cepphus grylle), common eiders (Somateria mollissima), and savannah sparrows (Passerculus sandwichensis). Muskrat (Ondatra zebethica) and snowshoe hare (Lepus americanus) also occurred on the study area.

Figure 1: Map of Kent Island, New Brunswick showing the study area (hatched) at the south end.



□ buildings

KENT ISLAND

300 m

The study area was censused once daily during egg laying from 20 May to 17 June 1986 and from 18 May to 19 June 1987. Excessively cold and wet conditions precluded censuses on four days in 1986 and two days in 1987. Each new nest with eggs was marked individually with a numbered wooden stake, and its approximate location relative to prominent landmarks determined. This enabled us to locate specific nests later with minimal searching.

Eggs were individually marked according to their laying order (first-laid egg = a-, second = b-, and third = c-) with a permanent felt-tip marker. Eggs were checked at approximately 10-day intervals throughout the incubation period and fading marks were replaced. In this way, laying dates were known and estimates could be made of expected hatching dates based on average hatch times for each egg (Drent 1970). Except where otherwise stated, all work was done using nests with natural three-egg clutches.

2.2.1 Behaviour

To document changes during the transition from incubation to care of chicks, parental behaviour at the nest was recorded throughout the incubation and hatching periods (mid-May to late July) in 1986. Observations were made from portable canvas blinds, and also from three semi-portable wooden blinds.

In most cases the arrival of the observer caused incubating gulls in the immediate vicinity to flush from their nests. Observations began when the returning bird of interest re-entered the nest. When the intended subject did not flush, as may occur in the very late stages of incubation, observations began when the alarm in the area had died down (when alarm calls and alarm posturing ceased).

One focal nest was observed during each 1-hr sampling period. This sampling method provides a maximum amount of data on a single individual, allowing a very detailed analysis of behaviour (Altmann 1974).

Data recorded included nest number, date, and time, as well as all parental behaviours while the attending parent was on the nest. Parental behaviours included time spent off the nest, duration of sitting spells, occurrence and timing of rising and resettling, whether settlings were 'complete' (if they contained quivering, Beer 1961), number of egg-shifts, nest reliefs, and feedings on the nest. In 1987, all feedings and chick begging off the nest were also recorded.

When calculating duration of sitting spells, only those spells that began and ended within the 1-h sampling period were used. As a result, long sitting spells are not included, and therefore the estimate of the median length of sitting spells does not represent the true median. This may

affect comparisons between different stages of pipping since sitting spells are expected to shorten as hatching progresses (Beer 1962, Drent 1970). Differences between stages will therefore be more difficult to show statistically.

In 1986, calls of embryos at focal nests were recorded with a small microphone buried under the nest, connected by a long lead to a Sony reel-to-reel tape recorder in the blind. Once the a-chick hatched, this method was no longer useful in recording calls from embryos since some types of chick calls were indistinguishable from embryonic calls. As a result, embryo vocalizations were only recorded during the pipping of the a-egg.

In 1986, 54 nests were observed over the first 25-26 days of incubation (full incubation period = 27 to 30 days from laying to hatching of the a-egg, Drent 1970). These nests were observed an average of 2.3 times each over this period for a total of 124 hours of observation. Baerends et al. (1970) stated that the intra-individual variability in incubation behaviour on different days is just as great as the variability between individuals. For this reason, they felt that multiple observations on a single nest could be used without invalidating the independence assumption necessary for most statistical analyses as long as the observations occurred several days apart.

Partial nest predation was high on Kent Island in 1986 relative to the 1987 season, particularly early in incubation, and the number of usable nests with complete clutches was limited. Because of this I decided that repeated observation of nests and the larger sample size allowed by this was the best option. A one-way ANOVA (SAS GLM) on the ranked data from these 124 observation periods showed that there was no difference between nests, or, in other words, the variability within a nest on different days was at least as great as the variability between nests. Based on this test it appeared that the assumption of independence of observations on the same nest on different days was valid for data collected.

In addition to these 124 h of observation in the first 25-26 days of incubation, 24 nests where no eggs were hatched but the a-egg was pipping were observed for one hour each (Table 1). Thirteen nests where the a-egg was hatched and the b-egg was pipping, and 14 nests where the a- and b-eggs were hatched and the c-egg was pipping were also observed for one hour each. For convenience, these three periods will be referred to as the a-pip, b-pip, and c-pip stages, respectively.

In 1987, observations were not made prior to pipping. Parental behaviour during pipping of each egg was recorded at 12 a-pip nests, 15 b-pip nests, and 20 c-pip nests (Table 1). Samples taken at a- and b-pip nests were of 1-h dura-

TABLE 1

Schedule showing the number of observation periods at herring gull nests during the two seasons of study.

| stage | sample size | |
|----------------|-------------|-----------------------|
| | 1986 | 1987 |
| prior to a-pip | 124 | |
| a-pip | 24 | 12 |
| b-pip | 13 | 15 |
| c-pip | 14 | 20 (b-chick 24 h old) |
| | | 4 (b-chick 12 h old) |
| | | 5 (b-chick 48 h old) |

tion, as before. To obtain more information on chick feeding and other potential proximate causes of the decline in parental incubation responses during the c-pip stage, samples taken at this time were extended to 2-h duration and were taken when the b-chick was approximately one day old. When various measures were compared between stages, hourly rates were used.

To determine the effect of increasing time since the b-chick hatched on the level of incubational disruption of the c-egg, additional 2-h observations were made at four c-pip nests where the b-chick was 12 hours old, and on five nests where the b-chick was approximately two days old or older. These data were compared with those recorded when the b-chick was about one day old (described above).

2.2.2 Egg Temperature

Pipped egg temperatures ($^{\circ}\text{C}$) were determined with a Yellow Springs Instruments Thermistemp model 46TUC temperature meter. The tip of the small (YSI probe size 402) flexible thermistor probe was inserted about two cm into the pip hole so that it was surrounded by body parts of the embryo and not touching the inside of the shell where it could be cooled much quicker and would be less likely to record embryonic body temperature (T_e) within the egg. The probe

was secured to the outside of the egg with tape and attached to the meter in the blind by an extension cable. Temperatures were recorded every 10 minutes for one h at each nest. Temperatures of 43 pipped eggs, 14 or 15 at each stage (a-, b-, and c-pip) were recorded over the two years of the study.

2.2.3 Obligate vs Facultative Neglect

To determine whether the same degree of neglect of the c-egg occurs when one egg has been lost as when the complete clutch is retained, T_e from a-b-c- (complete clutches) and a-c- nests (previously 3-egg clutches but with the b-egg removed) as well as ambient temperature (T_a) were measured every 15 min, 24 hours a day throughout hatching in 1987. Temperatures for each nest examined were recorded to the nearest 0.2 °C on a digitized temperature data logger (Model SQ-2, Grant Instruments, Cambridge, England). Because of the fragility of the egg shell of pipped eggs, c-eggs were removed and replaced with more durable dummy eggs implanted with thermistors.

Dummy eggs were constructed by emptying the contents and drying the shells of real eggs, then applying a thin layer of fibreglass inside to provide strength and to act as a vapor barrier (Evans, in press). A thermistor was then imp-

lanted and carefully positioned at the center of the egg. The egg was filled with a 1.5g/100ml solution of agar (Van Sheik 1985), and the cap glued back on. The agar concentration of the filling was such that it very closely mimicked the response of a real egg to changing temperature (Evans, in press). Temperatures recorded by these dummy eggs are lower than real pipped egg temperatures, since by mid-incubation, the embryo is producing heat itself (Drent 1970). However, this does not affect comparisons of two- and three-egg nests where dummy eggs are used in both, since recorded temperature is a measure of parental time spent incubating the eggs in both treatments.

Mean temperatures for the period between the hatch of the a-egg and the expected hatch of the c-egg (for a-c- nests n=7, for a-b-c- nests n=3), and between the hatch of the b-egg (or expected hatch in a-c- nests) and expected hatch of the c-egg (for a-c- nests n=7, for a-b-c- nests n=5) were compared between a-c- and a-b-c- nests. Since time was limited and all types of egg combinations could not be examined, a-c- as opposed to b-c- nests were chosen here. There is a longer interval between the hatch of the a- and c-chicks than between the hatch of b- and c-chicks (mean a- to c- hatch interval in 1987 = 3.0 ± 1.0 (S.D.) days, mean b- to c- hatch interval = 2.1 ± 0.6 days, n=29). I reasoned that if parents were still going to incubate the c-egg less after loss of a prior egg, they would be more likely to do

so in a-c- nests where they would have to continue incubation longer after the first egg hatched than in b-c- nests. Examination of a-c- nests was therefore expected to be the most conservative test of the hypothesis that parents neglect the c-egg more in complete clutches than in incomplete ones.

2.2.4 Data Analysis

I have used parametric tests where possible. However, some of the data were non-normal, and in much of it variances were not homogeneous among groups. In these cases, where a transformation would not stabilize variances, non-parametric tests were used. Where sample distributions appeared to be highly skewed, I reported median values (\pm S.E.median) as opposed to means (\pm S.D) (Zar 1974). An alpha level of 0.05 was used throughout. I have followed Zar (1974) and Daniel (1978) in my use of various statistical tests.

2.3 RESULTS

2.3.1 Behaviour

In 1986 the amount of time the parents left the nest uncovered (Fig. 2) was low during the first 25-26 days of incubation and during the a-pip stage, but increased significantly in the b-pip stage, after the a-chick had hatched (SAS GLM one-way ANOVA on log-transformed data, $P=0.0001$, with Tukey's multiple comparison $P<0.05$). There was a further non-significant increase in neglect during the c-pip stage, after the b-chick hatched. In 1987, differences were in the same direction as in 1986 and were significantly different during the pipping of each egg (Fig. 2, a- vs b- vs c-, Kruskal-Wallis ANOVA on ranked data, $P<0.0001$; Mann-Whitney U-test, a- vs b- $P=0.0189$, a- vs c- $P<0.0001$, and b- vs c- $P=0.0024$). There was no difference between years in amount of time/hour the parents spent off the nest during the stages of hatch (Mann-Whitney U test, $P=0.2168$). For both years combined, there was a significant difference in time off the nest during each pip stage (Kruskal-Wallis ANOVA on ranked data, a- vs b- vs c-, $P<0.0001$; Mann-Whitney U-test, a- vs b- $P=0.0125$, a- vs c- $P<0.0001$, b- vs c- $P=0.0009$).

During the c-pip stage, there was a non-significant trend for the amount of time parents spent off the nest to

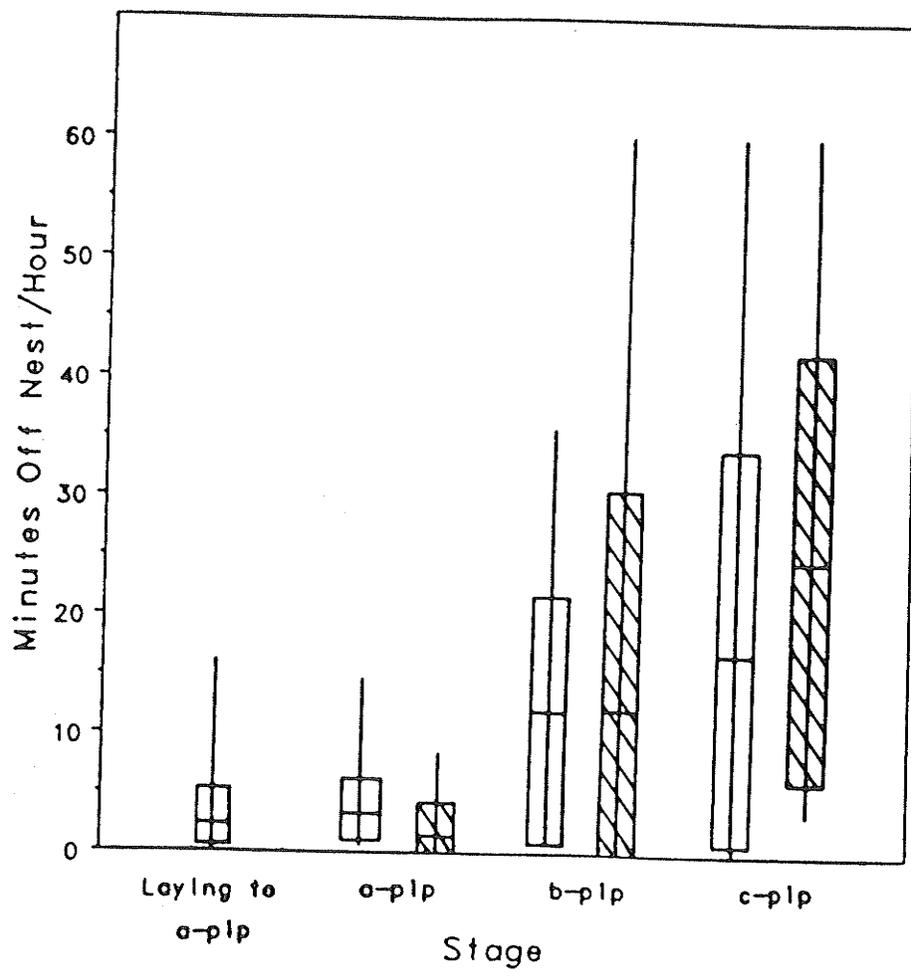
increase with time after the b-chick hatched (Kruskal-Wallis ANOVA $P=0.0990$). Parents left the c-egg uncovered an average of 10.7 min/h (± 5.0 S.D., $N=4$) at 12 h, 39.3 min/h (± 29.2 , $N=20$) at 24 h, and 43.8 min/h (± 40.8 , $N=5$) at 48 h after the b-chick hatched.

Feedings of young away from the nest contributed substantially to the time parents spent off the nest during the c-pip stage. Twenty 2-h observation periods in 1987 at nests where b- was approximately one day old, yielded 77 feedings, with a mean of 1.9 ± 1.4 (S.D.) feedings/hour/nest. Forty-three percent of these feedings were performed away from the nest. The parent clearly led the chick(s) in 77% of the feedings that occurred away from the nest.

Besides time spent feeding chicks, parents also spent relatively large amounts of time off the nest standing or sitting nearby during the c-pip stage (when the b-chick was one day old). Preening sometimes also occurred at this time. An average of $25\% \pm 29\%$ (S.D. $n=20$) of the time the attending parent was off the nest was spent in these activities.

Results of the other parental behaviour measures recorded are given in Table 2. The duration of sitting spells declined significantly as hatching progressed in both years (Table 2a, Kruskal-Wallis one-way ANOVA on ranked data, a- vs b- vs c-, 1986 $P<0.0001$, 1987 $P=0.0234$, combined years

Figure 2: Incubational neglect of herring gull eggs before pipping and during the a-, b-, and c-pip stages. Shown are means (horizontal lines) \pm S.D. (bars), and ranges (vertical lines). Open bars indicate data from 1986, and hatched bars from 1987.



$P < 0.0001$, no significant difference between years $P = 0.1426$). The number of times the incubating parent rose and resettled on the eggs (Table 2b) increased over hatching but the change was significant only for 1986 and for both years combined (a- vs b- vs c-, 1986 $P = 0.0005$, 1987 $P = 0.1532$, combined years $P = 0.0001$). There was also no significant difference between years ($P = 0.2911$) for this variable. The percent of settling sequences that were complete (Table 2c, an indication of how well parents fit the eggs to their brood patches) declined significantly over hatching in both years (a- vs b- vs c-, 1986 $P < 0.0001$, 1987 $P = 0.0003$). There was a significant difference between years ($P = 0.0001$), so tests were not done on data from both years combined. The values for 1987 appear to be lower and to drop off more rapidly than those for 1986. Number of egg-shifts (Table 2d) declined significantly over hatching but this difference was only significant in 1986 and for data from both years combined (a- vs b- vs c-, 1986 $P = 0.0372$, 1987 $P = 0.1728$, combined years $P = 0.0017$). There was no difference between years in number of egg-shifts/h ($P = 0.1964$).

Calls by pipped a-eggs ranged from 1 to 349 calls/h (median = 67.00 ± 23.38 S.E.). There was a significant positive correlation between number of calls/h from embryos and number of egg-shifts/h by the parent (Kendall's tau Rank Correlation, $\tau = 0.3357$ $P < 0.05$). Correlations between calls and other variables were not statistically signifi-

Table 2. Parental behaviours (median minutes±S.E. of the median) during the hatching period for 1986, 1987, and both years combined.

| Variable | Stage | 1986 | 1987 | Combined years |
|-------------------------------------|-------|---------------------------|---------------------------|--------------------------|
| a. Duration of sitting spells (min) | a-pip | 11.00±3.95 ¹ | 9.50±3.32 ¹ | 11.00±2.51 ¹² |
| | b-pip | 5.90±1.76 ¹ | 5.70±2.22 | 5.85±1.36 ¹ |
| | c-pip | 3.05±0.81 ¹ | 4.40±0.78 ¹ | 3.70±0.40 ² |
| b. Number of settlings/h | a-pip | 3.00±0.58 ¹ | 3.75±0.89 | 3.00±0.58 ¹² |
| | b-pip | 5.00±0.87 ¹ | 5.00±1.15 | 5.00±0.87 ¹ |
| | c-pip | 10.00±2.60 ¹ | 5.00±1.01 | 6.25±0.87 ² |
| c. Percent complete settlings | a-pip | 75.00±10.97 ¹² | 53.00±23.09 ¹² | - ³ |
| | b-pip | 7.00± 7.79 ¹ | 0.00± 9.53 ¹ | - |
| | c-pip | 0.00± 2.89 ² | 0.00± 0.00 ² | - |
| d. Number of egg-shifts/h | a-pip | 1.00±0.58 ¹ | 1.00±0.87 | 1.00±0.58 ¹² |
| | b-pip | 0.00±0.29 | 0.00±0.29 | 0.00±0.0 ¹ |
| | c-pip | 0.00±0.00 ¹ | 0.00±0.14 | 0.00±0.0 ² |

¹²The same number beside two medians in one year and one variable indicates

a significant difference between the two stages (Mann-Whitney U-test P<0.05).

³Years significantly different (see text), hence not combined.

cant. The embryos seemed to call most when the eggs were moved.

2.3.2 Egg Temperature

With incubational neglect came a concomitant drop in egg temperature (T_e , Fig. 3). In 1986, T_e was significantly lower during the b- and c-pip stages than during the a-pip stage (a- vs b- vs c-, Kruskal Wallis one-way ANOVA, $P=0.0008$, Mann-Whitney U-test a- vs b- $P=0.0025$, a- vs c- $P=0.0014$). There was also a trend for T_e to be lower during the c-pip stage than during the b-pip stage, but this difference was not statistically significant (b- vs c- $P=0.1482$). Sample sizes for 1987 were small and statistical differences were not present (Fig. 3, Kruskal-Wallis one-way ANOVA, $P=0.0810$). Means tended to be slightly higher than in 1986, but differences between years were not significant ($P=0.2042$, Kruskal-Wallis one-way ANOVA). For both years combined, nest temperatures were different during each pip stage (a- vs b- vs c-, $P=0.0003$, a- vs b- $P=0.0444$, a- vs c- $P=0.0002$, b- vs c- $P=0.0082$). Variance in egg temperature was not homogeneous among groups (Levene's test $P=0.0021$). Greater variance while the c-egg was pipping reflected the frequent rising and resettling on the nest at that time, causing T_e to fluctuate much more widely than

previously. Mean T_a (ambient temperature, Fig. 4) was always lower than T_e , indicating that cooling of c-eggs could be directly related to reduced effectiveness of incubation at that time.

Figure 3: Herring gull pipped-egg temperatures during the a-, b-, and c-pip stages. Shown are means (horizontal lines) \pm S.D. (bars) and ranges (vertical lines). Open bars indicate data from 1986, and hatched bars from 1987.

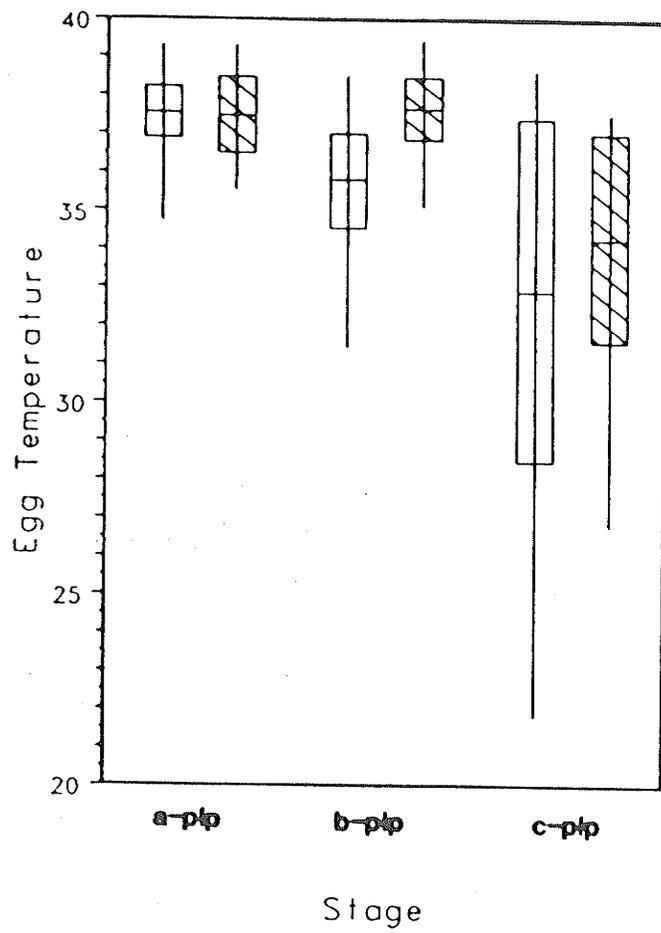
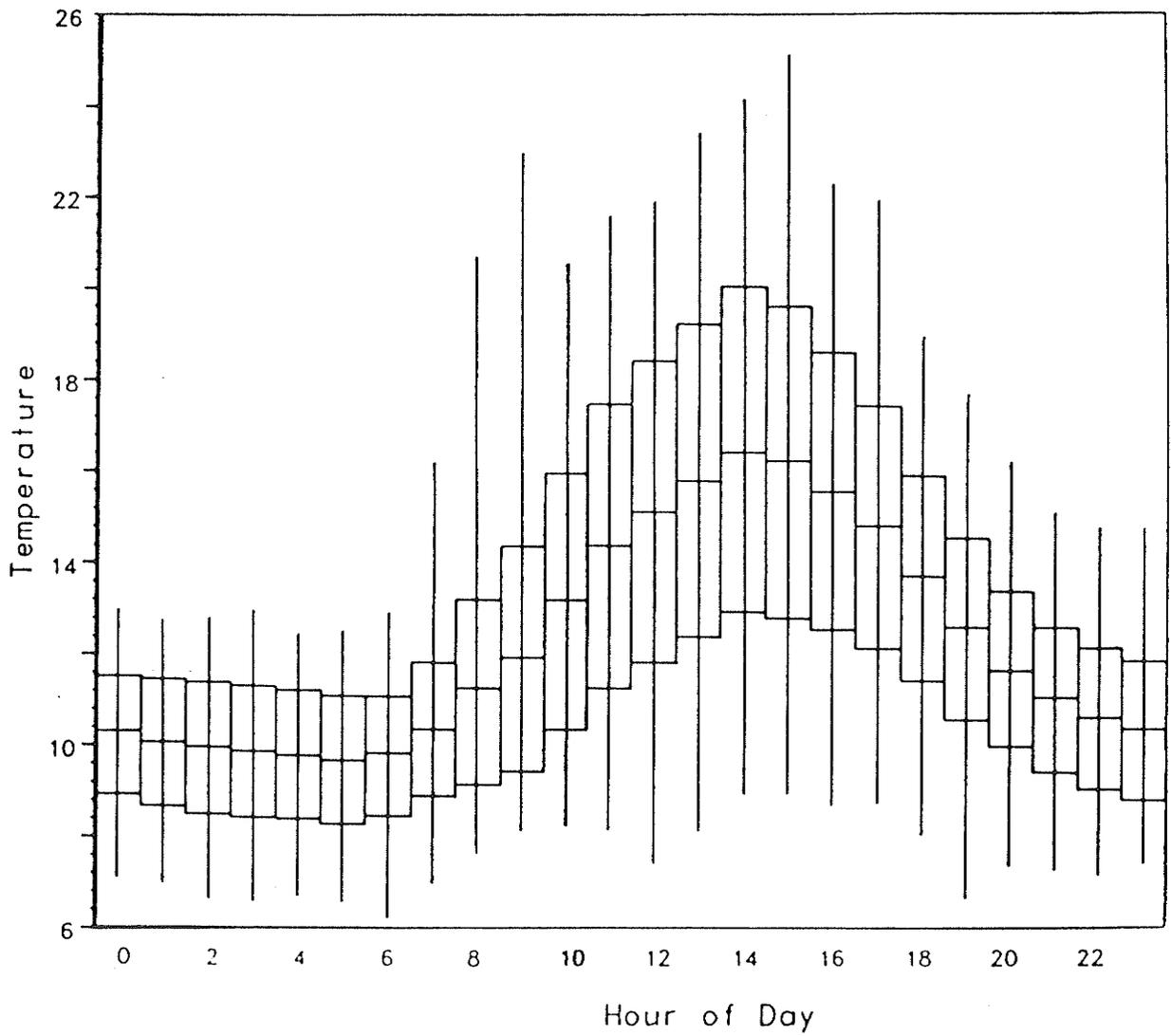


Figure 4: Mean hourly ambient temperature for all days from 29 May to 15 July 1987, on Kent Island. Shown are means (horizontal lines) \pm S.D. (bars) and ranges (vertical lines).

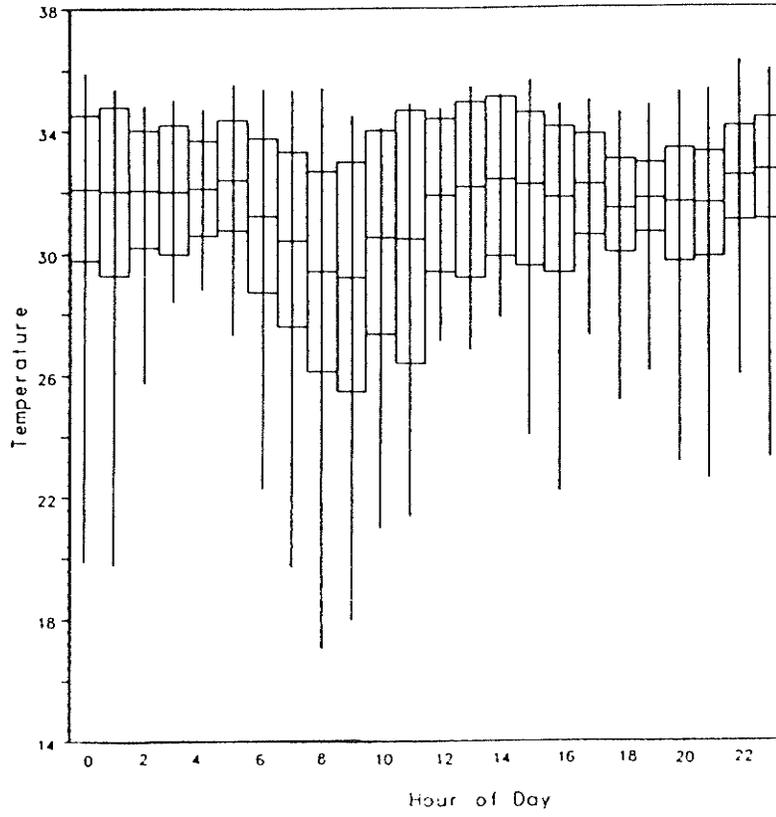


2.3.3 Obligate vs Facultative Neglect

Egg temperature data taken every 15 minutes 24 hours per day during hatching from a-c- and a-b-c- nests showed that a-c- nests had higher mean temperatures for the period between the hatch of the a-egg and the expected hatch of the c-egg (Fig. 5, Mann-Whitney U-test, $P=0.025$). A-c- nests also had higher mean temperatures for the period between hatch of the b-egg (or expected hatch of b- for a-c- nests) and the expected hatch of the c-egg (Fig. 6, Mann-Whitney U-test, $P=0.01$). Therefore the c-egg was neglected less when there was only one other (a-) chick in the nest than when both a- and b-chicks were present. At all nests monitored, there was a tendency for eggs to be cooler during the morning than at other times of the 24-h day, possibly reflecting a higher level of parental activity and incubational disruption at that time.

Figure 5: Hourly dummy egg temperature during the a- to c- hatch interval in a-b-c- nests (a), and in a-c- nest (b). Shown are means (horizontal lines)±S.D. (bars) and ranges (vertical lines).

a.



b.

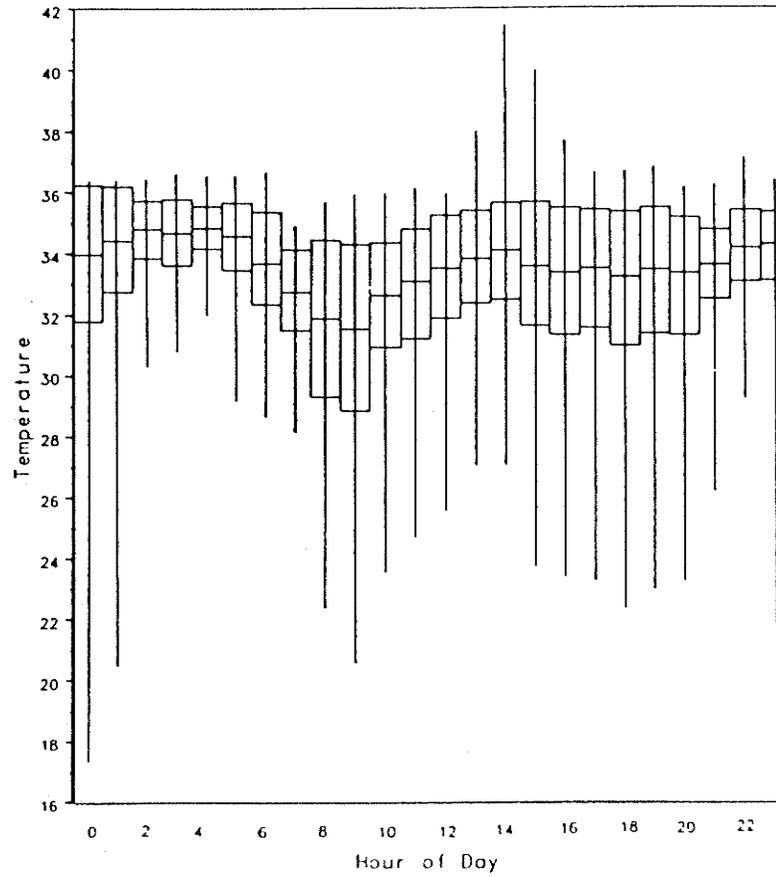
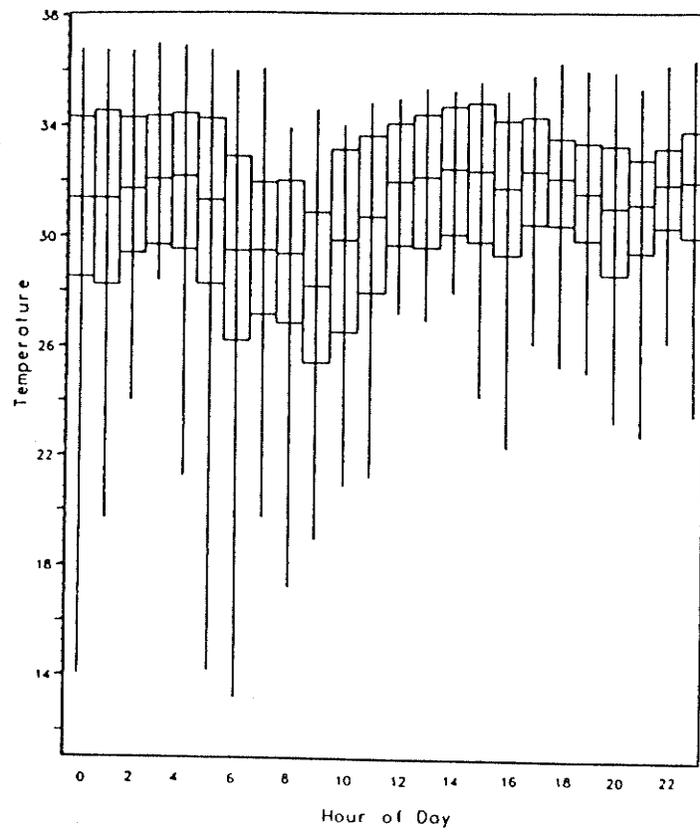
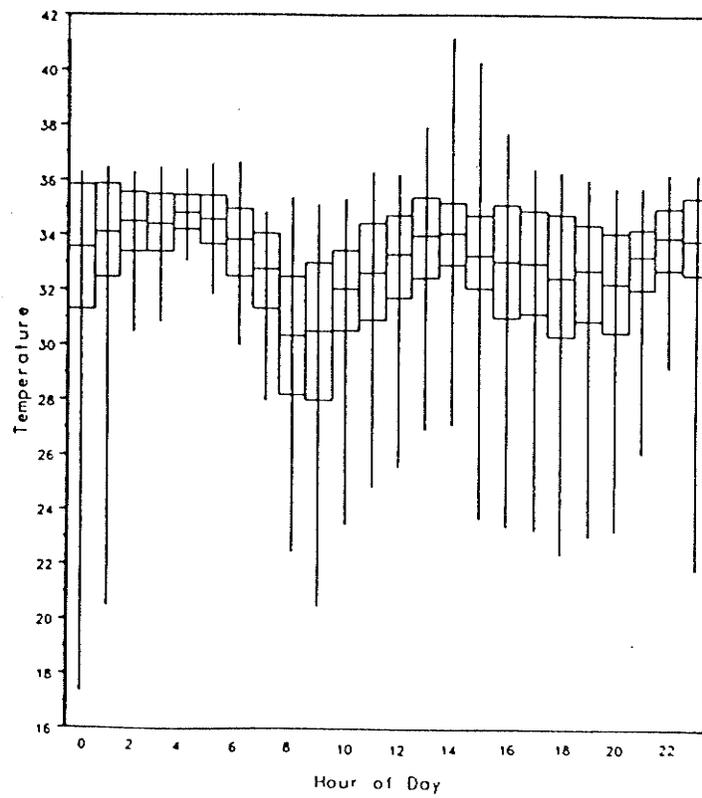


Figure 6: Hourly dummy egg temperature during the b- to c- hatch interval in a-b-c- nests (a), and in a-c- nests (b). Shown are means (horizontal lines) \pm S.D. (bars) and ranges (vertical lines).

a.



b.



2.4 DISCUSSION

In both years, substantially different conditions existed in the nest during the pipping of each egg. Parental incubation behaviour was relatively constant during the a-pip stage. Occurrences of rising and resettling on the eggs were infrequent at this time, resulting in the eggs being maintained at a relatively high and constant temperature. Movement of the eggs and changes in light intensity associated with rising and resettling would presumably also have been infrequent at that time.

Incubation during the b-pip stage was less constant. The parent was off the eggs for several minutes each hour, and as a result, egg temperature was lower and more variable than during the a-pip stage. Similarly, fluctuations in mechanical, and probably visual and auditory stimuli occurred more often during the b-pip stage.

After the b-egg hatched (c-pip stage), parental incubation became very irregular. The parent spent extended periods off the nest, leaving the c-egg uncovered. Mean egg temperature declined further and was even more variable than for the b-egg. Exposure to mechanical stimuli was probably not much different than for b-, but the pipping c-egg was exposed to lower ambient temperature for prolonged periods, and probably also to higher levels of light and sound. These changes tended to become more pronounced with time

after b- hatched. This effect of time after the b-egg hatched on incubational neglect of the c-egg was also found by Beer (1966) for black-headed gulls.

In general, similar results were obtained in both years of the study. Quantitative differences between years in percent complete settlings very likely stem from the fact that June and July, 1987, had higher average maxima, average minima and mean temperatures and a larger number of growing degree days than for the same period in 1986 (Table 3, R. Cunningham, unpublished report, 1987). As a result, egg cooling may have been less rapid and parents therefore less apt to sit tightly on their eggs in 1987. This seems a reasonable conclusion when one notes that parents tended to spend more time off the eggs during the hatching period, but still had slightly higher pipped egg temperatures in 1987 than in 1986 (Fig. 2 and 3).

Although there was a strong association between lower, more variable T_e and less intense incubation behaviour, other behaviours of the parent also appeared to be related causally to changes in T_e . In particular, the tendency for parents to feed the a- and b-chicks away from the nest undoubtedly contributed to the decrease in time spent incubating during the c-pip stage. Feeding off the nest (also in Ring-billed gulls, Evans 1970, Uin 1984) was typically initiated by the parent, not the chicks, as was suggested by Graves et al.(1984). This behaviour may have a number of

Table 3. Weather statistics from Kent Island for the months of June and July
 (taken from R. Cunningham, 1987, unpublished report).

| Month | Variable Measured | 30-year Mean | 1986 | 1987 |
|-------|---|--------------|------|------|
| June | ave. daily max. °C | 14.2 | 14.0 | 14.4 |
| | ave. daily min. °C | 7.3 | 7.8 | 8.1 |
| | daily ave. °C | 10.7 | 10.9 | 11.3 |
| | no. of growing degree days ¹ | 117 | 109 | 124 |
| July | ave. daily max. °C | 16.8 | 16.4 | 16.8 |
| | ave. daily min. °C | 9.4 | 10.2 | 10.2 |
| | daily ave. °C | 13.1 | 13.3 | 13.4 |
| | no. of growing degree days | 194 | 192 | 199 |

¹The number of degree days each day equals the average of the max. and min. temperatures for the day minus 5.5°C - which is the temperature at which grass begins to grow (Man. Dept. Agri.).

functions, such as to prevent soiling the nest with uneaten food and hence the potential infestations of pests and/or parasites. Maggots were observed in a few nests at Kent Island where rotting eggs had broken, and may be more likely if uneaten food remains in the nest. However, this is not likely to be the main reason for feeding the chicks away from the nest since over half of the feedings were performed in the nest throughout the hatching period in this and other studies (see Uin 1984). Intraspecific predation on chicks is often a major source of early mortality in herring gulls (Tinbergen 1953, Knudsen 1987). Parents may feed chicks away from the nest to force them to practise moving about, learning the characteristics of the territory, and so enable them to avoid predation by other gulls. It is also possible that feedings away from the nest are one way the parent can ensure that the c-egg is not warmed by the parents' own body heat or that of the chicks, i.e. the parent 'intentionally' exposes the c-egg to low temperatures (and other stimuli present when the egg is exposed). The possible significance of this neglect is discussed below.

Parents also spent substantial amounts of time off the nest loafing. Some preening that did occur during this time may have required that the bird stop incubating temporarily. However, for the most part it appears that these activities do not need to occur off the nest. Parents leave the c-egg exposed, and often this does not appear to be necessitated

by any event or condition on the territory or surroundings. This behaviour seems to lend credibility to the suggestion given above that parents 'intentionally' leave the c-egg exposed. Norton (1972) also found that sandpiper parents spent considerable amounts of time just standing near the nest during the period between the hatching of the first and last eggs.

According to Beer (1962, 1966) and Drent (1970), the behavioural transition from incubation to care of chicks is not an efficient one. Parents appear not to be behaving optimally during this period. However, I must assume that this behaviour has been and is subject to natural selection and that parents would continue to incubate the c-egg at a higher rate, more similar to levels during pipping of a- and b-eggs, if it were in their best interests to do so.

Brood reduction theory suggests one way incubational neglect could benefit parents that lay more eggs than they can, on average, raise to independence (Parsons 1970). In years when food is limited, parents and surviving siblings may benefit from the death of one offspring if the fitness of the entire brood would otherwise suffer due to poor quality offspring or total brood loss due to starvation (Lack 1954, 1968, O'Connor 1978). When all three eggs in a herring gull clutch hatch, the c-chick commonly does not survive the first week (Paynter 1949, Paludan 1951, Parsons 1969, Kadlec et al. 1969, Haycock and Threlfall 1975). The c-egg is

believed to play an insurance role (Dorward 1962), usually surviving only if the a- or b-egg is not successful (Nisbet and Drury 1972, Graves et al. 1984, Hebert and Barclay 1986, but see chapter 3). Smaller egg size (and subsequently smaller hatch size and yolk reserves available during the early post-hatch period) and asynchronous hatching (and resultant relative immaturity and lower competitive ability) have been documented as being at least partially responsible for the very high c-chick mortality observed soon after hatching in herring gulls (Parsons 1970 1972 1975, Hebert 1985). Graves et al. (1984) suggest that another way parents may reduce brood size is to stop incubating the third egg when the other two chicks have hatched.

If, however, the b-egg is lost before it hatches, the results indicate that the c-egg is subject to nest conditions much more like those experienced by the a- or b-eggs during pipping. Mean temperatures during pipping of the c-egg in a-c- nests were significantly higher than in a-b-c- nests, indicating that the parents were more attentive, probably rising and resettling less frequently. Under these conditions, further brood reduction would presumably be less advantageous, parents having evidently been selected to remain attentive to at least two eggs.

Whether the c-egg is actually disadvantaged by incubational neglect remains problematical. The results presented here show that real differences do, in fact, exist among the

nest conditions just prior to the hatch of a-, b-, and c-chicks. The irregularities in parental incubation behaviour that develop as hatching progresses could potentially have negative consequences for c-egg/chick survival. Romanoff (1936) and other authors (see Lundy 1969) have shown that lower temperature during the last days before hatching can result in longer time to hatch in artificially incubated chicken eggs. If a similar result occurs in the herring gull under natural conditions then an increase in asynchrony would result, causing greater differences in competitive abilities between chicks than if such cooling did not occur.

On the other hand, other work (Russian workers in Lundy 1969, Hess 1970, Norton 1972) indicates that short-term fluctuations in nest conditions may actually improve the circumstances of embryos that develop under such regimes. Norton (1972), in his field study of calidrine sandpipers, found that when the hatching period coincided with good weather, parents' incubation behaviour became irregular after hatching began. Eggs cooled but tended to hatch fairly synchronously. When the weather was not good, parents sat tightly on nests throughout hatching. At these times the eggs were kept warmer, but hatched a day later and more asynchronously than those that hatched in good weather. This seems to indicate that fluctuating conditions during the hatching period accelerate and synchronize the hatching process (Norton 1972). It is therefore possible that incu-

bational disruption during pipping of the c-egg in the herring gull may act to decrease hatching asynchrony and minimize competitive differences between chicks. This possibility is considered further in the following chapter.

Chapter III

THE CONSEQUENCES OF INCUBATIONAL NEGLECT IN HERRING GULLS: DOES THE THIRD CHICK REALLY SUFFER?

3.1 INTRODUCTION

According to brood reduction theory, parents and surviving siblings are expected to favour the early demise of one or more offspring when food is not sufficiently abundant for all to be raised successfully (O'Connor 1978). Those parents that decrease their brood size in times of food stress have higher reproductive success than those that try to raise the entire brood on inadequate resources (Lack 1954, 1968). Brood reduction is facilitated by parents establishing competitive asymmetries within the brood through declining egg size with laying order and incubation prior to the laying of the last egg resulting in asynchronous hatching (Lack 1954, 1968).

Many gull species normally lay 3 eggs, the third of which is significantly smaller than the first two, and hatches one to four days later than its siblings (Paynter 1949, Paludan 1951, Parsons 1970, MacRoberts and MacRoberts 1972, Hebert

and Barclay 1988). This third chick (hereafter called the c-chick; the first and second will be called the a- and b-chicks, respectively) suffers a disproportionately high mortality rate, especially during the first week post-hatch (Paynter 1949, Paludan 1951, Parsons 1969, Kadlec et al. 1969, Haycock and Threlfall 1975). In the herring gull the c-chick rarely fledges unless at least one of its siblings dies soon after hatching (Graves et al. 1984, Hebert and Barclay 1986, but see chapter 3). Egg size and hatch asynchrony have been shown to be major factors contributing to this high mortality (Parsons 1970, 1975).

Graves et al. (1984) have suggested that a third factor besides egg size and hatch asynchrony may be involved in brood reduction in gulls. Parents typically go through a transition period when the eggs begin to hatch, gradually altering their behaviour from incubation of eggs to brooding and feeding of chicks. Incubation becomes increasingly disrupted as hatch proceeds. This "inefficiency" of parental incubation during the hatch of the c-egg may be partially responsible for the lower viability of the c-egg sometimes reported in the literature (Beer 1962 1966, Kadlec et al. 1969, Drent 1970, and Haycock and Threlfall 1975). Failure to hatch, and increased hatch asynchrony (with subsequently increased competitive disadvantage or abandonment), presumably due to suboptimal incubation temperatures, have been cited as probable consequences of disruption of incubation

during hatch (Paludan 1951, Beer 1962 1966, Drent 1970, Haycock and Threlfall 1975).

The transition period between incubation and hatching was studied in detail in herring gulls (Chapter 1). In each of two years the c-egg in 3-egg clutches (hereafter called C/3 nests) but not in 2-egg clutches (called C/2 nests), experienced a much less constant nest environment than the b-, and especially the a-egg. The c-egg in C/3 nests was subject to lower temperatures and to frequent fluctuations in temperature, light, and probably movement, sound and gaseous environment as a consequence of frequent and sometimes extended periods during which the attending parent left the nest uncovered. This neglect in C/3 nests appeared to be under parental control. It commonly was associated with feeding the a- and b-chicks off the nest, but parents sometimes left the nest uncovered for no apparent reason.

The effect of such environmental fluctuations on naturally incubated avian embryos is unknown (Drent 1972, Shilov 1973, Webb 1987). Almost all work done has examined the effects of various artificial incubation regimes on hatchability, growth, etc. of domestic chickens (e.g. Romanoff 1936, see Lundy 1969 for a review). Results of these studies vary depending on the levels of incubation parameters examined and the timing of their application. None has attempted to simulate natural conditions during hatching. Consequently, causal predictions concerning the effects of

fluctuations of the environment within the nest during hatching cannot yet be made with confidence.

In this study I examined the effect of incubational disruption and neglect of the c-egg that occurs naturally during the hatching period in herring gulls. Does parental behaviour during the transition from incubation to care of chicks directly or indirectly facilitate brood reduction and the early demise of the c-chick? Specifically, I tested the hypotheses that incubational disruption and neglect of the c-egg causes a decline in hatch success, an increase in hatch asynchrony, and a subsequent drop in growth rate and survival compared with c-eggs which are not subject to such neglect during hatch.

3.2 METHODS

3.2.1 Field Methods

In 1987 a segment of the Kent Island (Bay of Fundy, New Brunswick, see Chapter 1) herring gull colony was censused daily during laying. Each nest was marked and the date of laying of each egg recorded. Eighty nests marked during laying were monitored during hatching and for one week following hatching. Each nest was checked twice a day at approximately 12-h intervals from the first sign of pipping of the a-egg until the entire clutch had hatched. Each

chick was banded with individually numbered plastic expandable leg bands, weighed, and its tarso-metatarsus measured during the first nest check after it hatched. Each chick was then weighed at approximately the same time every morning until the c-chick in that nest was 7 days old. At some nests we returned to the nest 10 or 12 days after the c-chick hatched to remove leg bands, and survival in these nests was also recorded at this time.

Forty-four of the 80 nests were controls in which hatch was allowed to proceed normally. The other 36 nests were experimentally manipulated. In these nests, the c-egg was removed (and replaced with an egg from another, later nest) and put into a surrogate nest that was sufficiently later than the experimental nest to allow the implanted c-egg to hatch before the other two eggs in the surrogate nest. This c-egg was therefore not subject to incubational disruption and neglect as were control c-eggs. Experimental c-eggs hatched under conditions that are expected to be identical to those experienced by the a-eggs during hatch. The experimental c-eggs were also checked twice a day until hatch, at which time they were weighed, measured, and immediately returned to their original nest (and the replacement egg returned to its original nest). Hatchability, hatch intervals, hatch size, growth rates, and survivorship were determined and compared between control and experimental groups.

Eleven additional nests in which the b-egg had been removed before the a-egg started to hatch were also monitored (C/2, a-c- nests). Parents at a-c- nests are known to neglect the c-egg significantly less during its hatch than parents with full C/3 clutches (see Chapter 1). Hatch intervals in a-c- nests were therefore predicted to be similar to hatch intervals between a- and c-eggs in experimental (unneglected) nests.

3.2.2 Analysis of Weight Data

Growth of chicks was estimated using two methods. First, overall growth rate was calculated using linear regression. A nest was removed from the regression analysis if the c-chick died before it was four days old, or if the a- or b-chicks died before the end of the experiment. Growth rates (slopes of regression lines) were then compared using the SAS statistical test for homogeneity of slopes (GLM). Secondly, a number of measures were calculated from the daily weight data that allow comparisons of weight changes for specific subsets of the experimental period. Nests where one chick died before the end of the experiment were not included in these calculations. These measures are: total weight gain to days five and seven (to lessen the effects of recent feedings on weights the total weight was taken as the average of the weights on the last two days (after Graves et

al. 1984), proportionate weight gain to days five and seven (total weight gain/hatch weight), and daily proportionate weight gain for days two to seven (24-h weight gain/hatch weight). Daily weights for c-chicks that died before the end of the experiment were also compared between the two groups. Note that chicks hatch on day one.

3.3 RESULTS

Deaths during pipping were too rare for statistical analysis. Three such deaths occurred in control nests; one a- and two c-eggs. One experimental c-chick died immediately after hatch but none was found dead during pipping. Overall hatchability was significantly higher in experimental nests (chi-square=4.5702, df=1, $P < 0.05$). This was not the result of significantly lower hatchability of any particular egg in control nests, although there was a minor tendency for c-eggs to hatch less well in control nests (Table 4). The same proportion of a-, b-, and c-eggs hatched in both groups (chi-square=0.0808 df=2, $P > 0.95$).

In nests where all eggs hatched, experimentals and controls did not differ in the proportion of broods in which all three chicks survived to one week after the c-chick hatched (Table 5, 70.4% of 27 control broods, and 73.3% of 30 experimental broods; chi-square=0.0022, df=1, $P > 0.95$).

TABLE 4

Hatchability of a-, b-, and c-eggs in control and experimental nests.

| group | n (nests) | number of chicks hatched(%) | | | |
|--------------|--------------|-----------------------------|--------|--------|---------|
| | | a-eggs | b-eggs | c-eggs | total |
| control | 44 | 36(82) | 41(93) | 37(84) | 114(86) |
| experimental | 36 | 33(92) | 35(97) | 35(97) | 103(95) |

Log-likelihood tests, control vs experimentals:
a-eggs $P > 0.25$, b-eggs $P > 0.75$, c-eggs $P > 0.10$.

There was also no difference between groups in number of c-chicks that survived to one week (chi-square=0.0379 df=1, $P>0.75$), ratios of a-, b-, and c-chicks that survived to 1 week (chi-square=0.0054 df=2, $P>0.995$), to 10 days (chi-square=0.3161 df=2, $P>0.75$) or to 12 days (chi-square=0.3369 df=2, $P>0.75$).

Hatch weight, tarso-metatarsus length, and tarso-metatarsus length/hatch weight of a-, b-, and c-chicks (Table 6) did not differ between control and experimental nests.

Hatch asynchrony differed significantly among groups (Fig. 7a). A significantly higher proportion of c-eggs in experimental nests (71.9%) hatched after the median a- to c-hatch time of 2.5 - 3.0 days, while a higher proportion in control nests (57.7%) hatched before the median (2.5 or less) (control vs experimentals, chi square=4.0229 df=2 $P<0.05$). The interval between hatching of a- and c-eggs at a-c- nests was similar to experimentals (in 72.7% of a-c-nests the c-egg hatched 2.5 or less days after the a-egg, binomial test for differences between proportions $P=0.66$), but different from controls (binomial test for differences between proportions $P=0.0384$).

There were no significant differences between controls and experimental nests in hatch intervals other than a- to c- hatch intervals (Fig. 7b and c, a-egg hatch to b-egg hatch $P>0.95$, b-egg hatch to c-egg hatch $P>0.25$) or in pip

Table 5. Survival of a-, b-, and c-chicks in control and experimental nests where all three eggs hatched.

| group | egg | 7 days (n ¹) | 10 days ² (n) | 12 days ² (n) |
|--------------|-----|--------------------------|--------------------------|--------------------------|
| control | a- | 25 (27) | 9 (11) | 7 (7) |
| | b- | 25 | 10 | 7 |
| | c- | 22 | 10 | 7 |
| experimental | a- | 28 (30) | 8 (9) | 6 (7) |
| | b- | 28 | 7 | 6 |
| | c- | 24 | 6 | 4 |

¹n is number of nests checked at a-given age.

²Only nests where three chicks were alive at 7 days were used.

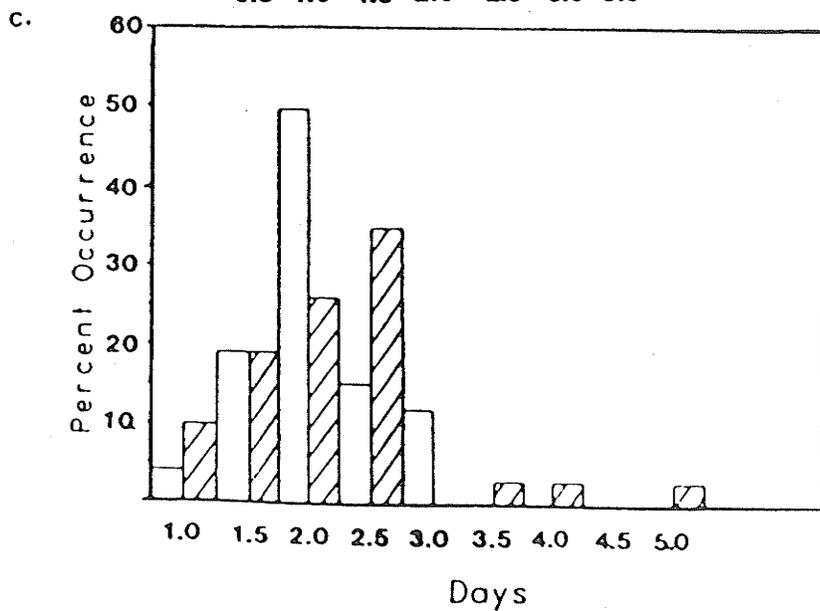
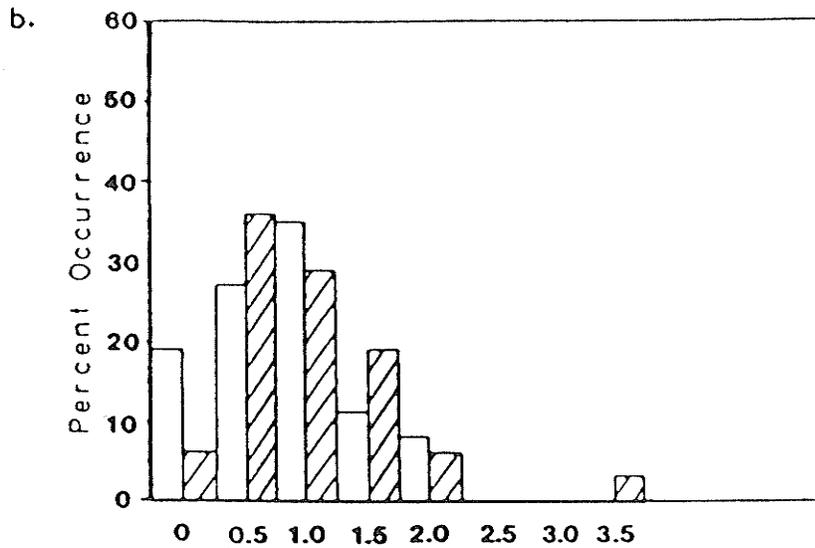
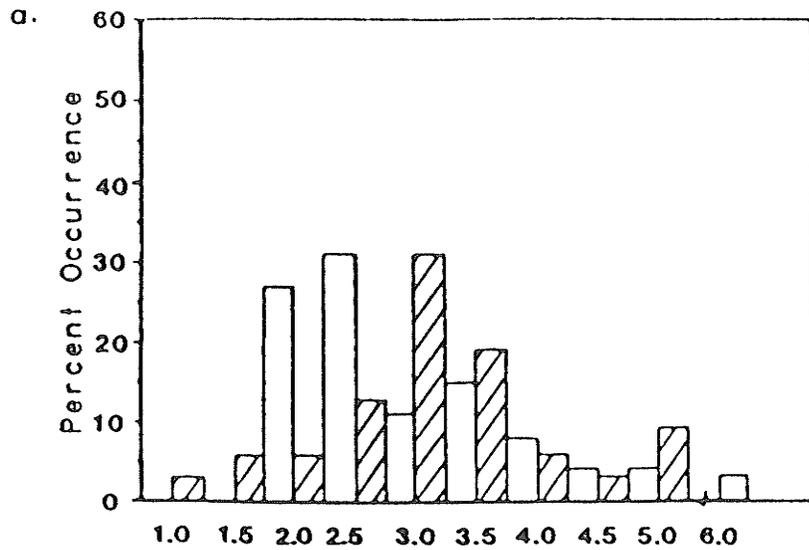
Table 6. Measurements (mean±S.E.) of control and experimental herring gulls at hatching.

| variable ¹ | egg | controls (n) | experimentals (n) | P ² |
|-----------------------|-----|-----------------|-------------------|----------------|
| hw(g) | a- | 67.68±6.46 (35) | 66.74±4.81 (34) | 0.49 |
| | b- | 66.83±5.99 (35) | 66.94±4.76 (35) | 0.93 |
| | c- | 60.55±5.81 (31) | 60.20±4.70 (34) | 0.80 |
| t(mm) | a- | 58.88±2.62 (35) | 58.65±2.62 (34) | 0.72 |
| | b- | 58.64±2.21 (35) | 58.78±2.05 (35) | 0.78 |
| | c- | 57.04±2.59 (31) | 57.40±1.63 (34) | 0.50 |
| t/hw | a- | 0.88±0.07 (35) | 0.88±0.05 (34) | 0.69 |
| | b- | 0.88±0.07 (35) | 0.88±0.06 (35) | 0.92 |
| | c- | 0.95±0.08 (31) | 0.96±0.07 (34) | 0.58 |

¹hw = hatch weight, t = tarso-metatarsus length.

²P-values are for unpaired t-tests.

Figure 7: Hatch intervals at control and experimental 3-egg nests. Open bars represent control nests and hatched bars represent experimental nests. a). Hatch intervals between a- and c-chicks, control n=26, experimental n=32. b). Hatch intervals between a- and b-chicks, control n=26, experimental n=31. c). Hatch intervals between b- and c-chicks, control n=26, experimental n=31.



to hatch intervals, (Fig. 8, chi-square tests, a-eggs $P > 0.50$, b-eggs $P > 0.90$, and c-eggs $P > 0.25$), pip to pip intervals (Fig. 9a-c, a-egg pipping to b-egg pipping $P > 0.90$, b-egg pipping to c-egg pipping $P > 0.90$, and a-egg pipping to c-egg pipping $P > 0.95$). There was a minor tendency for c-pip to hatch intervals (Fig. 8c) and b- to c- hatch intervals (Fig. 7c) to be longer in experimental nests. Therefore, the significantly higher proportion of longer a- to c-hatch intervals in experimental nests appears to be due mainly to an overall lengthening of the c- pip to hatch interval. C- pip to a-hatch intervals were very similar in both treatments (Fig. 10, $P > 0.50$), suggesting that the c-egg hatched faster after the hatch of the a-chick in control nests than in experimental nests.

Growth rates for a- and b-chicks did not differ between treatments (Table 7, a-chicks $P = 0.4716$, b-chicks $P = 0.2586$), but control c-chicks grew significantly faster than experimentals ($P = 0.0142$). There was also a minor, non-significant trend for c-chicks in control nests to have slightly but consistently higher means for the growth measures calculated from weight data (Table 8). There were no significant differences in weights between experimental and control c-chicks that died before the end of the experiment (Table 9).

Figure 8: Pip-to-hatch intervals at control and experimental 3-egg nests. Open bars represent control nests and hatched bars represent experimental nests. a). a-eggs control n=23, experimental n=26. b). b-eggs, control n=19, experimental n=26. c). c-eggs, control n=30, experimental n=35.

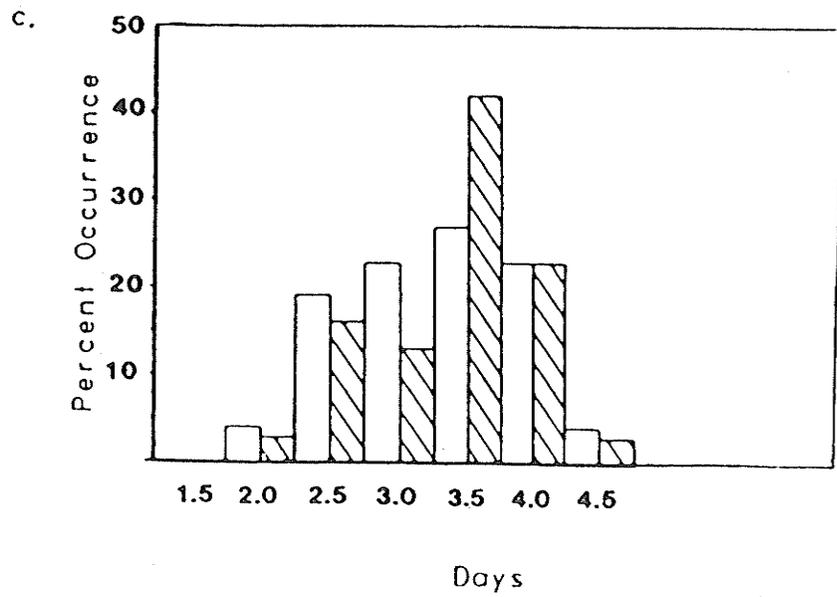
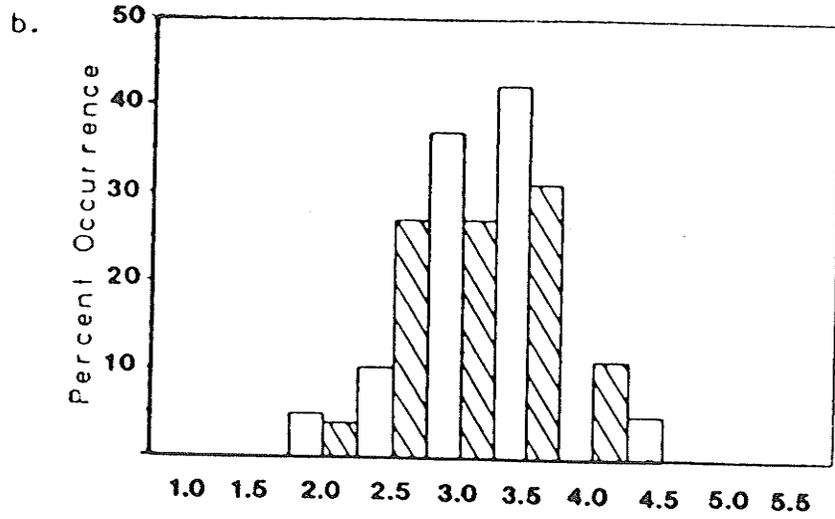
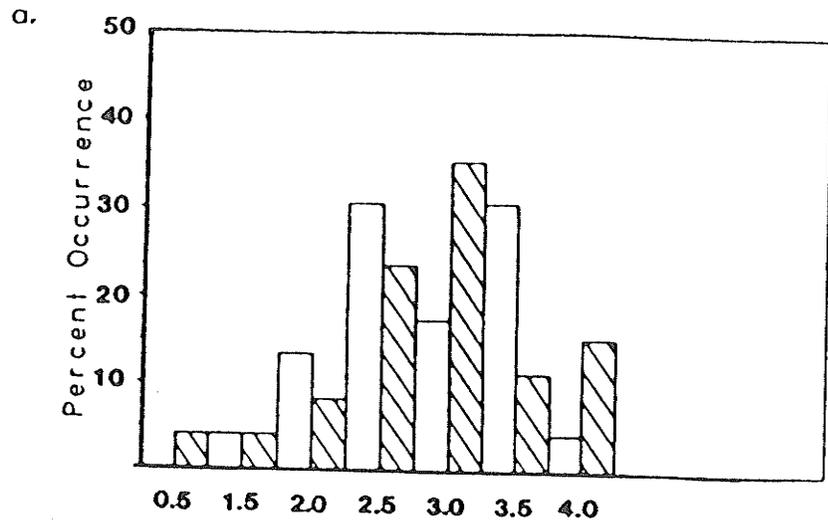


Figure 9: Pipping intervals between eggs at control and experimental 3-egg nests. Open bars represent control nests and hatched bars represent experimental nests. a). a- to b- pipping interval, control n=23, experimental n=23. b). b- to c- pipping interval, control n=25, experimental n=30. c). a- to c- pipping interval, control n=25, experimental n=30.

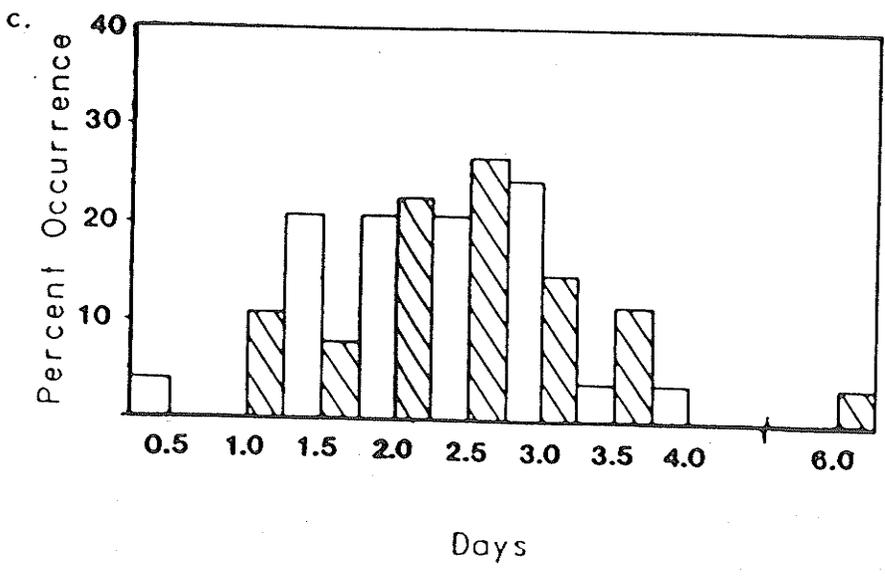
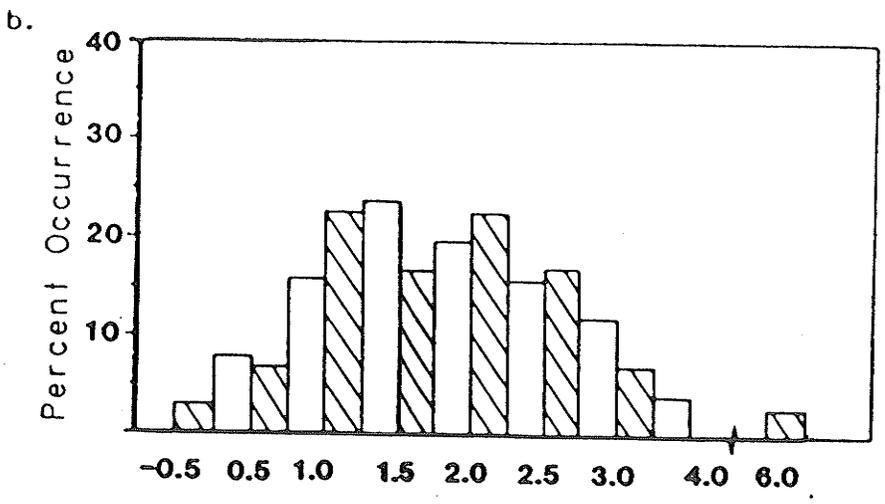
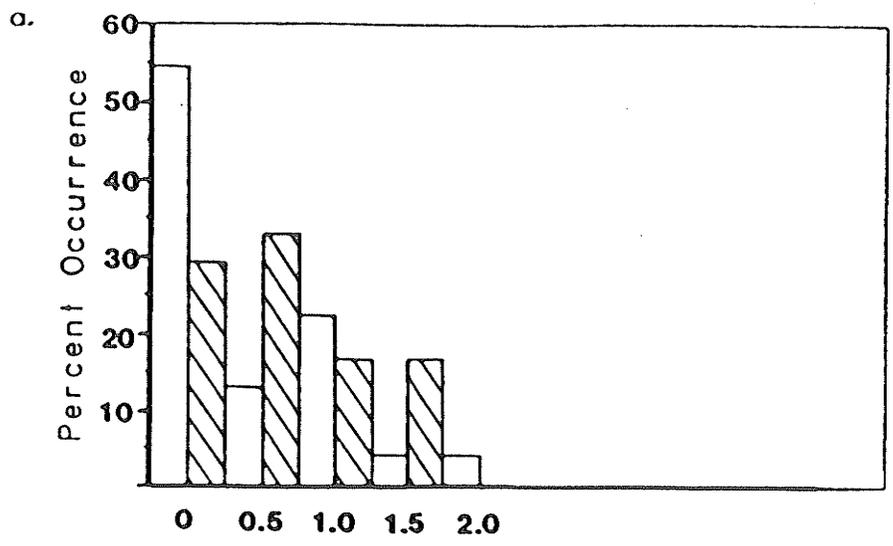


Figure 10: C- pip to a- hatch intervals in 3-egg nest.
Open bars represent control nests and
hatched bars represent experimental nests.

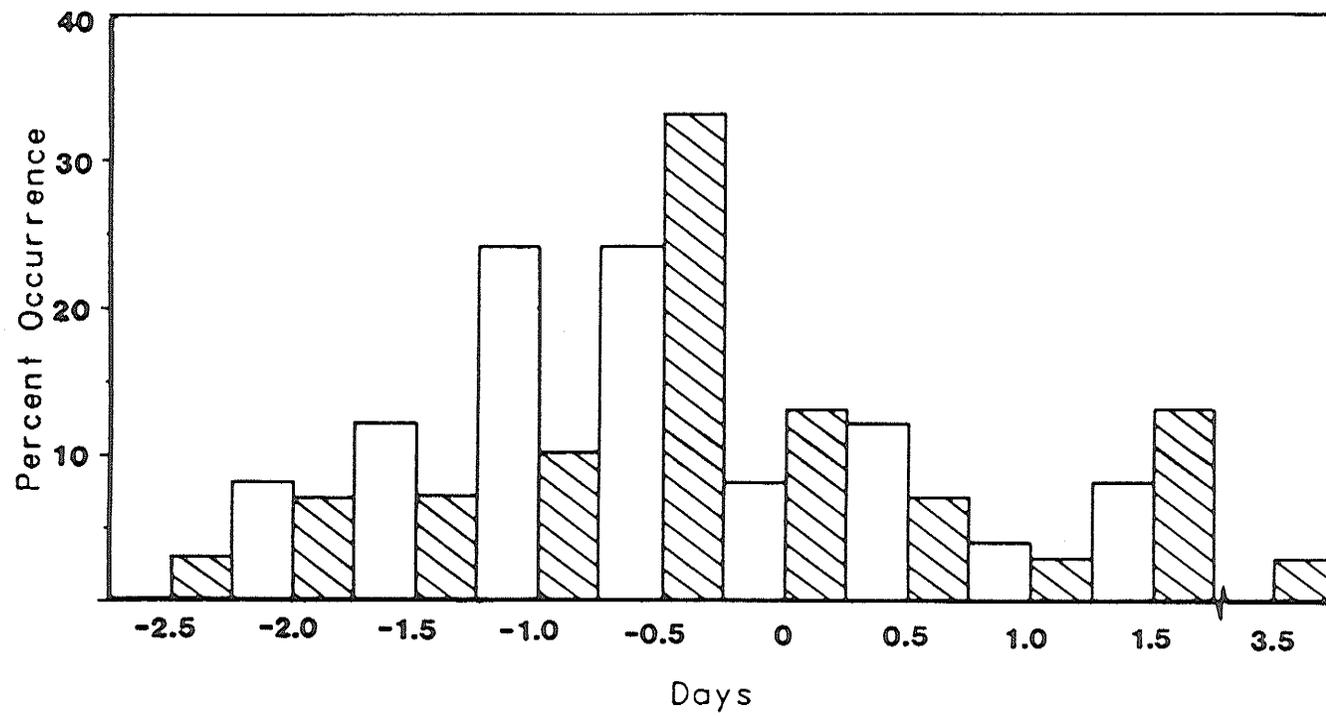


Table 7. Comparisons of herring gull growth rates (\pm S.E.) up to 7 days days post-hatch, for control and experimental nests with 3 eggs.

| group | egg | n | slope (ln g/day) | y-intercept (ln g) |
|--------------|-----|----|----------------------|---------------------|
| control | a- | 21 | 0.1260 \pm 0.0042 | 4.1416 \pm 0.0214 |
| | b- | | 0.1232 \pm 0.0052 | 4.1268 \pm 0.0248 |
| | c- | | 0.0927 \pm 0.0070* | 4.0348 \pm 0.0248 |
| experimental | a- | 25 | 0.1212 \pm 0.0049 | 4.1326 \pm 0.0253 |
| | b- | | 0.1164 \pm 0.0034 | 4.1427 \pm 0.0161 |
| | c- | | 0.0697 \pm 0.0062* | 4.0456 \pm 0.0218 |

*c-chick slopes significantly different, P=0.0142.

TABLE 8

Comparison of means of growth measures for c-chicks in control and experimental nests.

| variable | control(S.E.) | n | experimental(S.E.) | n | P ¹ |
|-------------------|---------------|----|--------------------|----|----------------|
| tot.wt.gn. to | | | | | |
| day 5 | 14.92(10.90) | 20 | 10.88(8.14) | 22 | 0.18 |
| day 7 | 37.60(17.36) | 19 | 28.27(17.79) | 22 | 0.10 |
| prop.wt.gn. to | | | | | |
| day 5 | 0.24(0.18) | 20 | 0.18(0.13) | 22 | 0.21 |
| day 7 | 0.60(0.28) | 19 | 0.46(0.28) | 22 | 0.11 |
| prop.daily wt.gn. | | | | | |
| day 2 | -0.01(0.07) | 24 | 0.01(0.06) | 29 | 0.35 |
| day 3 | 0.06(0.09) | 23 | 0.03(0.06) | 27 | 0.15 |
| day 4 | 0.09(0.07) | 22 | 0.06(0.07) | 24 | 0.27 |
| day 5 | 0.18(0.15) | 20 | 0.11(0.13) | 22 | 0.11 |
| day 6 | 0.18(0.16) | 18 | 0.13(0.14) | 21 | 0.25 |
| day 7 | 0.18(0.17) | 19 | 0.19(0.17) | 22 | 0.75 |

¹P-values are for unpaired t-tests.

Table 9. Weights (mean+S.E.) of c-chicks that died before they reached 7 days post-hatch.

| variable | controls | n | experimentals | n | p ¹ |
|-----------------|-------------|---|---------------|---|----------------|
| hatch weight | 59.50± 7.32 | 4 | 60.00± 6.26 | 6 | 0.9146 |
| weight on day 2 | 59.00± 3.46 | 3 | 62.00± 8.92 | 6 | 0.6973 |
| day 3 | 61.00± 4.24 | 2 | 63.67±11.52 | 6 | 0.8676 |
| day 4 | 64.00±12.73 | 2 | 67.24±15.69 | 4 | 0.8170 |
| day 5 | 48.00 | 1 | 69.00±26.87 | 2 | 0.5403 |

¹P-values are for Wilcoxon's two-sample test.

3.4 DISCUSSION

These results clearly indicate that incubational disruption and neglect of the c-egg during hatching did not significantly disadvantage the c-egg/chick in any way tested. There were no statistical differences between controls and experimentals in hatchability or survival of c-chicks. There were also no differences for a- and b-chicks. The two groups did differ in degree of hatch synchrony and in overall growth rates, but the results were the opposite of what was expected, with neglected c-chicks in normal, control nests hatching sooner after their siblings, and growing faster than those in experimental nests which were not subject to neglect during hatching. The finding that c-chicks from a-c- nests (not subject to neglect) were similar to experimental nests but different from controls in degree of hatch asynchrony lends further support to this conclusion.

The effects on hatch synchrony were similar to those found by Norton (1972). Norton studied three species of calidrine sandpipers which have precocial young (as opposed to semiprecocial young in gulls) that must leave the nest soon after hatch in order to feed. Incubation attentiveness in these birds fell during hatch only when temperatures ranged from +5 to +10 °C, and clutches that hatched during these times did so quite synchronously. When hatch occurred during bad weather (temperature range: -1 to +4 °C), parental attentiveness did not decline and the interval between

the hatch of the first- and last-hatching chicks was about a day longer than for nests that hatched during mild weather. Norton (1972) suggested that fluctuating conditions of temperature, sound, light, and movement that occurred when incubation attentiveness was disrupted during hatching acted to stimulate and accelerate hatching, whereas constant nest conditions acted to delay hatching. Results of the present study are consistent with this interpretation, in that hatching of c-eggs was more rapid at control nests where attentiveness was normally disrupted during hatching of the c-egg (Chapter 1).

The possibility exists in the present study that increased synchrony in control nests was mediated by exposure of the c-embryo to auditory stimuli emanating from its pipped or hatched nest-mates. Hatching c-eggs in normal, control nests are continuously exposed to calls and clicks from pipping and/or hatched siblings. While a synchronizing effect of such calls has not been shown in herring gulls (Drent 1970), it does occur in many other avian groups, particularly in those species where the hatch must be synchronous in order for the brood to leave the nest to forage soon after hatch (Vince 1966, 1968). However, hatch was also less synchronous in a-c- nests than in controls. C-eggs in a-c- nests were subject to little or no neglect during hatch (Chapter 1), but were exposed to vocalizations of the a-egg/chick prior to hatch, albeit to a lesser degree than in con-

trol C/3 nests. This result tends to support the view that differences in hatch asynchrony between controls and experimentals were the result of other differences in incubational disruption and neglect during the hatch of the c-egg, and not the result of differences in exposure to siblings' calls.

Earlier studies have shown that hatch asynchrony is a very important factor in determining the relative competitive abilities of chicks within a brood (Parsons 1970, 1972, 1975, Hahn 1981, Hebert 1985). This leads to the expectation that c-chicks hatching soon after their siblings will be less disadvantaged in competition for food than c-chicks that hatch relatively later. Specifically, then, in contrast to the original hypothesis, one might now expect c-chicks in control nests to have survived better or grow faster than those in experimental nests. There was no significant difference in survival between the two groups, but growth rates (Table 6) were higher for the neglected control c-chicks. Graves et al. (1984) found that c-chicks at nests given food supplements in the first five days post-hatch had significantly higher fledging success than c-chicks at non-supplemented nests. This increased fledging success was apparently entirely due to higher growth rates during the first five days. Although chicks in my study were not followed to fledging, the work by Graves et al. (1984) suggests that a difference in fledging success between the two treatments could have occurred.

The strong indication that typical levels of neglect did not harm c-embryos, and may even have helped them, leads to the question of why parents should incubate hatching c-eggs much more continuously in nests where the b-egg has been lost (a-c- nests) than in nests where both a- and b-chicks are present (Chapter 1). This occurrence suggests there may be costs associated with egg neglect during hatching, and that in C/2 nests, these costs are not outweighed by potential benefits from increased hatch synchrony brought about by neglect. Although slight, there could be a cost in terms of hatchability, since there was a tendency for (normally) neglected c-eggs to hatch less successfully. Similarly reduced hatchability of c-eggs has been reported by Beer (1962) and Haycock and Threlfall (1975). Also, competition for food would be considerably less in C/2 nests, so the effects of hatch asynchrony on growth should be less critical.

It seems paradoxical that herring gull parents would first create asymmetries within the clutch by beginning incubation on or before the laying of the penultimate egg and by laying a relatively small final egg, then ameliorate the effects of these asymmetries by increasing hatch synchrony through neglecting the c-egg. It may be that high predation rates during laying, when parents are not yet incubating full time (Drent 1970) also influence the time at which effective incubation is begun. The initiation of

incubation may thus represent a balance between prevention of egg loss to predation (Ricklefs 1969, Clark and Wilson 1981) and the degree of hatch asynchrony that maximizes the parents' ability to control brood reduction.

It is also possible that the egg neglect, evidently responsible for greater synchrony, arises in large part as a consequence of other adaptive behaviour. For example, feeding the a- and b-chicks away from the nest, which is one correlate of c-egg neglect (Chapter 1), may reduce fouling of the nest and render the young less susceptible to predation (Tinbergen 1953, Knudsen 1987), or it may facilitate the development of the feeding hierarchy within the brood (Graves et al. 1984). According to this interpretation, the asynchronizing effects of an early onset of incubation would presumably need to be exaggerated to take account of this later synchronizing effect of c-egg neglect so that an optimal degree of hatch asynchrony is eventually produced. Further work is required to assess these possibilities, and to determine whether the degree of hatch asynchrony normally present at C/3 nests is, in fact, optimal.

It remains to be determined whether the results obtained here can be generalized to other gull species, or even to herring gulls breeding under other more, or less extreme temperature conditions. Variability in the degree of c-chick disadvantage and brood reduction is evidenced in herring gulls (Chapter 3). A similar degree of variability

in third-egg neglect and the consequences of it would therefore not be unexpected. Additional studies will be needed to clarify this possibility.

Chapter IV

MORTALITY IN HERRING GULL CHICKS: OBLIGATE VS FACULTATIVE BROOD REDUCTION

4.1 INTRODUCTION

Classical brood reduction theory suggests that in species where females lay larger clutches than they can raise in an average year, the number of offspring that are successfully raised depends on food availability. Larger clutch sizes evolved to allow parents to take full advantage of a fluctuating unpredictable food supply (Lack 1954, 1968). In good years, parents may fledge the entire brood, whereas in years when food is in short supply, one or more offspring are eliminated soon after hatch, and the probability of fledging for the remainder of the brood is consequently increased (Lack 1954, 1968, O'Connor 1978).

An alternative explanation for the evolution of clutch sizes larger than parents can normally raise is the "insurance-egg hypothesis", first proposed by Dorward (1962) and supported experimentally by Cash and Evans (1986). This hypothesis differs from classical brood reduction in that the survival of the smallest and usually youngest brood member(s) depends on the survival of older siblings. In the

most extreme form of the insurance-egg hypothesis, the youngest offspring never survive except as replacements for older siblings that do not hatch, or that die soon after hatching. Here, egg or offspring quality, rather than food availability per se, determines the probability of survival of youngest brood members (Clark and Wilson 1981).

Graves et al. (1984) and Hebert and Barclay (1986) have suggested that brood reduction in the herring gull constitutes an example of the insurance-egg phenomenon. Herring gulls lay three eggs, the third of which is relatively small and hatches one to four days after the first two (Paynter 1949, Paludan 1951, Kadlec et al. 1969, Parsons 1969, Haycock and Threlfall 1975, this study, Chapter 2). The third, or c-chick suffers disproportionately high mortality during the first week post-hatch and, according to Nisbet and Drury (1972), Graves et al. (1984), and Hebert and Barclay (1986), rarely survives unless one of its siblings is lost during the egg or early post-hatch stages.

During the course of a study on egg temperatures and hatching intervals in the herring gull (Chapter 2), survival of chicks was also recorded during the first week post-hatch, when most chick mortality normally occurs (e.g. Haycock and Threlfall 1975, Parsons 1975). Contrary to previous findings, results indicate that the c-egg/chick does not function solely or perhaps even primarily as insurance against the loss of older brood members in herring gulls.

4.2 METHODS

Forty-three naturally occurring nests with three-eggs (C/3) and 15 artificial two-egg nests (C/2) for which laying order was known were checked daily during hatch of the clutch and the week following the hatch of the c-egg at each nest. For C/2 nests, six had the a-egg, and nine had the b-egg removed before the a-egg hatched. Chicks were banded with individually numbered plastic leg bands as soon as they hatched. Presence or absence and weight of each chick was recorded at each visit.

Overall brood survival and growth rates of a-, b-, and c-chicks were compared (slopes of regression lines, SAS GLM test for homogeneity of slopes) between broods of three (B/3) and of two (B/2). For some analyses, C/3 nests that hatched only two chicks were classed as broods of two (B/2) and combined with B/2 broods derived from C/2 nests.

4.3 RESULTS

At unmanipulated C/3 nests, one egg failed to hatch at 14 nests and none hatched at two nests, producing 14 and two B/2 and B/0 nests, respectively. Overall survival (Table

10) up to one week of age was very high (0.8450 chicks/egg laid in unmanipulated nests). In total, only 11 chicks died in the 56 successful nests. Hatchling survival was significantly greater (binomial test for differences between proportions, $P < 0.05$) for chicks at B/2 nests derived from C/3 clutches, than for young at B/3 nests. A similar but non-significant trend ($0.05 < P < 0.10$) was present for all B/2 broods (from C/2 and C/3 nests combined). Despite slightly better survival at B/2 nests, B/3 nests averaged 2.67 chicks/nest at the end of the experiment, whereas all B/2 nests combined averaged 1.93 chicks/nest (Mann-Whitney U test $P < 0.0001$).

Seventy percent of the 27 nests where all three eggs hatched still had three chicks at the end of the experiment when c-chicks were one week of age. In these nests there was no statistically significant difference in the number of a- (25 chicks), b- (25 chicks), and c- (22 chicks) chicks surviving, i.e. c-chicks did not suffer higher mortality than a- or b-chicks ($\chi^2 = 0.25$, $df = 2$, $P > 0.75$).

Growth rates (Table 11) were significantly higher for a-, b-, and c-chicks in B/3 nests than in B/2 nests (from C/2 and C/3 nests combined). Evidently, parents could feed three chicks as well or better than two chicks, and a- and b-chicks did not suffer lower growth as a result of parents feeding a third chick.

Table 10. Survival in C/3 (3 eggs), C/2 (2 eggs), B/3 (3 chicks), and B/2 (2 chicks, from C/2 and C/3 nests) nests to one week post-hatch.

| Nest type | Nests (N) | Chicks hatched | Chicks died | Hatchling survival | Surviving chicks/nest | Surviving chicks/egg laid |
|-----------|-----------|----------------|-------------|---------------------|-----------------------|---------------------------|
| C/3 nests | | | | | | |
| B/3 | 27 | 81 | 9 | 0.89 ^{1 2} | 2.67 ³ | 0.889 |
| B/2 | 14 | 28 | 0 | 1.00 ¹ | 2.00 | 0.667 |
| B/0 | 2 | | | | | |
| Total | | 109 | 9 | | | 0.845 |
| C/2 nests | | | | | | |
| B/2 | 15 | 30 | 2 | 0.93 | 1.67 | - |
| B/2 nests | 29 | 58 | 2 | 0.96 ² | 1.93 ³ | - |
| All nests | | | | | | |
| Total | 58 | 139 | 11 | 0.92 | 2.21 | - |

¹P<0.05.

²0.05<P<0.10.

³P<0.0001.

TABLE 11

Growth rates (ln g/day) to 7 days of a-, b-, and c-chicks in B/3 and B/2 broods.

| Brood Category | Egg | N | Slope (S.E.) ¹ | y-intercept (S.E.) |
|------------------|-----|----|---------------------------|--------------------|
| B/3 | a- | 21 | 0.1260 (0.0042) | 4.1416 (0.0214) |
| | b- | 21 | 0.1233 (0.0052) | 4.1268 (0.0248) |
| | c- | 21 | 0.0927 (0.0070) | 4.0348 (0.0248) |
| B/2 ² | a- | 19 | 0.0971 (0.0104) | 4.1296 (0.0506) |
| | b- | 18 | 0.1048 (0.0058) | 4.1037 (0.0256) |
| | c- | 25 | 0.0692 (0.0066) | 4.0118 (0.0236) |

¹Comparison of slopes between B/3 and B/2:

a-chicks P=0.0059, b-chicks P=0.0208, c-chicks P=0.0158.

²B/2 includes C/3 nests where only two chicks hatched (a-b-, a-c-, and b-c- broods) as well as artificial C/2 (a-c- and b-c-) nests. Therefore the b-chick growth rate in this category includes both b-chicks that hatched first (b-c- nests) and last (a-b- nests). Growth rates of b-chicks in these two categories did not differ significantly (P=0.2130), and hence were combined.

4.4 DISCUSSION

Results of this study provide strong evidence that herring gulls can sometimes rear three young. Although I did not follow chicks through to fledging and so did not record fledging success, most sources (Paynter 1949, Paludan 1951, Fordham 1964, Kadlec and Drury 1968, Kadlec et al. 1969, Parsons 1970, 1975, Haycock and Threlfall 1975, Gillett et al. 1975, and Hunt and Hunt 1976) indicate that mortality during the remainder of the pre-fledging period is much lower than during the first week post-hatch. Therefore, it is probable that fledging success would also have been high, and would have included a large proportion of broods in which all three chicks fledged.

The weather at Kent Island during the course of this study was unusually mild. Average daily mean and minimum temperatures were higher than normal and the total number of days with fog in June, July, and August was the second lowest (tied with five other years) in 41 years of records (R. Cunningham 1987, unpublished report). Hebert (1987), in his work at the same herring gull colony, found a correlation between fog, constituents of parental regurgitate, and chick survival during the first five days post hatch. During clear weather a high proportion of parental regurgitates contained fish (90%) and a low proportion contained euphausiids (24%). This trend was reversed in foggy weather

(36.8% fish, 65.8% euphausiids), and chick survival was lower during foggy weather.

According to Boecker (arctic terns Sterna paradisaea, 1967 in Lemmetyinen 1972) and Spaans (herring gulls, 1971) young chicks that are not yet able to thermoregulate require soft, high calorie food that is easy to digest. When chicks are very young, one parent at a time forages, since the other must brood the chicks and protect them from predators. It is therefore likely that parents would, when possible, bring the chicks a large proportion of fish, which is highly nutritional and contains little indigestible material relative to molluscs or crustaceans (Spaans 1971). Hebert's (1987) results therefore suggest that herring gull parents bring a higher proportion of suboptimal food during foggy weather, likely leading to the higher mortality rates he found during an extended foggy period. Cool damp weather may also lead to thermoregulatory stress in newly hatched chicks, especially if parents spend less time brooding as a result of the need to increase foraging effort (Hebert 1987). Hence, weather, or at least fog, appears to affect the quality of parental care by influencing foraging efficiency and/or the availability of various prey types. Similar effects of weather on foraging in terns have been found by Dunn (1973, 1975), Lemmetyinen (1972), and Whitlock (1927 in Dunn 1975).

When my study was conducted, in 1987, fewer days with fog, and possibly the warmer than usual temperatures may thus have created exceptionally favourable foraging conditions for parents. The greater growth rates of chicks in this study compared with those reported by Hebert (1985), (approximately 100% greater in this study) support this conclusion. However, these growth rates are not strictly comparable with mine since they reflect growth to 40 days, whereas mine reflect growth to only seven days. The higher mortality seen in B/3 nests as opposed to B/2 nests appears contrary to the growth rate data, but may indicate that, while parents had no trouble feeding three chicks, they sometimes had trouble brooding or protecting three chicks from predators (as in Knudsen 1987).

The tendency for chicks in B/3 nests to grow faster than those in B/2 was unexpected, and lends further support to the conclusion that food was unusually abundant in 1987. Greater growth rates at B/3 nests could have been the result, for example, of increased begging stimuli from more chicks causing parents to bring proportionately more food to the nest (cf. Henderson 1975). An increase in the number of potential competitors, as well as social facilitation of feeding (Turner 1965, Wilson 1975), could possibly have increased the amount of food B/3 chicks ate when faced with abundance.

Early survival in herring gull chicks may only rarely reach the high levels found in this study. However, if high chick survival was the result of the low number of days with fog during the pre-fledging period, then such high survival may not be all that uncommon. According to R. Cunningham (1987 unpub. data), summers with similar or lower levels of fog as in 1987 can be expected to occur about once every six years on Kent Island (7 of 41 seasons had an equal or lower number of days with fog in June, July, and August). Herring gulls are long-lived birds, often surviving to breed 12 to 15 times (Davis 1975, Chabrzyk and Coulson 1976). Therefore, on Kent Island, a herring gull can expect to encounter two or more years with as good or better conditions as in 1987 during its' reproductive life-span.

The results presented here strongly suggest that herring gull parents can raise three chicks on those occasions when environmental conditions permit. I suggest that survival of the c-chick ultimately does depend on food availability. When food is very abundant or accessible, whole broods can be raised, but when it is in short supply, the c-egg/chick functions as insurance, its survival depending upon that of its older siblings. The c-chick is therefore valuable as insurance whenever parents cannot provide for and raise the entire brood. Potentially, however, the reproductive benefits arising from the occasional occurrence of favourable conditions that allow parents to raise all three chicks may

be primarily responsible for the evolution of a clutch size of three in this species. According to this interpretation, the insurance value of the c-egg/chick would be a secondary factor, ameliorating the strength of counter selection pressures against a three-egg clutch in years when food is scarce.

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