

Some Effects of Asynchronous and Synchronous Hatching and
Parental
Investment on Reproductive Success of The Herring Gull on
Kent Island, New Brunswick

by

Percy Norman Hébert

A thesis
presented to the University of Manitoba
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in
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Cette these est dedie a ma grandmere, Valeda Hebert

ABSTRACT

The purpose of this study was to examine, A) the effects of clutch size on parental investment, chick fitness, and parental reproductive success; and B) the significance of asynchronous hatching on reproductive success in the Herring Gull. The experiments were conducted at Kent Island, Bay of Fundy, New Brunswick, during the summer of 1984.

Data for both experiments were collected on egg weight and chick weight, culmen length, and tarsometatarsus length, both at hatch and every three to four days thereafter. Behavioural observations were made from blinds located in the colony. Data were collected on the occurrence of feedings and aggression, and the chicks involved.

In three-egg clutches, A-eggs were only significantly heavier than B-eggs at moderate clutch weights, whereas C-eggs were always significantly lighter than B-eggs. In two-egg clutches, A-eggs were always significantly heavier than B-eggs.

Survivorship of the A- and C-chicks in three-chick broods was correlated with hatch weight, which was also correlated to tarsometatarsus length at hatch for the C-chick. In two-chick broods, survivorship was not correlated with hatch weight.

Hatching success (eggs/nest) was greatest in control three-egg nests, and lowest in control two-egg nests, with experimental two-egg nests (three-egg nest minus the C-egg) being intermediate. In control three-egg nests, the C-egg provided insurance for the loss of 25 % (n=45) of the A and 23 % (n=45) of the B-eggs. Growth rates were similar for all chicks within and between groups (C3, C2, E2), however there was a trend for chicks in experimental two-chick broods to grow at a faster rate than those in control three and two-chick broods. Survivorship up to five days post-hatch was similar for all chicks, with the exception of C-chicks in control three-chick broods which survived fewer days than their elder sibs, and B-chicks from control two-chick broods which survived less well than their counterpart in control three-chick broods.

The above results suggest that increase in egg weight enhances survivorship of the chicks, while extra parental investment to produce a C-egg increases hatching and possibly fledging success, as well as providing insurance against the loss of the A- or B-egg. The observed growth rates suggest that the C-chick has a negative effect on the growth of its elder sibs, and that parental experience affects chick growth in a positive manner.

Twenty-eight nests containing either three A-, three B-, or three C-eggs of similar weight, and laydate, which hatched synchronously, were followed, and compared to control nests where the eggs hatched asynchronously.

Hatch weights were similar for all chicks, except the control C-chicks which hatched lighter than their brood mates, and the experimental C-chick. Similarly, control C-chicks exhibited slower growth rates compared to brood mates and experimental C-chicks. Comparisons between the other chicks revealed no significant differences in their growth rates. In comparing survivorship, to 40 days post-hatch, there was a trend for experimental A- and B-chicks to have lower survival probabilities compared to their control counterparts. On the other hand, control C-chicks exhibited a lower probability of survival compared to experimental C-chicks. This is due to the fact that control C-chicks were only able to obtain food in 20 % (n=15) of the observed feedings.

The above results support Lack's (1954) hypothesis, in that, A) survivorship in asynchronous nests was concentrated in the older, and presumably fitter, chicks (i.e., A and B), whereas in experimental (synchronous) broods, the A- and B-chicks had a similar chance of survival as the C-chick; and B) the C-chick in control nests was lost soon after hatching, and thus its elder sibs could expect to obtain more food, and hence a higher level of fitness.

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GENERAL INTRODUCTION

The reproductive effort of birds and probably animals in general, in any given year, represents a delicate balance between the expected lifetime reproductive success, and the proportion of that future reproductive success represented by the current offspring (Williams 1966; Trivers 1972, 1974; Dawkins and Carlisle 1976). The weight that each of these elements receives towards determining the amount of reproductive effort during any given reproductive season may be affected by several factors. Two of these factors, which are not mutually exclusive, are food availability, and parental age or experience. That is, if food conditions become less than optimal, parents should reduce the amount of care they provide their offspring, and intuitively, this should be more pronounced in younger, less experienced adults (Skutch 1967; Carlisle 1982).

In species of birds of the family Laridae, reproductive effort during a single breeding season may be examined by comparing investment patterns within a clutch/brood, and between clutches/broods, assuming that egg and clutch sizes are affected by food availability and parental experience. Since gulls, in general, subsist on an ephemeral food supply, they have evolved several strategies which enable them

to maximize their reproductive effort according to food availability and parental experience. It was the purpose of this study, to examine the effect of varying egg and clutch sizes, and hatching asynchrony on parental reproductive success in the Herring Gull.

The American Herring Gull (Larus argentatus smithsonianus Coues) (Godfrey 1966) is a neritic, colonial nesting species, eurytopic in its choice of breeding habitat (Buckley and Buckley 1980). Although it prefers to nest on the rocky cliffs and meadows of islands (Drury and Nisbet 1973; Haycock and Threlfall 1975; Buckley and Buckley 1980; Pierotti 1982) it also nests in salt marshes (Burger 1977), barrier beaches (Erwin et al. 1981), trees and rooftops (Monaghan 1979; Buckley and Buckley 1980) and along the margins of inland lakes and streams (Southern 1980). As with many larid species (Burger 1979), the Herring Gull nests in association with other larids, most notably Great Black-backed Gulls (L. marinus L., Paynter 1949; Erwin 1971; Parnell and Soots 1975), Ring-billed Gulls (L. delewarensis Ord., Schoen and Morris 1984; Southern and Southern 1984), and Laughing Gulls (L. atricilla L., Burger 1977, 1979).

The Herring Gull has a type-c territory (Hinde 1956), which serves as a mating and nesting territory and also provides chicks with protection from neighboring adults (Tinbergen 1956). The size of the territory varies through the breeding cycle and according to the type of intruder (Burger

1980). That is, there is a "unique" territory which is defended against all intruders, and "primary" and "secondary" territories which are defended against neighbors and non-neighbors, respectively (Burger 1980). The size of the "unique" territory averages between 20 m during the pre-incubation stage and 60 m during the chick stage (Burger 1980). Average inter-nest distances range from 1-2 m on debris beaches and up to 10-15 m in meadows (Drury and Nisbet 1973).

The modal clutch size of the Herring Gull is three, with clutches of two being common, while four- and five-egg clutches are infrequent, and possibly the result of female-female pairs (Tinbergen 1953; Kadlec and Drury 1968; Parsons 1970; Drury and Nisbet 1973; Graves et al. 1984; Nisbet and Drury 1984). Even though the common clutch-size is three, most pairs fledge on average one chick (Paynter 1949; Harris 1964; Kadlec and Drury 1968; Haycock and Threlfall 1975). Three-egg clutches are more successful than two-egg clutches (Harris 1964; Kadlec and Drury 1968; Haycock and Threlfall 1975). The first objective of this study was to examine the effects of clutch-size on parental investment with respect to chick fitness levels and parental reproductive success. In addition, the clutch manipulations undertaken provided a test of the "insurance-egg" hypothesis (Dorward 1962).

In three-egg clutches, the laying interval between the first and third egg averages four days (MacRoberts and Mac-

Roberts 1972), and consequently the last chick hatches 1-4 days after the first and second chicks (Haycock and Threlfall 1975). In addition to hatching later than its elder sibs, the last-hatched chick is lighter at hatching (Parsons 1975a). In combination, asynchronous hatching and the small size of the last-hatched chick increase its mortality rate during the first week post-hatch (Parsons 1970, 1972, 1975a) compared to its brood mates. The second objective of this study was to examine the effects of asynchronous and synchronous hatching on chick fitness and survival (up to 40 days post-hatch), parental reproductive success, and brood reduction.

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Chapter I

SOME EFFECTS OF CLUTCH SIZE ON REPRODUCTIVE SUCCESS

1.1 INTRODUCTION

Parental investment (PI) as defined by Trivers (1972) is, "...any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." In birds, "other" offspring may be seen as either future offspring (from another reproductive effort), or as contemporaneous members of a clutch or brood. In the first instance, the cost to the future offspring of current investment levels is difficult to quantify, and may be compounded by many factors. Egg-size in gulls and terns, for example, is positively correlated to female age and/or breeding experience (e.g., Davis 1975; Coulson and Horobin 1976; Mills 1979; Thomas 1983; Nisbet et al. 1984). Conversely, egg-size is negatively correlated with time of laying (Parsons 1972; Mills 1979). Operative sex-ratios may also affect egg-size (Trivers 1974; Howe 1976; Ryder 1983).

It may be assumed that the above factors which compound the effects of differential investment between seasons are

constant within a season, and within a clutch. However, variability may be expected to occur between clutches with respect to the age and experience of the pairs within the population. Consequently the cost of increased investment in one egg/chick at the expense of a contemporary may be readily examined by comparing relative parameters of investment within a clutch or brood.

There is substantial evidence indicating that females can vary egg weight within a clutch. In general, small altricial birds increase egg weight with laying order (Clark and Wilson 1981, and references therein). In gulls, (Herring Gull: Parsons 1970, Davis 1975; Great Black-backed Gull: Harris 1964; Laughing Gull: Hahn 1981; Red-billed Gull L. novaehollandiae Stephens., Mills 1979), terns [Common Tern Sterna hirundo L., Nisbet 1978a; Caspian Tern S. caspia (Pallas), Quinn 1980] some penguins (Williams 1980) and eagles (Gargett 1982; Edwards and Collopy 1983, and references therein) egg weight decreases with laying order.

In gulls the factors that affect decreasing egg weight with laying order have received considerable attention. In three-egg clutches, the A- and B-eggs are similar in weight, and both are significantly larger and heavier than the C-egg (Parsons 1970, 1975a; Mills 1979; Hahn 1981; Thomas 1983). Parsons (1970, 1972) argued that the proportionately higher mortality of Herring Gull C-chicks in the first week post-hatch resulted directly from hatching after the A- and B-

chick, but especially due to its smaller size (Parsons 1975a). Lundberg and Vaisanen (1979) came to a similar conclusion from their work on Black-headed Gulls (L. ridibundus L.).

Parsons (1972) concluded that the proximate cause of the smaller C-egg was the onset of incubation which reduces albumin secretion. In addition, Parsons found that the C-egg had relatively less yolk. The smaller size of the C-egg, however, reduces its incubation period and hence also the degree of intra-clutch hatching asynchrony. Ultimately this reduces the C-chick's probability of mortality in the first week post-hatch (Parsons 1972). Nisbet (1973) found a correlation between quality of courtship feeding and the weight of the C-egg in Common Terns. However, no such correlation has been found in Herring Gulls (Niebuhr 1981).

Parsons (1971a, in Parsons 1975b) experimentally removed eggs and showed that Herring Gulls could lay more than three eggs/clutch, and suggested that reduced egg and clutch sizes were not due to a lack of food for the production of eggs.

Hatching asynchrony has been proposed as an adaptation which in concert with the smaller size of the C-egg/chick, facilitates brood reduction (O'Connor 1978; Hahn 1981; Braun and Hunt 1983; but see Clark and Wilson 1981 for an opposing view, and counter argument by Richter 1982). However, Parsons (1975a) manipulated clutches in which C-eggs hatched

first, and despite this advantage the C-chicks did not survive as well as A- or B-chicks. Consequently, Parsons concluded that egg-size and subsequently chick-size contributed most importantly to brood reduction in the Herring Gull.

It appears that egg size can be controlled by the female and that chick survival is correlated to egg size. Thus it may be hypothesized that if adequate resources are available, a female will invest proportionately more in her eggs, especially the C-egg, since its probability of survival depends directly on its size. The first aim of this study was to examine parental investment patterns within clutches of three and two eggs, by comparing egg weights as a function of clutch weight.

Lack et al. (1957) have argued that the most common clutch-size would, on average, be the most successful. In many gulls the most common clutch size is three, although clutches of two are not uncommon (Harris 1964; Parsons 1970; Burger 1974; Davis 1975; Ryder 1975; Davis and Dunn 1976; Lundberg and Vaisenen 1979). Several researchers have reported that Herring Gulls that laid three eggs experienced higher hatching and fledging success than those that laid two eggs (Paynter 1949; Harris 1964; Kadlec and Drury 1968; Haycock and Threlfall 1975; Parsons 1975b), despite the fact that adults rarely raise three fledglings in one breeding season (Davis 1975; Parsons 1975b; Chabrzyk and Coulson 1976; Monaghan 1979). In fact, Nisbet and Drury (1972)

found that two was the optimum fledgling number in Herring Gulls, since parents could not care adequately for three flying young. This agrees with Graves et al. (1984) who found that raising a brood of three greatly increased reproductive effort of Herring Gulls. Graves et al. (1984) also found that in those broods where the C-chick survived for three days or more, the B-chick gained weight more slowly. By providing some pairs with additional food, they significantly increased the number of C-chicks that fledged. Thus the C-chicks' chances of survival are minimal unless the food supply is unusually good, or if either or both the A- or B-chicks are lost early (Graves et al. 1984). Graves et al. (1984), hypothesized, that the benefit of the C-egg/chick is in its insurance value against the loss of the A- and/or B-eggs/chicks.

Dorward (1962) first proposed the "insurance egg" hypothesis as an adaptation for the second egg in White (Sula dactylatra Lesson.) and Brown [S. leucogaster (Boddaert)] boobies. These species lay two eggs, but rarely fledge both chicks. The second egg is hypothesized to insure against the loss or infertility of the first laid egg and/or the early demise of the first-hatched chick. If the first egg/chick is healthy, then the second chick is eliminated through obligate siblicide (Dorward 1962; Mock 1984). Kessler (1969) found in the Blue-faced (=White) Booby, that B-chicks survived in 22 % of the nests. Cash (1985) obtained

similar results conducting experiments on the American White Pelican (Pelicanus erythrorhynchus Gmelin).

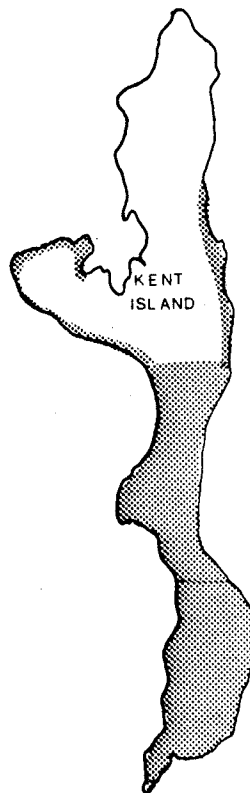
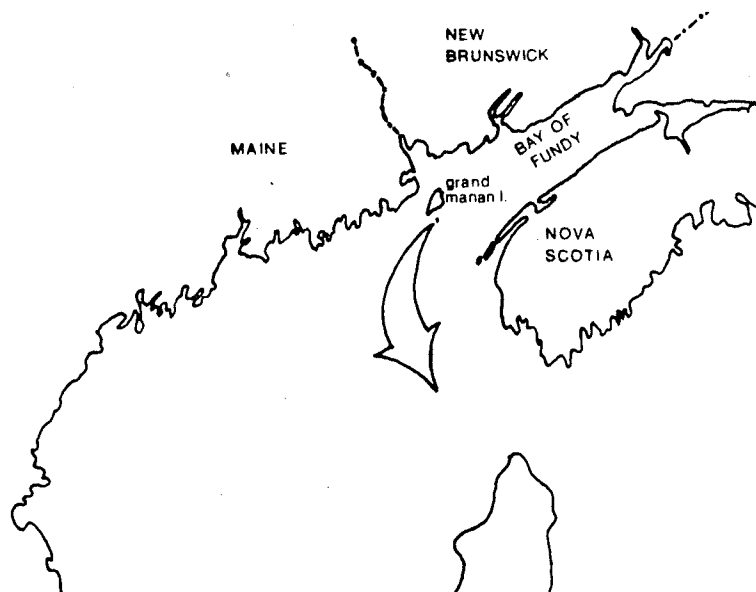
The cost of laying an insurance egg is presumably compensated for by an increase in parental reproductive success (Kepler 1969). In Herring Gulls, for example, adults laying three eggs do better than those laying two. The cost of the insurance egg may be more exacting in Herring Gulls since, as reported by Graves et al. (1984), the presence of the C-chick reduces the fitness levels of B-chicks. Graves et al. (1984) did not test the insurance egg hypothesis directly through clutch manipulation, as suggested by Mock (1984). Consequently, the second objective of this first project was to test the insurance egg/chick hypothesis in the Herring Gull, through clutch manipulation.

1.2 STUDY AREA

Kent Island, Bay of Fundy, New Brunswick, Canada (44° 35'N ; 66° 45'W) is approximately five km west of Whitehead, N.B., and 25 km southeast of Grand Manan, N.B.(Fig.1). Kent Island is at the southern extremity of the Grand Manan archipelago (Cannell and Maddox 1983), and runs in a north-south direction.

This 75.0 ha. island is divided roughly into three general habitat types (excluding the rocky shoreline): a spruce [Picea mariana (Mill.)] BSP. forest at the north end, a flat

Figure 1. Map of Kent Island, Bay of Fundy,
New Brunswick, Canada (44' 35" N;
66' 45" W). Stippling indicates
areas censused.



meadow in the centre, and a hilly meadow occupying the southern portion. The Herring Gull population used for this study was located at the south end of the island (Paynter 1949)(Fig.1). Dominant vegetation types in the colony included: dead spruce trees (at the northern edge of the colony), leafy-bracted aster (Aster subspicatus, Nees, 41.8 % relative cover), sheep sorrel (Rumex acetosella, L., 19.2 % relative cover), raspberry(Rubus idaeus L., 18.2 % relative cover), and hair grass [Deschampsia flexuosa(L.) Trin., 11.8 % relative cover] (A. McIlraith, pers. comm.).

Other bird species nesting in the colony included approximately 25 pairs of Common Eiders [Somateria mollissima (L.)] and about 10 pairs of Great Black-backed Gulls. Muskrats (Ondatra zibethica L.) and snowshoe hare (Lepus americanus Erxleben) were also present.

1.3 METHODS AND MATERIALS

I searched each day for nests beginning on 7 May 1984 through to 18 June, and on 20 and 22 June. The same route was used if possible to minimize disturbance.

All Herring Gull nests initiated in the study area were marked with numbered and/or lettered wooden stakes. Eggs were weighed to the nearest 0.5 g using a 100-g Pesola spring scale, and to the nearest 1.0 g using a 300-g Pesola when the egg weighed more than 100 g. Egg lengths and widths were recorded to the nearest 0.01 mm using calipers.

As the colony was visited almost daily, it was possible to determine the identity of eggs within the laying sequence. Each egg was marked either A, B or C, on the blunt end using a non-toxic felt marker.

1.3.1 Parental Investment And Clutch/Brood Size

C-eggs were removed from 31 3-egg clutches (experimental 2-egg clutches), from 1-30 days post-laying. In addition, 102 natural (control) 2-egg and 49 natural (control) 3-egg nests were followed from laying to hatching.

Chicks were weighed at hatching to the nearest 0.5 g using a 100-g Pesola spring scale. When chicks weighed more than 100 g, they were weighed to the nearest 1.0 g with a 300-g Pesola spring scale, and once they had exceeded 300 g, were weighed to the nearest 5.0 g using a 2000-g Chatillon kitchen spring scale with 25.0-g divisions. Culmen and tarsometatarsus (to tip of middle toe) were measured to the nearest 0.5 mm using calipers and/or a steel ruler. Chicks were banded at hatching with coloured plastic bands, and colour marked with non-toxic felt markers, to permit individuals to be identified. U. S. Fish and Wildlife Service aluminum bands were added when chicks were large enough. Weight, culmen, and tarsometatarsus measurements were taken every day until 3 days post-hatch of the A-chick, or until the last chick hatched, and every third day thereafter until 40 days post-hatch. If both A- and B-chicks hatched on the

same day, the chick with the drier plumage and/or no egg-shell fragments attached to it was assumed to be the A-chick. Since only one control B-egg was recorded to have hatched before the A-egg in this study (n=182), the above assumption seems valid.

Data were also collected on the contents of chick regurgitations, and the presence of wounds or bare skin patches on chicks.

1.3.2 Statistical Analysis

Data were analyzed using tests from the SAS package. Correlation between fresh egg weight versus total clutch weight was analyzed using Spearman Rank correlation tests. This relationship was also examined using linear regression (Zar 1984). Mean fresh egg weights were compared within and between experimental groups using the t-test in the SAS package. Since sample sizes were drastically reduced at hatch, chick mass, culmen and tarsometatarsal measurements at hatch are analyzed using the SAS non-parametric program (Wilcoxon Rank Sum Test).

Chick growth rates (up to 40 days post hatch) were estimated using three parameters: chick weight (ln g/day), culmen length (mm/day) and tarsometatarsus (mm/day). The rate of growth for each of these parameters was calculated for each chick through linear regression. The resultant slopes

and y-intercepts were then averaged for each chick type (i.e. control A, etc.). However, only data from chicks surviving to at least the third day post-hatch were used in this analysis. The slopes were then compared using the Wilcoxon Rank Sums test in the SAS package. Survivorship probabilities were calculated and analyzed using the Mayfield (1975) method (see Appendix C for sample calculation).

1.3.3 Behavioural Observations

Six blinds (1.5 m x 1.5 m x 1.5 m) made of particle board were placed in the colony during the week of 14-21 May. Two were eventually used for this study. Observations were made each morning from 16-25 May to determine the onset of egg laying, and to gain familiarity with possible nest locations.

Observations of broods were made on 2, 6, 9 July and every day thereafter, fog permitting, through to 12 August. Observations were made on "cohorts" (focal group, Altmann 1974) of 2-6 broods. The size of the cohort varied according to the survival of chicks in it. Cohorts were observed for one hour each/day. Data collected during observation periods included: 1) the order in which chicks arrived at a parental regurgitate (i.e., first=1, second=2 etc., ties were given the average rank), 2) which chicks obtained food, and 3) aggression between chicks, and the identity of the chicks involved.

1.4 RESULTS

1.4.1 Egg Laying

The first egg was found on 18 May. Clutch initiation peaked on 4 June, and by 8 June 75.3 % of all 2- and 3-egg clutches had been initiated ($n=320$) (Fig. 2). Clutch initiation for 3-egg clutches ($n=151$) peaked on 4 June, and 83.4 % of all 3-egg clutches recorded were initiated by 8 June (Fig. 2). Initiation of 2-egg clutches ($n=169$) peaked on 6 June, and by 10 June 82.5 % of all 2-egg clutches had been initiated (Fig. 2).

1.4.2 Clutch Apportionment

The fresh weight of A-, B-, and C-eggs in 3-egg clutches and A- and B-eggs in 2-egg clutches were all strongly positively correlated with total clutch weight (Table 1). Regression slopes of fresh egg weight versus clutch weight were similar between A- and C-eggs, and B- and C-eggs in 3-egg clutches (Table 1). However, A-eggs increased significantly more rapidly in fresh weight versus clutch weight than did B-eggs ($t=2.09$, $df=170$, $P<0.05$) (Table 1). For 2-egg clutches, the regression slopes of fresh egg weight versus clutch weight for A- and B-eggs differed significantly ($t=2.55$, $df=154$, $P<0.02$) (Table 1).

To examine further the relationship between egg weight and clutch weight in 3-egg clutches, the 87 clutch weights observed were

Figure 2. Frequency distribution of clutch initiation dates
for 3- and 2-egg clutches, in three day intervals.

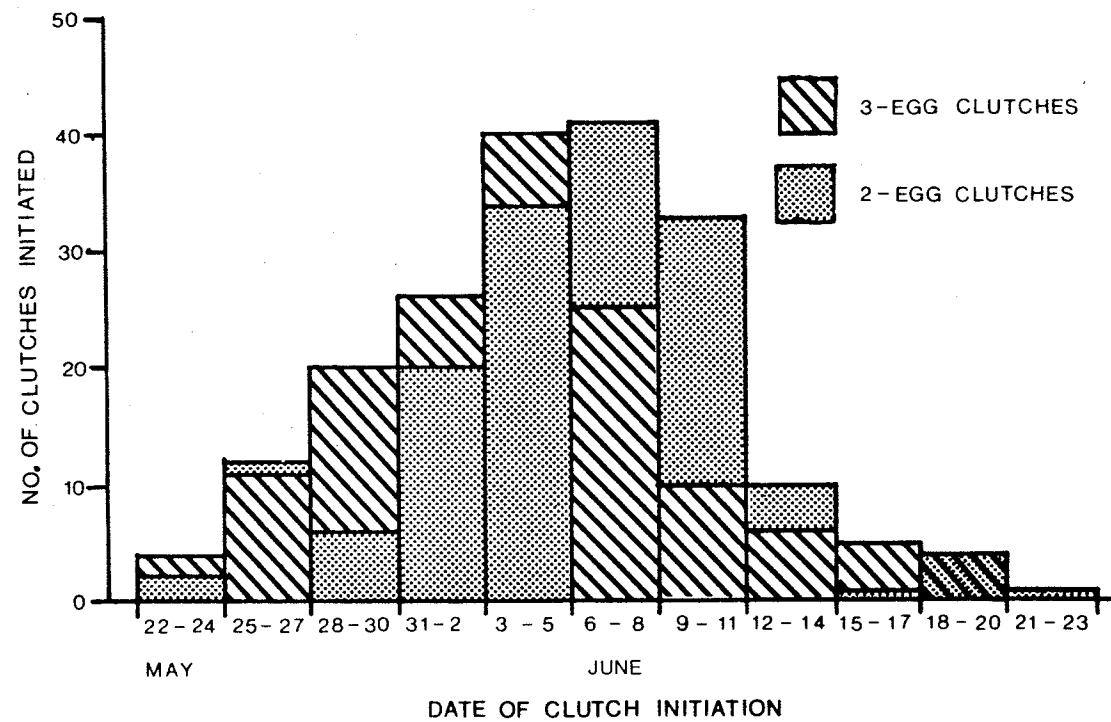


Table 1. Spearman Rank Correlations, and linear regression coefficients of egg weight versus clutch weight.

CLUTCH TYPE	EGG	N	SPEARMAN CORRELATION		SLOPE (g)	Y-INTERCEPT	r^2
			COEFFICIENT	P			
CONTROL 3	A	138	0.8453	0.0001	0.3519	-1.72	0.81
	B	138	0.8973	0.0001	0.3101	7.93	0.88
	C	138	0.8476	0.0001	0.3285	-3.99	0.81
CONTROL 2	A	160	0.9297	0.0001	0.5287	-2.48	0.93
	B	160	0.8977	0.0001	0.4709	2.54	0.91

grouped into three equal sized classes: light, moderate and heavy. The mean weights of A-, B-, and C-eggs were then calculated for each group (Table 2). The difference in the slope of egg weight versus clutch weight between A- and B-eggs was mainly due to a significant difference in their means in moderately heavy clutches ($t=3.98$, $df=102$, $P<0.001$). A similar trend was observed when the mean weights of B and C-eggs were compared. B-eggs were significantly heavier than C-eggs, but especially so in moderately heavy clutches (Table 2). These results are paralleled by the fact that the regression coefficient for the B-egg is greater than those of A- and C-eggs (Table 1).

1.4.3 Egg Loss

Egg loss within five days of laying was recorded, within five days of clutch completion, for 3- and 2-egg clutches not involved in manipulations within five days of clutch completion. Egg loss was highest for A-eggs in both 2- and 3-egg clutches, but was significantly higher in 2-egg clutches ($X=6.20$, $df=1$, $P<0.025$; Fig. 3). There was no difference in the proportion of B-eggs lost between 3- and 2-egg clutches ($X=1.72$, $df=1$, $P>0.10$). In 3-egg clutches there was no significant difference in the rate at which A-, B- and C-eggs were lost ($X=2.33$, $df=2$, $P>0.25$; Fig. 3), while in 2-egg clutches, significantly more A- than B-eggs were lost within five days of laying ($X=6.35$, $df=1$, $p<0.02$;

Table 2. Mean fresh egg weights ($g \pm S.E.$) from light, moderate and heavy 3-egg clutches.

CLUTCH WEIGHT	MEAN WEIGHT OF EGGS		
	A	B	C
LIGHT (43) ¹	83.55 \pm 3.29	83.03 \pm 1.51	75.40 \pm 3.67
MODERATE (52)	91.79 \pm 1.44	89.56 \pm 0.87	81.74 \pm 1.80
HEAVY (43)	96.90 \pm 4.92	95.58 \pm 3.08	88.15 \pm 3.15

() = no. of clutches

Figure 3. The proportion of eggs lost within five days of laying in 3-egg (hatched) and 2-egg (stippled) clutches. S. indicates a significant difference between A-eggs from 3- and 2-egg clutches, at $P=0.05$, using Chi-Square analysis.

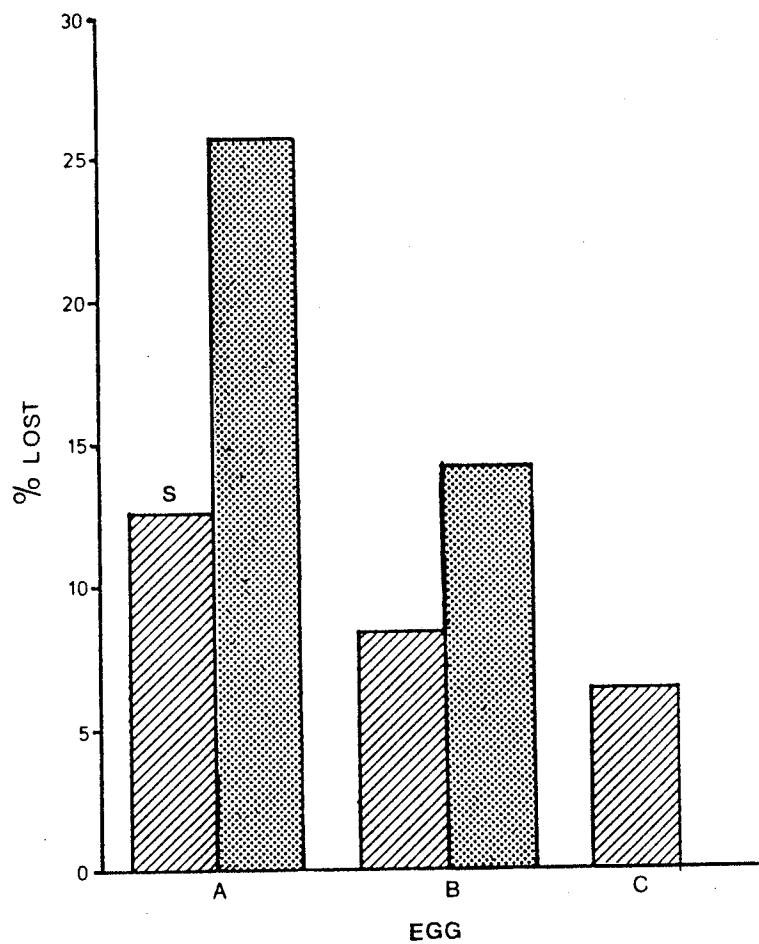


Fig. 3). Overall, egg loss within five days of egg laying was significantly greater in 2-egg as compared to 3-egg nests (20.21 % vs 9.21 % ; $X = 13.57$, $df=1$, $P<0.001$).

1.5 EFFECT OF CLUTCH/BROOD SIZE ON CHICK FITNESS

1.5.1 Egg Laying

Peak clutch initiation in 2-egg control nests occurred on 6 June, while initiation of experimental 2-egg and control 3-egg clutches peaked on 4 June and 2 June, respectively.

Mean fresh weights of A- and B-eggs in control 2-egg clutches were significantly different ($t=3.97$, $df=202$, $P<0.001$). This may be partially the result of finding a three-egg nest after the A-egg was lost, and then calling it a two-egg nest. There was no significant difference ($t=1.021$, $df=60$, $P>0.20$) in the mean fresh weights of experimental A- and B-eggs (Table 3) or control 3-egg A- and B-eggs ($t=0.52$, $df=96$, $P>0.50$). Both A- and B-eggs were heavier in experimental clutches than those in control 2-egg nests (A vs A, $t= -2.52$, $df=131$, $P<0.02$; B vs B, $t=-5.34$, $df=131$, $P<0.001$; Table 3). Since experimental 2-egg clutches were originally 3-egg clutches, they had similar weights as A- and B-eggs in control 3-egg clutches (Table 3). A-eggs were similar between control 3- and 2-egg clutches ($t=1.12$, $df=149$, $P>0.20$), however, B-eggs in control 3-egg clutches were significantly heavier than those in control 2-egg clutches ($t=6.45$, $df=149$, $P<0.001$; Table 3).

Table 3. Comparison of mean fresh egg weights within 3- and 2-egg control clutches, and experimental 2-egg clutches.

CLUTCH TYPE	EGG	N	\bar{x} WEIGHT \pm S.E. (g)	COMPARISON	t	df	P
CONTROL 3	A	49	89.03 \pm 0.96	A vs B	0.52	96	>0.50
	B	49	88.36 \pm 0.85	B vs C	6.04	95	<0.01
	C	48	80.32 \pm 1.03	A vs C	6.17	95	<0.01
CONTROL 2	A	102	87.67 \pm 0.75	A vs B	3.97	202	<0.01
	B	102	82.94 \pm 0.25				
EXPERIMENTAL 2	A	31	91.05 \pm 1.06	A vs B	1.02	60	>0.20
	B	31	89.62 \pm 0.90				

1.5.2 Hatching Success

Hatching success (#eggs hatched /clutch) in control 3-egg nests was almost twice that of control 2-egg nests (Table 4; $t=-4.48$, $df=149$, $P<0.001$). Experimental 2-egg clutches also had a higher mean hatching success as compared to control 2-egg clutches ($t=-3.26$, $df=131$, $P=0.001$). Control 3-egg clutches and experimental 2-egg clutches had similar mean hatching success ($t=-0.79$, $df=78$, $P=0.42$; Table 4).

1.5.3 Hatching Sizes

Within brood types, chicks in experimental 2-chick (E2) broods had similar hatching weights, culmen lengths and tarsometatarsal lengths at hatch (Table 5). In control two-chick broods (C2), A-chicks hatched significantly heavier than B-chicks ($Z=2.96$, $P=0.003$), and also had longer culmens ($Z=2.69$, $P=0.007$) but tarsometatarsal lengths were similar (Table 5). In control 3-chick (C3) broods, A- and B-chicks were significantly heavier, and had longer tarsometatarsi at hatching, compared to C-chicks. Culmen lengths at hatch were similar between the three chicks.

Among groups, the respective A- and B-chicks had similar hatch weights, except for B-chicks in C2 broods which hatched significantly lighter than their E2 ($Z=4.03$, $P=0.001$) and C3 counterparts ($Z=2.89$, $P=0.003$; Table 5). Similarly only C2 B-chicks had significantly smaller culmen

Table 4. Hatching success (eggs/nest) in control 3, and 2,
and experimental nests.¹

CLUTCH TYPE	$\bar{x} \pm \text{S.E.}$	% EGGS HATCHING (n)
CONTROL 3	1.73 ± 0.16^A	58.5 (147)
CONTROL 2	0.95 ± 0.09^B	48.0 (204)
EXPERIMENTAL 2	1.54 ± 0.13^A	77.0 (62)

1. Means with the same letter are not statistically different
at $P=0.05$, using a two-tailed t-test.

Table 5. Comparison of chick weight, and culmen and tarsometatarsus (to tip of middle toe) lengths at hatch, for chicks in control 3-, 2-, and experimental 2-chick broods.

BROOD TYPE	CHICK	HATCH WEIGHT		CULMEN LENGTH		TARSOMETATARSUS	
		($\bar{x} \pm$ S.E.) (g)	n	($\bar{x} \pm$ S.E.) (mm)	n	($\bar{x} \pm$ S.E.) (mm)	n
CONTROL 3	A	63.32 ± 1.32^A ¹	14	17.50 ± 0.24^A	13	60.96 ± 0.76^A	13
	B	63.42 ± 1.66^A	14	17.25 ± 0.23^A	14	59.85 ± 0.52^A	14
	C	57.00 ± 2.08^B	14	17.00 ± 0.27^A	11	57.00 ± 1.19^B	11
CONTROL 2	A	61.45 ± 0.85^A ²	28	17.65 ± 0.18^A ³	26	58.90 ± 0.43^A ⁴	26
	B	57.59 ± 0.80^B ²	28	16.83 ± 0.19^B ³	26	57.90 ± 0.67^A ⁴	26
EXPERIMENTAL 2	A	63.88 ± 1.21^A	20	17.65 ± 0.18^A	20	58.95 ± 0.15^A ⁵	19
	B	64.13 ± 1.11^A	19	17.67 ± 0.21^A	18	58.72 ± 0.60^A	18

1. See Table 4. for explanation

2. Significantly different (P 0.05) compared to C3 and E2 counterparts

3. Significantly different compared to E2 counterpart

4, 5. Significantly different compared to C3 counterpart

lengths at hatch compared to those in E2 broods ($Z=2.72$, $P=0.009$; Table 5). Finally, with respect to tarsometatarsus length at hatch, all chicks were similar except the C2 B-chick which had significantly shorter tarsometatarsi compared to C3 B-chicks ($Z=2.08$, $P=0.03$), and the E2 A-chick compared to the C3 A-chick ($Z=2.13$, $P=0.03$; Table 5).

Correlations between egg weight, hatch weight and tarsometatarsus length at hatch, and survivorship were examined using Spearman Rank Correlations. Egg weights for eggs in C3 and C2 clutches were all positively correlated to hatch weight (Table 6). Hatch weights were also positively correlated to tarsometatarsus length at hatch, but only significantly so for B- and C-chicks in C3 broods, and B-chicks in C2 broods. Hatch weight of A-chicks in C3 broods was positively correlated with survivorship, and C-chicks nearly so ($P=0.065$). Tarsometatarsal length was also positively correlated to survivorship for the C-chick (Table 6).

1.5.4 Chick Weight

A- and B-chicks in C2 broods gained weight at a similar rate ($Z=-0.54$, $P=0.58$) as did A- and B-chicks in E2 broods ($Z=0.35$, $P=0.71$; Table 7). A- and B-chicks in C3 broods had similar growth rates ($Z=0.09$, $P>0.92$), and these were both significantly greater than that of the C-chick (A vs C, $Z=2.16$, $P=0.03$; B vs C, $Z=2.20$, $P=0.02$).

Table 6. Spearman Rank Correlations between egg weight (EWT), hatch weight (HWT), tarsometatarsus (to tip of middle toe) length at hatch (TAR), and the number of days post-hatch (up to 40 days) a chick survived (DAYS). Only significant results are presented.¹

		<u>EWT vs HWT</u>	<u>HWT vs TAR</u>	<u>HWT vs DAYS</u>	<u>TAR vs DAYS</u>
		CORR. COEFF.			
		N			
CLUTCH TYPE	CHICK				
<hr/>					
CONTROL 3	A	0.7231		0.5726	
		14		15	
	B	0.8101	0.7468		
		13	14		
	C	0.8884	0.6429		0.5881
		12	11		11
CONTROL 2	A	0.5574			
		28			
	B	0.8147	0.6367		
		27	25		

1. $P \leq 0.05$

Table 7. Comparison of chick growth rates, up to 40 days post-hatch, for chicks in control 3-, 2- and experimental 2-chick broods. Growth rates were similar for A- and B-chicks between all groups.

BROOD SIZE	CHICK	n	\bar{x} SLOPE (ln g/day)	(\bar{x}) Y-INTERCEPT
			(\pm S.E.)	(\pm S.E.)
CONTROL 3	A	14	0.07 ± 0.01^A	4.20 ± 0.04
	B	14	0.06 ± 0.01^A	4.24 ± 0.03
	C	6	0.03 ± 0.01^B	4.11 ± 0.09
COANTROL 2	A	23	0.07 ± 0.01^A	4.17 ± 0.03
	B	17	0.06 ± 0.01^A	4.09 ± 0.03
EXPERIMENTAL 2	A	18	0.09 ± 0.01^A	4.19 ± 0.04
	B	12	0.08 ± 0.01^A	4.17 ± 0.05

1. See Table 4 for explanation

A-chicks from all three brood types grew at similar rates (C2 vs C3, $Z=0.70$, $P=0.48$; C2 vs E2, $Z=1.43$, $P=0.15$; C3 vs E2, $Z=-0.70$, $P=0.48$; Table 7). Similarly, B-chicks grew at the same rate (C2 vs C3, $Z=0.81$, $P=0.41$; C2 vs E2, $Z=1.57$, $P=0.11$; C3 vs E2, $Z=1.15$, $P=0.24$; Table 7).

1.5.5 Culmen and Tarsometatarsal Growth

Culmen and tarsometatarsus growth rates were similar for all chicks within and between groups (Table 8, 9). The lack of significant differences, especially those involving the C3 C-chick, are probably due to the small sample size ($n=4$).

1.5.6 Chick Survivorship

The Average Survivorship Probability/Day (ASP/D) for A and B-chicks was the same in C2 ($X = 1.94$, $df=1$, $P>0.10$) and E2 broods ($X = 1.15$, $df=1$, $P>0.25$; Table 10). There were also no differences for the A-chicks ($X = 0.02$, $df=1$, $P>0.75$) or B-chicks ($X = 0.07$, $df=1$, $P>0.75$; Table 10) between the groups.

There were no differences between A-chicks from C2 and C3 broods ($X = 0.66$, $df=1$, $P>0.25$). B-chicks from C3 broods had a higher ASP/D than did those from C2 broods, and this difference approaches significance ($X = 3.55$, $df=1$, $0.10>P>0.05$; Table 10).

Table 8. Comparison of growth rates for chicks in control 3-, 2-, and experimental 2-chick broods. Slopes were similar for all chicks.

BROOD SIZE	CHICK	n	\bar{x} CULMEN SLOPE (mm/day)	(\bar{x}) Y-INTERCEPT
			(\pm S.E.)	(\pm S.E.)
CONTROL 3	A	12	0.7 ± 0.09	16.67 ± 0.28
	B	11	0.5 ± 0.08	16.79 ± 0.28
	C	4	0.4 ± 0.19	17.12 ± 0.41
CONTROL 2	A	22	0.5 ± 0.07	17.33 ± 0.25
	B	16	0.6 ± 0.06	16.57 ± 0.26
EXPERIMENTAL 2	A	16	0.5 ± 0.07	17.45 ± 0.29
	B	12	0.4 ± 0.09	17.31 ± 0.31

Table 9. Comparison of tarsometatarsus (to tip of middle toe) growth rates.

Slopes were similar between all chicks.

BROOD SIZE	CHICK	n	\bar{x} TARSOMETATARSUS SLOPE (mm/day)	(\bar{x}) Y-INTERCEPT
			(\pm S.E.)	(\pm S.E.)
CONTROL 3	A	13	2.22 \pm 0.33	60.39 \pm 1.05
	B	11	1.86 \pm 0.26	59.89 \pm 0.59
	C	4	1.08 \pm 0.64	60.45 \pm 2.31
CONTROL 2	A	22	2.12 \pm 0.24	59.22 \pm 0.66
	B	16	1.79 \pm 0.24	57.63 \pm 1.07
EXPERIMENTAL	A	16	2.10 \pm 0.31	59.67 \pm 1.34
	B	12	2.24 \pm 0.20	58.85 \pm 1.27

Table 10. Comparison of Average Survivorship Probability/Day¹(ASP/D) for chicks in control 3-, 2- and experimental 2-chick broods.³

BROOD TYPE	CHICK	n	EXPOSURE DAYS	CHICKS DISAPPEARING	ASP/D
CONTROL 3	A	15	68	5	0.9256 ^{A2}
	B	15	65	5	0.9231 ^A
	C	15	33	12	0.6364 ^B
CONTROL 2	A	28	108	12	0.8889 ^A
	B	28	83	15	0.8193 ^A
EXPERIMENTAL 2	A	20	77	8	0.8162 ^A
	B	20	61	10	0.8361 ^A

1. See Appendix C for a sample calculation.

2. See Table 4. for explanation

3. ASP/D values were similar ($P > 0.05$) between respective A- and B-chicks

A-chicks from E2 and C3 broods had similar ASP/D's ($X = 0.39$, $df=1$, $P>0.50$). Although not statistically significant ($X = 2.35$, $df=1$, $P>0.10$), B-chicks from C3 broods had a higher ASP/D than did B-chicks in E2 broods (Table 10). C-chicks in C3 broods had a significantly lower ASP/D than A-chicks ($X = 10.51$, $df=1$, $P<0.005$) and B-chicks ($X = 10.12$, $df=1$, $P<0.005$).

1.5.7 Life Expectancy

Chick life expectancy, up to 40 days post-hatch, was calculated by taking the mean of the age at which chicks in each category disappeared (Table 11). Mean life expectancy of A- and B-chicks in C2 broods were not significantly different ($Z=0.98$, $P=0.31$). Mean life expectancy was similar for A- and B-chicks from E2 broods ($Z=0.69$, $P=0.48$; Table 11). A- and B-chicks from both groups had similar mean life expectancies (A vs A, $Z=-0.08$, $P=0.93$; B vs B, $Z=0.20$, $P=0.84$; Table 11).

In C3 broods, A- and B-chicks survived significantly longer than the C-chick (A vs C, $Z=10.51$, $P=0.005$, B vs C, $Z=10.12$, $P=0.005$). A-chicks from C3 broods survived, on average, three more days than A-chicks from C2 broods. However, this difference was not significant ($Z=1.15$, $P=0.24$; Table 11). Also there was no difference between the life expectancies of C3 and C2 B-chicks ($Z=1.49$, $p=0.13$; Table 11). Mean life expectancies of A- and B-chicks in C3 and E2

Table 11. Mean life expectancy (days \pm S.E.), up to 40 days post-hatch, for chicks in control 3,2 and experimental 2-chick broods.

BROOD SIZE	CHICK	N	\bar{x} LIFE EXPECTANCY
CONTROL 3	A	15	13.13 \pm 3.65
	B	15	9.20 \pm 2.40
	C	15	4.66 \pm 2.57
CONTROL 2	A	28	10.07 \pm 3.65
	B	28	8.75 \pm 2.35
EXPERIMENTAL 2	A	20	9.90 \pm 2.71
	B	20	9.05 \pm 2.80

broods were similar (A vs A, $Z=1.27$, $P=0.20$; B vs B, $Z=1.23$, $P=0.21$; Table 11).

1.5.8 Fledging Success

Fledging success was low in all groups (Table 12) (see Appendix B for a discussion) and statistical analysis was not attempted. However, C3 broods had the highest mean fledging success.

1.5.9 Behavioural Observations

Observations were made on 33 days between 2 July and 12 August. The following results involve only complete broods (unless chick-hours are stated) since the aim of these observations was to document interactions between chicks.

C2 broods were observed for 132 chick-hours (i.e., 1 hour observing two chicks=two chick-hours, etc.), and E2 broods were observed for 160 chick-hours. C3 broods were observed for 150 chick-hours.

On average A- and B-chicks from C2, C3 and E2 broods had equal chances of arriving first or second (or third) at a parental regurgitate, both within and between groups (Table 13). The slightly higher rank averages for C3 chicks is due to the fact that it was possible for these chicks to arrive in position number 3, and hence this would elevate their average.

Table 12. Fledging success (chicks/nest \pm S.E.)
for control 3, 2 and experimental
2-chick broods.

BROOD SIZE	N	\bar{x} CHICKS FLEDGING
CONTROL 3	45	0.33 ± 0.21
CONTROL 2	56	0.21 ± 0.09
EXPERIMENTAL 2	45	0.20 ± 0.13

Table 13. Mean rank (\pm S.E.) of position of arrival
at a parental regurgitate for chicks in
control 3, 2 and experimental 2-chick
broods.

BROOD TYPE	CHICK	\bar{x} RANK (n)
CONTROL 3	A	2.03 ± 0.19 (15)
	B	1.63 ± 0.13 (15)
	C	2.34 ± 0.18 (15)
CONTROL 2	A	1.57 ± 0.07 (7)
	B	1.42 ± 0.07 (7)
EXPERIMENTAL 2	A	1.56 ± 0.52 (9)
	B	1.44 ± 0.52 (9)

I observed 13 feeds in C2 broods, and 12 and 15 for E2 and C3 broods, respectively. In C2 broods, A and B-chicks participated in 92.3% and 100% of the feeds, respectively. In E2 broods, A- and B-chicks were each involved in 91.6% of the feeds. These differences are not significant within groups or between groups. A- and B-chicks in C3 broods were involved in 73.3% and 80.0% of observed feeds, respectively, whereas C-chicks participated in only 20.0%. This is significantly lower (A vs C, $X = 8.57$, $df=1$, $P < 0.005$; B vs C, $X = 10.80$, $df=1$, $P < 0.005$).

No acts of aggression were observed in C2 or E2 broods. However, 17 sib-sib altercations were observed in C3 broods, and they occurred at a rate of 0.11/chick-hour.

One A-chick (2.5%) from an E2 brood had a wound, as did three chicks (2xA, 1xB) (5.4%) from C2 broods. In C3 broods, 8 chicks (2xA, 3xB, 3xC) (17.2%) had wounds. Whether these wounds were inflicted by siblings or adults is not known.

1.6 DISCUSSION

Parsons (1970) and Nisbet (1973) found, in Herring Gulls and Common Terns, respectively, that chick survivorship was positively correlated with egg size. A similar situation exists in Black-headed Gulls (Lundberg and Vaisanen 1979) and the European Swift [Apus apus (L.)] (O'Connor 1979). Assuming offspring fitness rather than the number of off-

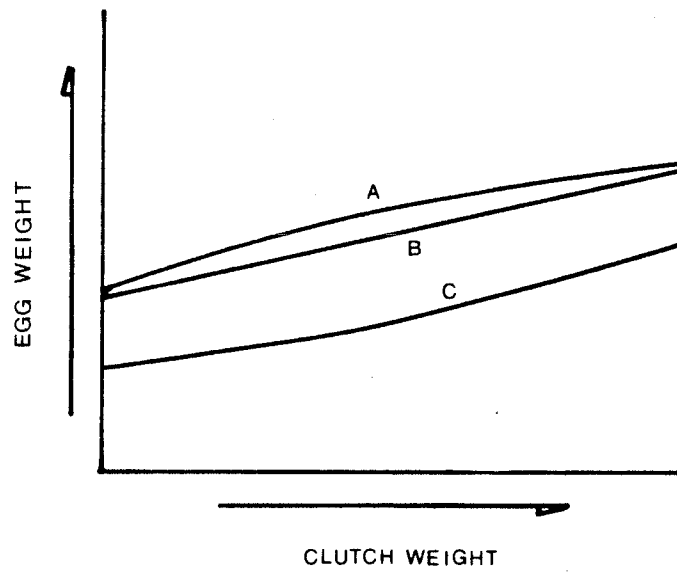
spring has been optimized by natural selection (Brockelman 1975) we may hypothesize that, given a set clutch size, a female should maximize her investment in each egg. That is, the more energy a female has for egg production, the more she should invest in each egg, so that its chance of survival is increased.

Evidence for this strategy may be found by comparing egg weight versus clutch weight. An increase in egg weight obviously increases the clutch weight. More important, however, is the pattern of investment within a clutch.

In 3-egg clutches the egg weight versus clutch weight slope of the A-egg was significantly steeper than that of the B-egg. This difference is due mainly to the fact that A-eggs in moderately heavy clutches were significantly heavier than B-eggs. There was also a trend for the weight of the C-egg to increase at a faster rate than the B-egg. Even though the B-egg was consistently heavier than the C-egg, the difference was slightly reduced at light and heavy clutch weights (Table 2). The average clutch apportionment patterns indicated by the above results can be graphed as in Fig. 4.

Several conclusions may be drawn from the above model. At light clutch weights (low energy reserves to invest in eggs) female Herring Gulls invest as much energy in the A-

Figure 4. Model approximating pattern of clutch apportionment for eggs in three-egg clutches. A, B and C indicate laying order.



as the B-egg, at a cost to the C-egg. To invest more into the A-egg would presumably reduce the amount of energy remaining for the B- and especially the C-egg, possibly below the level required to produce a viable C-egg. In fact, Parsons (1975a) found that females laying B-eggs smaller than 72 ml generally did not lay a third egg. He suggested that the reduction in clutch size is an adaptation which prevents the production of small eggs with a reduced chance of survival.

At heavier clutch weights (i.e., more energy invested in eggs) female Herring Gulls increase their investment in A- and B-eggs in similar proportions. The benefit in increasing the apportionment to already heavy A-eggs may not be significant since it may not significantly increase the A-chicks chance of survival, and may significantly reduce the chance of survival of the C-chick and possibly the B-chick (Smith and Fretwell 1974). This strategy is presented in Fig. 4, where the rate of increase in the weight of the A-egg tapers off at heavy clutch weights.

In the moderately heavy clutches, the B-egg is put at a disadvantage due to the proportionately greater increase in the weight of the A-egg. It may, however, benefit by having a shorter incubation period. As a result this would tend to decrease the size discrepancy between the A- and B-chick at hatch, and thus put the B-chick in a more favorable position should the A-chick be lost.

There is also a trend for female Herring Gulls laying heavier clutches to invest proportionately more into the C-egg compared to the B-egg. This seemingly paradoxical situation, however, may be resolved. In the Herring Gull, and other larid species, chick mortality in the first week post-hatch is usually greatest in the last-hatched chick (Brown 1967; Kadlec and Drury 1968; Davis 1975; Nisbet and Cohen 1975; Parsons 1975a; Haycock and Threlfall 1975; Lundberg and Vaisenen 1979; Braun and Hunt 1983). This mortality is often associated with starvation or cannibalism of wandering chicks as a result of an inefficient transition from incubation to chick rearing behaviour by the parents (Kadlec and Drury 1968; Parsons 1972, 1975a; Haycock and Threlfall 1975; Graves et al. 1984). Chicks hatching from heavier eggs have higher energy and water levels, which have been hypothesized to increase their probability of survival during this transition period (Parsons 1972). Since the B-egg has an advantage over the C-egg (both in weight and hatching date), regardless of clutch weight, a female Herring Gull may benefit more by investing proportionately more into the C-egg rather than the B-egg. Such a strategy would increase the C-chicks probability of survival, and yet the advantages accrued to the B-chick (as a result of hatching heavier and before the C-chick) are maintained.

As with other studies (Parsons 1970; Davis 1975; Thomas 1983), I found a positive correlation between hatch weight

and survivorship, but only significantly so for A-chicks in 3-chick broods and nearly so for C-chicks. Similarly, tarsometatarsus length at hatch was positively correlated to hatch weight, but only significantly so for the B- and C-chicks. The lack of a significant correlation between hatch weight and survivorship for B-chicks may be obscured by the effects of asynchronous hatching and was possibly confounded in this study by an extended period of fog which occurred during peak hatching (see Appendix B for a discussion). Examination of the effect of hatch weight on survivorship in an 'asynchronous' subsample of synchronously hatching broods (see Chapter 2) also produced similar results. Hence the survivorship of the B-chick may depend not only on its hatch weight, but also on the presence or absence of the A- and possibly the C-chick. Since B-chicks have similar hatch weights as A-chicks it is possible that survivorship in the B-chick is more dependent on the presence of the A-chick rather than the hatch weight of the B-chick.

That the survivorship of the A-chick is correlated to hatch weight, agrees with observations made by Parsons (1970) and Nisbet (1978a). This correlation is probably because heavier chicks hatch from heavier eggs, and hence have more stored energy. That the 'extra' weight of the A-egg indicates an increase in weight of the A-chick, and not its size per se, is evidenced by the fact that neither its egg weight or hatch weight were correlated to culmen or tarsome-

tatarsus length at hatch. Thus this reserve may be important when the parents switch from incubating to brooding. As previously mentioned the inefficiency of this transition has been suggested to be a major cause of chick mortality in the first week post-hatch.

Unlike the B-chick, the probability of the C-chick surviving is correlated to hatch weight. Intuitively, this is probably because the C-chick is invariably lost in the first week post-hatch (Parsons 1970, 1975a) and hence mortality may be slightly delayed in those C-chicks heaviest at hatching as suggested by the results of the present study.

That tarsometatarsus lengths at hatch for the B- and C-chicks are correlated to hatch weight, may indicate yet another pattern of differential investment by females in their eggs. In addition, there was also a significant correlation between tarsometatarsus length at hatch and survivorship of the C-chick, as well as a trend in the same direction for the B-chick. C-chicks hatched with proportionately longer tarsometatarsi as evidenced by the fact that, although, A-chicks hatched 10 % heavier than C-chicks, on average, the difference in tarsometatarsal lengths was only five percent.

The above results are important with respect to the breeding ecology of the Herring Gull. Firstly, the C-chick hatches between 1 and 4 days after the A-chick (Parsons 1975a; Haycock and Threlfall 1975; this study), at a time

when the parents have presumably begun the transition from incubating to brooding. That this transition begins before the C-egg hatches is supported by the fact that in this study, the C-egg had a relatively high rate of hatch failure (22.2 %, n=45). Second, the need for nutrient reserves in the C-chick, although important, is not at a premium as in the A- and possibly the B-chick, but rather well developed tarsometatarsi may have an adaptive significance. The adaptive value of relatively long tarsometatarsi is readily observed if we consider the fact that at about the time the C-egg hatches, the parents are beginning to feed the chicks away from the nest (Graves et al. 1984; this study), which presumably puts the C-chick at a further disadvantage. However, this disadvantage may be reduced if C-chicks hatched with proportionately longer tarsometatarsi, which presumably enhances their ability to locomote.

To my knowledge, there is no suggestion in the literature that females can control how embryos use the available nutrients in the egg. One possible mechanism, would have the female vary the ratio of nutrients in the egg. Hence, the C-egg and to some degree the B-egg may contain relatively greater proportions of specific nutrients required for bone development.

Clutch apportionment in 2-egg clutches was similar to that of 3-egg clutches. The relationship between egg weight and clutch weight had a higher regression coefficient, how-

ever. This is probably due to the fact that there are only two eggs (i.e. variables) as opposed to three.

Unlike 3-egg clutches, the weight of A-chicks in 2-egg clutches did not correlate significantly with survivorship. Smaller clutches are in general laid by younger less experienced birds (Coulson and White 1958; Mills 1979; Coulson and Horobin 1976). Thus it may be argued that younger birds which lay large eggs are not able to profit from this increased investment in a consistent manner. Also, the effectiveness with which young birds make the transition from incubation to brooding may vary to such an extent as to mask any benefits that might result from laying heavier eggs.

As with B-chicks from three-chick broods, an increase in B-chick hatching weight did not affect survivorship. Presumably the reasons for this are similar to those discussed for B-chicks in three-chick broods. Tarsometatarsus length at hatch was positively correlated to hatch weight, but not to survival. Presumably the same arguments put forth for B-chicks in three-chick broods are also in effect here.

In summary, it appears that female Herring Gulls can vary the apportionment of energy and nutrients in eggs according to their position in the laying order. Differences in egg weights appear to increase survivorship in the A- and C-chicks, in three-chick broods. Although a similar relationship was not found for B-chicks, its existence may be ob-

scured by several factors. Survivorship of the C-chick also appears to be dependent on tarsometatarsal length at hatch, and this may also be under parental control.

In addition to varying PI between eggs, there is evidence that PI varies between pairs in that some gulls lay two eggs rather than three. The last-laid egg in birds that typically lay two eggs has been hypothesized to act as an insurance egg against infertility of the first-laid egg, or the early demise of the first-hatched chick. Evidence for the "insurance egg" hypothesis is generally circumstantial. It is comprised of reports that pairs laying the modal clutch size have a higher hatching and fledging success than those pairs laying smaller clutches (Dorward 1962; Nisbet and Cohen 1975; Stinson 1979). In the Herring Gull, considerable evidence suggests that parents with 3-egg clutches are on average more successful than those with 2-egg clutches (Harris 1964; Kadlec and Drury 1968; Parsons 1975b). In addition, Graves et al. (1984) succeeded in increasing fledging success in Herring Gulls with 3-chick broods by supplementing them with food for the first five days post-hatch of the A-chick. The increase in the fledge rate was due to an increase in the number of broods fledging the C-chick. Graves et al. (1984) concluded that although food demands are low, the parents are not providing enough food to ensure the survival of the entire brood. From this, they argued that because the C-chick is usually lost shortly after hatching,

and its extended survival reduces the growth rate of the B-chick, the C-egg/chick must therefore be an insurance egg/chick.

The results of this study clearly suggest that the C-egg acts as an insurance egg in Herring Gulls. Overall hatching success in control three-egg clutches was significantly greater than that of control two-egg clutches. This is due to the fact that the loss of one egg in 3-egg nests reduces hatch success by one-third, whereas in 2-egg clutches the loss of one egg reduces hatch success by one-half. These data agree with the insurance egg hypothesis, but are not proof, since the higher hatching success is a result of having three eggs, and not solely due to the presence of the C-egg.

Critical evidence supporting the insurance egg hypothesis may be found in the fact that the C-egg provided insurance for the hatching failure of A- and B-eggs at a rate of 25 % (n=45) and 23 % (n=45), respectively (including loss due to predation). If only non-hatching by the A- and B-egg is examined, the C-egg paid off in 50 % of these occasions (n=6). There is a clear benefit to laying a third egg as insurance. That the insurance is collected often enough to favor selection for an insurance egg is supported by findings of Haycock and Threlfall (1975) who recorded hatch failure (excluding predation) in 14.7 % and 12.5 % of the A- and B-eggs respectively, in their sample.

Two-egg clutches lost more eggs within five days of laying compared to three-egg clutches. Parents with three eggs were more attentive than those with two-egg clutches, an observation also made by Beer (1961) and Brown (1967). Prior to clutch manipulation there was a trend for A-eggs to be lost more often than B- or C-eggs. Hence the third egg increases the probability of future reproductive success, and consequently the parents provide more PI in the form of efficient incubation attentiveness, compared to two-egg clutches.

The C-egg may also eventually serve as an insurance chick against the early demise of either the A- or B-chick, as suggested by Cash (1985) in explaining the adaptive significance of the B-egg in the American White Pelican. However, only one C-chick fledged during the present study, and its elder sibs also fledged. The remaining fledglings in three-chick broods were all A-chicks. These data do not allow me to properly assess the insurance chick hypothesis.

Parental investment also involves providing chicks with food, something that can be directly quantified through observation, and indirectly through chick growth. Graves et al. (1984) and others (Harris 1964; Nisbet and Drury 1972; Parsons et al. 1976) have found that chicks from three-chick broods fledge lighter than those from smaller broods. However, in this study, the growth rates of A- and B-chicks in C3 broods were similar to that of A- and B-chicks in C2

broods. This is probably because 80 % (n=15) of the C-chicks did not survive past four days post-hatch. Thus it initially appears that the effect of the C-chick on growth in C3 broods was not a factor, and thus indirectly in agreement with Graves et al. (1984). Evidence that the C-chick affects growth rates is suggested in the trend for A- and B-chicks in E2 broods to gain weight more rapidly than their counterparts in C3 broods. This suggests that the presence of the C-chick in a brood for any length of time depresses the growth rate of its older sibs.

Since growth rates of C3 and C2 chicks were similar, parents of the two brood types provided similar amounts of PI per chick, in terms of food. Although feeding rates were similar for C3 and C2 broods, indicating that chicks in C3 broods received proportionately less food, C-chicks in C3 broods were involved in only 20 % (n=15) of observed feedings. Hence, the A- and B-chicks were obtaining the majority of the food provided by the parents. Although initially parents of C3 broods invested less per chick, this initial difference was eliminated as a result of brood reduction involving the C-chick.

When the growth rates of C3 and C2 broods were compared, the cost of laying a third egg appears negligible. However, the higher growth rates of E2 versus C3 chicks indicates that the cost of the C-chick may be substantial if the brood is not reduced quickly, especially in times of food stress.

E2 chicks generally grew faster than C2 chicks, perhaps because parents of C2 broods provided less PI than E2 parents, and thus may indicate that clutch size and reproductive success are affected by parental experience and/or age. Also, by laying smaller clutches, and providing less PI, younger birds may be maximizing their probability of future reproductive success.

In summary, PI in the Herring Gull varies among eggs, and clutch sizes. The benefits of increased PI in terms of laying larger eggs lies in enhanced survivorship of the chicks. Extra PI in the form of an "extra" or C-egg benefits parents by increasing hatching success and presumably fledging success. In addition, the C-egg in Herring Gulls provides the parents, with an insurance marker against loss or hatching failure of the A- or B-egg. PI levels measured indirectly by growth of chicks and directly by feeding rates were similar between C3 and C2 broods, due to the early demise of the C-chick in most of the C3 broods. The higher growth rates of E2 chicks along with the slower feeding rate, of those chicks suggests that: A) In C3 broods, the presence of the C-chick does have a negative effect on the early growth rate of A- and B-chicks; B) reproductive effort (feeding rates) does increase with clutch size, and C) parental experience has a positive effect on chick growth rates, assuming that that two-egg clutches are laid by younger birds.

Chapter II

EFFECT OF ASYNCHRONOUS/SYNCHRONOUS HATCHING

2.1 INTRODUCTION

Herring Gulls generally lay their eggs two days apart, and begin incubating upon laying the penultimate egg. Thus the eggs hatch asynchronously over a period of one to four days (Haycock and Threlfall 1975; this study). This asynchronous hatching, Lack (1954, 1968) hypothesized, is a mechanism by which the parents facilitate brood reduction, especially during periods of food stress. Hatching asynchrony, promotes a feeding hierarchy based on sibling size and age which enables the parents to channel food efficiently into the older, larger and probably fittest chick(s). Thus, when food is unpredictable, parents can adjust their brood size by eliminating the chick which would otherwise require the most future investment, not, as Hahn (1981) suggested, the one which has received the least investment. The probability of survival of the remaining brood is thereby increased and consequently parental reproductive success is optimized.

Several other hypotheses have been presented to explain the adaptive significance of asynchronous hatching. Hussell (1972) proposed the "Peak Load Reduction" hypothesis, where-

by asynchronous hatching is seen as a parental strategy to spread out the peak food demands of the brood. Intuitively this hypothesis is sound, and may actually benefit parents to some degree, but because the proposed benefits are rarely collected (fledging complete broods) in some species, such a strategy can not explain fully the evolution of asynchronous hatching.

As an alternate hypothesis, asynchronous hatching may reduce the probability of total nest failure (Clark and Wilson 1981). Clark and Wilson argued that in species where mortality is greatest in the egg stage, the parents should commence incubation on or before the penultimate egg, to reduce the amount of time only eggs are in the nest, and thus reduce the probability of total nest failure. However, one of the assumptions of their model is that all eggs/chicks in a nest have the same probability of survival. However, mortality is usually greatest in last hatched chicks (Ricklefs 1965; Parsons 1975a; see O'Connor 1978, for a review). Accordingly, Richter (1982) calculated the optimum daily survival rate required for asynchronous hatching to be favoured, with the assumption that the probability of survival of the last-hatched chick is less than that of its elder sibs. Richter found that several species which exhibit hatching asynchrony have a higher total nest failure rate than allowed by Clark and Wilson's (1981) model. Hence it appears that as an adaptation against total nest failure, asynchronous hatching is too costly (Richter 1982).

That brood reduction optimizes parental reproductive success has been established theoretically by O'Connor (1978). He constructed three models (based on the identity of the possible benefactor of brood reduction) using the concepts of kin-selection (Hamilton 1964) and parent-offspring conflict (Trivers 1974). These models predict that as the probability of mortality within a brood increases, so does the benefit of brood reduction. In other words, brood reduction will be favored if the probability of survival of the brood minus one chick is better than that of the original brood.

In addition to asynchronous hatching, brood reduction may also be facilitated by producing eggs of different sizes, and hence varying their energy or nutrient content. Such differences have been found in Herring Gulls, where the C-egg contains relatively less yolk and albumin compared to the A- and B-eggs (Parsons 1972). These differences facilitate brood reduction (Parsons 1975a). Parsons manipulated clutches to make the C-egg hatch first, and found that although survivorship of the C-chick improved, it still suffered significantly more mortality during the first week post-hatch than did its brood mates.

Finally, Hahn (1981) hypothesized that in addition to the brood reduction role, asynchronous hatching also reduced sibling rivalry, and thus minimized wastage of parental investment.

Brood reduction as a result of asynchronous hatching has been reported in a variety of avian groups: boobies (Dorward 1962), pelicans (Cash 1985), eagles (Meyburg 1974; Stinson 1979) egrets (Mock 1984), gulls (Parsons 1975a; Hahn 1981; Braun and Hunt 1983), terns (Nisbet and Cohen 1975), grackles (Howe 1976, 1978), wrens and thrashers (Ricklefs 1965). In gulls and some other species, the smaller size of the C-egg, as previously mentioned, has also been implicated as an important factor in brood reduction (Parsons 1970, 1975a; Nisbet 1973).

The purpose of the present study was to test, through clutch manipulation, the brood reduction and sibling rivalry hypotheses in Herring Gulls.

2.2 METHODS AND MATERIALS

General methods regarding the location and identification of nests, eggs and chicks used in this experiment are similar to those described in Chapter 1. The control nests used in this experiment are the same as those used in Chapter 1.

2.2.1 Significance of Asynchronous Hatching

To induce synchronous hatching within a clutch (i.e., A-C hatch interval <24 hrs) experimental clutches were created by exchanging eggs. These manipulations involved taking either three A-, three B-, or three C-eggs of similar weight,

and laying date, and placing them in a nest which previously contained 3 eggs. The mean weight difference (\pm S.E.) for eggs used within an experimental clutch was 4.84 ± 0.95 g, and the mean difference in laying dates was 0.28 ± 0.07 days. I used eggs with the same position in the laying sequence to eliminate bias associated with inherent differences between A-, B-, and C-eggs. In addition, choosing eggs of similar fresh weights reduced the possibility of size discrepancies between chicks at hatching (Hahn 1981). Finally, eggs with similar laying dates were used to produce the required hatching synchrony. Clutch manipulations were carried out from 1-17 days after completion of the clutches involved. If an experimental or control (A-C hatch interval > 24 hrs) egg disappeared before hatching, I tried to replace it with an egg similar in its position in the laying sequence, in weight and laying date. Control nests were selected randomly provided they were initiated within 10 days of the earliest and latest experimental nest. In doing so it is assumed that any age or experience bias associated with the timing of breeding (McCrimmon 1980) would be minimized.

2.2.2 Egg/Brood Success Of Control And Experimental Nests

Experimental and control nests were visited two to three days prior to the onset of hatching, every day thereafter until four days post-hatch and every fourth day thereafter.

In experimental nests where one egg had a smaller pip hole than another, the hole was enlarged to minimize the hatch interval between chicks within a clutch. Since the aim of this experiment was to examine the effect, if any, of asynchronous and synchronous hatching on chick individual fitness levels, some broods were supplemented with an extra chick if one of the original eggs did not hatch. Chicks were also added to a nest if one of the original chicks disappeared within a day of hatching. In all cases, replacement chicks were of similar weight. Chicks in experimental nests were randomly assigned to position A, B or C.

2.2.3 Behavioural Observations

Three blinds were used in this experiment, and data were collected as described in Chapter 1.

2.3 RESULTS

2.3.1 Hatching Success

Thirty-nine experimental and 49 control 3-egg nests were followed from laying to hatching. Hatching success in synchronously hatching nests was 64.9 % (n=117), with a mean (\pm S.E.) of 1.94 ± 0.16 eggs/nest. At least one egg hatched in 87.2 % (n=39) of the experimental nests. Hatching success of control nests was 58.5 % (n=147), with a mean of 1.73 ± 0.16 eggs hatching per nest. Of the 49 control nests, 73.5 % hatched at least one egg. The proportion of

nests hatching all 3 eggs (excluding predation) was 70 % (n=20) and 48 % (n=25) for experimental and control nests respectively. This difference was not significant ($X = 2.20$, $df=1$, $P>0.10$).

As a result of egg loss (mostly due to predation) only 28 synchronously hatching and 15 control nests could be used to investigate the effects of synchronous and asynchronous hatching on the individual fitness of chicks. The mean hatching interval (measured to the nearest day) between the A- and C-chick in experimental nests was 0.37 ± 0.09 days, and 2.28 ± 0.28 days in control nests. These means differed significantly ($t=-7.89$, $df=39$, $p=0.001$).

Hatch weights for A-, B- and C-chicks in experimental nests were not significantly different (Table 14). In control nests, A-chicks were not significantly heavier at hatching than B-chicks, but both A- and B-chicks hatched significantly heavier compared to C-chicks (Table 14). Hatch weights were similar between A-chicks and B-chicks in control and experimental nests (Table 14). Experimental C-chicks however, hatched significantly heavier than control C-chicks (Table 14).

Table 14. Within brood comparison of chick weight, and culmen and tarsometatarsus lengths at hatch for chicks in control (asynchronous) and experimental (synchronous) broods.

BROOD TYPE	CHICK	N	WEIGHT (g)	COMPARISONS			CULMEN LENGTH(mm)	N	COMPARISONS			TARSOMETATARSUS LENGTH(mm)	N	COMPARISONS		
			(\bar{x})(\pm S.E.)	CHICKS	Z	P	(\bar{x})(\pm S.E.)		CHICKS	Z	P	(\bar{x})(\pm S.E.)		CHICKS	Z	P
CONTROL	A	14	63.32 \pm 1.32	A vs B	0.09	0.92	17.50 \pm 0.24	13	A vs B	0.27	0.78	60.96 \pm 0.76	13	A vs B	0.95	0.34
	B	14	63.42 \pm 1.66	B vs C	2.20	0.02	17.25 \pm 0.23	14	B vs C	-0.83	0.40	59.85 \pm 0.52	14	B vs C	-2.17	0.02
	C	14	57.00 \pm 2.08	A vs C	2.16	0.03	17.00 \pm 0.27	11	A vs C	-1.00	0.31	57.95 \pm 1.19	11	A vs C	-2.49	0.01
EXPERIMENTAL	A	26	63.68 \pm 0.88	A vs B	-0.32	0.74	17.48 \pm 0.22	26	A vs B	-0.30	0.75	61.11 \pm 0.50	26	A vs B	1.52	0.12
	B	28	64.32 \pm 1.29	B vs C	-0.32	0.74	17.67 \pm 0.21	28	B vs C	-0.63	0.52	59.98 \pm 0.48	28	B vs C	0.27	0.78
	C	28	63.17 \pm 1.48	A vs C	0.07	0.93	17.44 \pm 0.22	26	A vs C	0.30	0.76	59.85 \pm 0.46	27	A vs C	1.67	0.09

Culmen lengths at hatch were similar for all chicks within and between groups (Table 14, 15). Mean tarsometatarsus lengths at hatch were also similar for A- and B-chicks within and between groups (Table 14, 15). However, control C-chicks had a smaller mean tarsometatarsal length at hatch compared to control A- and B-chicks, and experimental C-chicks (Table 14, 15).

2.3.2 Chick Growth

Growth rates were estimated for chick weight (g), culmen length (mm) and tarsometatarsus (to tip of middle toe) length (mm), and treated as in Chapter 1.

The mean slopes for growth with respect to chick weight were similar for control A- and B-chicks (Table 16). C-chicks in control nests, however, had significantly lower growth rates (Table 16). In synchronously hatching broods, the growth rates of A-, B- and C-chicks were similar (Table 16).

The growth rates of A- and B-chicks in control versus experimental nests were similar (A vs A, $Z=-0.25$, $P=0.80$; B vs B, $Z=-1.56$, $P=0.11$; Table 17). However, experimental C-chicks exhibited a significantly higher growth rate compared to control C-chicks ($Z=-2.58$, $P=0.009$) (Table 17).

Table 15. Between group comparisons of mean chick weight ($g \pm S.E.$), and mean lengths of culmen and tarsometatarsus ($mm \pm S.E.$) lengths at hatch.

PARAMETER	CHICK	CONTROL	N	EXPERIMENTAL	N	Z	P
HATCH WEIGHT	A	63.32 ± 1.32	14	63.68 ± 0.88	26	-0.34	0.73
	B	63.42 ± 1.66	14	64.32 ± 1.29	28	-0.45	0.64
	C	57.00 ± 2.08	14	63.17 ± 1.48	28	-2.27	0.02
CULMEN	A	17.50 ± 0.24	13	17.48 ± 0.22	26	-0.27	0.78
	B	17.23 ± 0.23	14	17.67 ± 0.21	28	-0.75	0.44
	C	17.00 ± 0.27	11	17.44 ± 0.22	26	-1.04	0.29
TARSOMETATARSUS	A	60.96 ± 0.76	13	61.11 ± 0.50	26	-0.41	0.67
	B	59.85 ± 0.52	14	59.98 ± 0.48	28	-0.10	0.91
	C	57.95 ± 1.19	11	59.85 ± 0.46	27	-2.63	0.01

Table 16. Comparison of mean ($\bar{x} \pm$ S.E.) chick growth rates (ln g/day) within control and experimental groups.

BROOD TYPE	CHICK	N	GROWTH SLOPE	Y-INTERCEPT	COMPARISON	Z	P
CONTROL	A	14	0.07 ± 0.01	4.20 ± 0.04	A vs B	0.02	0.98
	B	14	0.06 ± 0.01	4.14 ± 0.03	B vs C	-2.10	0.03
	C	6	0.03 ± 0.01	4.11 ± 0.09	A vs C	-2.10	0.03
EXPERIMENTAL	A	22	0.08 ± 0.01	4.16 ± 0.02	A vs B	1.08	0.27
	B	21	0.09 ± 0.01	4.21 ± 0.04	B vs C	-1.63	0.10
	C	20	0.08 ± 0.01	4.22 ± 0.03	A vs C	-0.27	0.78

Table 17. Between group comparison of mean ($\bar{x} \pm$ S.E.) chick growth rates (ln g/day) and culmen and tarsometatarsus growth rates (mm/day).

PARAMETER	CHICK	CONTROL	N	EXPERIMENTAL	N	Z	P
WEIGHT	A	0.07 ± 0.01	14	0.08 ± 0.01	22	-0.04	0.95
	B	0.06 ± 0.01	14	0.09 ± 0.01	21	-1.56	0.11
	C	0.03 ± 0.01	6	0.08 ± 0.01	20	-2.58	0.01
CULMEN	A	0.70 ± 0.09	12	0.67 ± 0.07	19	0.70	0.47
	B	0.51 ± 0.08	11	0.58 ± 0.06	17	-0.61	0.54
	C	0.43 ± 0.19	4	0.59 ± 0.06	18	-1.14	0.25
TARSOMETATARSUS	A	2.22 ± 0.33	12	1.86 ± 0.25	19	1.15	0.24
	B	1.86 ± 0.26	11	2.30 ± 0.23	17	-1.15	0.24
	C	1.08 ± 0.64	4	2.24 ± 0.16	18	-1.40	0.16

2.3.3 Culmen Growth

Mean culmen growth slopes were similar among control A-, B- and C- chicks, and among experimental A-, B- and C- chicks. Culmen growth rates were also similar between the respective chicks of the two groups (Tables 17, 18).

2.3.4 Tarsometatarsal Growth

Control A- and B-chicks had similar mean tarsometatarsal growth rates (Table 17). The mean tarsometatarsal growth rate of C-chicks was similar to that of B-chicks ($Z=-0.84$, $P=0.39$), but was almost significantly different from that of control A-chicks ($Z=-1.75$, $P=0.07$; Table 17). Experimental A-, B- and C-chicks all had similar mean tarsometatarsal growth rates (Table 17). No differences were found between corresponding experimental and control chicks (Table 18).

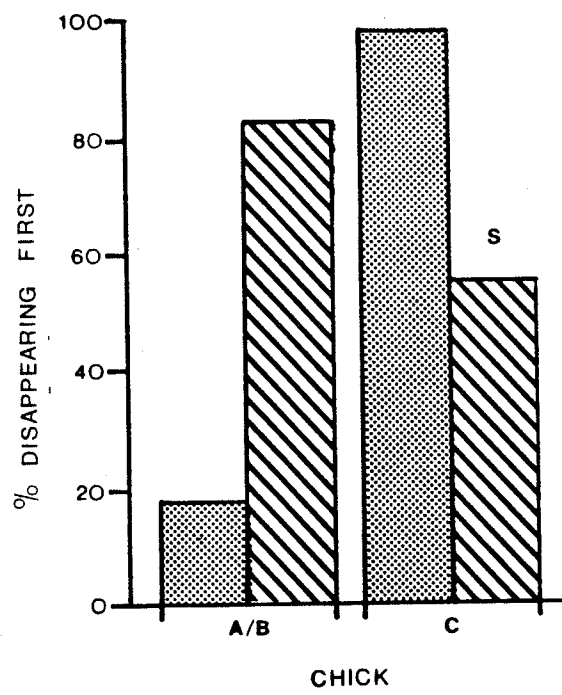
2.3.5 Chick Survivorship

The distribution of chick loss was recorded with respect to the order in which chicks disappeared. The data for A- and B-chicks were combined to provide adequate sample sizes. For control broods, A- and B-, and C-chicks did not disappear first at similar rates ($X=4.82$, $df=1$, $P<0.05$). The C-chick disappeared first most frequently. For experimental broods, A- and B-, and C-chicks disappeared first at similar frequencies ($X=0.93$, $df=1$, $P>0.25$ Fig. 5).

Table 18. Comparison of culmen and tarsometatarsus growth rates (mm/day) within control and experimental groups.

BROOD TYPE	CHICK	N	CULMEN	COMPARISON	Z	P	TARSOMETATARSUS	COMPARISON	Z	P
CONTROL	A	12	0.70 \pm 0.09	A vs B	-1.32	0.18	2.22 \pm 0.33	A vs B	-1.20	0.23
	B	11	0.51 \pm 0.08	B vs C	0.19	0.84	1.86 \pm 0.26	B vs C	-0.84	0.39
	C	4	0.43 \pm 0.19	A vs C	-1.39	0.16	1.08 \pm 0.64	A vs C	-1.75	0.07
EXPERIMENTAL	A	19	0.63 \pm 0.19	A vs B	-0.52	0.60	1.86 \pm 0.25	A vs B	1.20	0.22
	B	17	0.58 \pm 0.06	B vs C	-0.28	0.23	2.30 \pm 0.23	B vs C	0.21	0.83
	C	18	0.59 \pm 0.06	A vs C	-0.09	0.92	2.24 \pm 0.16	A vs C	1.35	0.17

Figure 5. The proportion of A-, B-, and C-chicks disappearing first in control (stippled) and experimental (hatched) broods. S. indicates a significant difference between control and experimental C-chicks, at P 0.05, using Chi-Square analysis. When two chicks in the same brood disappeared on the same day, both were recorded as having been lost first.



Control and experimental A- and B-chicks disappeared first at similar rates ($X = 3.41$, $df=1$, $P>0.05$), although there was a trend for experimental A- and B-chicks to disappear first more frequently than control A- and B-chicks. Control C-chicks, however, disappeared first more frequently than experimental C-chicks ($X = 3.99$, $df=1$, $P<0.05$; Fig. 5).

Survivorship probabilities of chicks up to five days post-hatch were estimated using the Mayfield (1975) method. The Average Survivorship Probability/Day (ASP/D) was similar for A- and B-chicks in control broods ($X = 0.005$, $df=1$, $P>0.90$). Control C-chicks had a significantly lower ASP/D compared to A-chicks ($X = 10.51$, $df=1$, $P<0.005$) and B-chicks ($X = 10.12$, $df=1$, $P<0.005$). Among experimental chicks, no differences were found in their ASP/D (A vs B, $X = 0.06$, $df=1$, $P>0.75$; A vs C, $X = 0.08$, $df=1$, $P>0.75$; B vs C, $X = 0.001$, $df=1$, $P>0.97$; Table 19).

Between groups, experimental A-chicks had a lower ASP/D than did control A-chicks, and this approached significance ($X = 3.44$, $df=1$, $0.10>P>0.05$). Likewise, experimental B-chicks had a lower ASP/D compared to control B-chicks, but this difference was not significant ($X = 2.45$, $df=1$, $P>0.10$). Experimental C-chicks did have a significantly higher ASP/D than did control C-chicks ($X = 4.63$, $df=1$, $P<0.05$; Table 19).

Mean life expectancies of A-, B- and C-chicks were calculated by averaging the number of days each chick was known

Table 19. Comparison of Average Survivorship Probability/Day¹ (ASP/D), up to five days post-hatch, for chicks in control (asynchronous) and experimental (synchronous) broods.

BROOD TYPE	CHICK	n	EXPOSURE DAYS	CHICKS DISAPPEARING	ASP/D
CONTROL	A	15	68	5	0.9256 ^A
	B	15	65	5	0.9231 ^A
	C	15	33	12	0.6364 ^{B2}
EXPERIMENTAL	A	28	98	17	0.8266 ^A
	B	28	94	15	0.8403 ^A
	C	28	95	15	0.8422 ^A

1. See Appendix C for a sample calculation

2. Only control C-chicks had a significantly lower ASP/D compared to their experimental counterparts

to have survived up to 40 days post-hatch. Control A-chicks survived longer than B-chicks, which survived longer than C-chicks (Table 20). A-, B- and C- experimental chicks had similar mean life expectancies (Table 20). The mean life expectancies of control and experimental A- and B-chicks were similar (A vs A, $Z = 1.77$, $P = 0.07$; B vs B, $Z = 1.00$, $P = 0.31$). However, experimental C-chicks had a significantly higher mean life expectancy compared to control C-chicks ($Z = -1.91$, $P = 0.05$; Table 20).

To examine further the effects of hatching asynchrony and hatch weight on life expectancy, the experimental group was divided into an asynchronous group (not all chicks hatched on same visit) and a synchronous group (all chicks found hatched on same visit). The mean life expectancies of chicks were then calculated with respect to hatching order, and hatch weight. In the "asynchronous" group ($n = 16$ nests), the chick hatching first survived significantly longer than the the last hatched chick ($Z = 2.10$, $P = 0.03$). There were no significant differences in the mean life expectancies between the assigned A-, B- and C-chicks in the "synchronous" group ($n = 12$ nests).

With respect to hatch weight in the "asynchronous" group, chicks hatching first, which also had the heaviest hatching weight within the brood, survived significantly longer than those first hatched chicks which did not have the heaviest hatch weight ($t = 3.46$, $df = 11$, $P < 0.005$). No differences were

Table 20. Within and between group comparisons of mean (days \pm S.E.) post-hatch survival, up to 40 days post-hatch.

ASYNCHRONOUS		SYNCHRONOUS		Z	P
CHICK	\bar{x} DAYS SURVIVING (\pm S.E.)	CHICK	\bar{x} days (\pm S.E.)		
A ^{A1}	13.13 \pm 3.65	A ^A	9.14 \pm 2.28	1.77	0.07
B ^A	9.20 \pm 2.40	B ^A	9.53 \pm 2.34	1.003	0.31
C ^B	4.66 \pm 2.57	C ^A	11.82 \pm 2.78	-1.91	0.05

¹ Chicks within a group with the same letter are not significantly different at P = .05

found between heavy and light B-chicks in the "asynchronous" group. A comparison of heavy and light C-chicks in the "asynchronous" group could not be done since only one C-chick had the heaviest hatch weight in the brood. In the "synchronous" group all chicks had similar life expectancies, regardless of whether they hatched heavier than their nest mates or not.

2.3.6 Fledging Success

As in the previous experiment fledging success was low in both the control and experimental groups. In the control group, five chicks (11.1 %) (3xA, 1xB, 1xC) fledged (40+ days post-hatch). Eleven experimental chicks (13 %, n=84) fledged (3xA, 3xB, 5xC). When considering their original position, in the laying sequence (i.e., in the nests from which they came) the 11 experimental fledglings included 6 A-chicks, 4 B-chicks, and 1 C-chick.

2.3.7 Behavioural Observations

Relative positions of arrival at a parental regurgitate were similar for A-, B- and C-chicks in experimental broods (Table 21). In control 3-chick nests, the C-chick arrived, on average, after the A- and B-chick but only significantly so after the B-chick ($t=-3.55$, $P<0.05$). The difference between the A- and B-chick was also significant ($t=2.00$, $df=28$, $P<0.002$). Control chicks were fed 0.32 feeds/hour

Table 21. Mean rank (\pm S.E.) of position of arrival at a parental regurgitate for chicks in control (asynchronous) and experimental (synchronous) broods.

BROOD TYPE	CHICK	\bar{x} RANK (n)
CONTROL	A	2.03 \pm 0.19 (15)
	B	1.63 \pm 0.13 (15)
	C	2.34 \pm 0.18 (15)
EXPERIMENTAL	A	2.06 \pm 0.14 (15)
	B	1.84 \pm 0.14 (15)
	C	2.10 \pm 0.17 (15)

(n=13), and experimental chicks 0.44 feeds/hour (n=18 feeds). In the control group, feeding rates between A-, B- and C-chicks were significantly different ($X = 13.34$, $df=2$, $P < 0.005$). A- and B- chicks obtained food at similar rates, which were significantly greater than those of the C-chick (A vs C, $X = 8.57$, $df=1$, $P = 0.005$; B vs C, $X = 10.80$, $df=1$, $P < 0.005$). In control nests, A- and B-chicks were involved in 77.3% and 80.0% of the feeds, while C-chicks were involved in 20.0% of the feeds. Experimental A-, B- and C-chicks all participated in 72.22% of the feeds. Between groups, A-chicks and B-chicks obtained food at similar rates, but the experimental C-chick obtained food more often than the control C-chick ($X = 8.93$, $df=1$, $P < 0.025$).

In synchronously hatching broods, 19 acts of aggression were observed at an average rate of 0.08 acts/chick hour. In control nests, 17 sib-sib altercations were observed, at 0.11 acts/chick hour. As previously mentioned, 8 chicks (17.7 %) from control 3-chick broods were observed to have wounds. In synchronous broods, 12 (A=5, B=3, C=4; 14.2 %) were observed with wounds.

2.4 DISCUSSION

In the Herring Gull, as in other larid species, the C-egg is lighter and hatches after the A- and B-egg (Parsons 1975a; this study). Lack (1954, 1968), hypothesized, that the resulting hatching asynchrony is a parental strategy

which facilitates brood reduction when food is scarce, by creating a sibling feeding hierarchy based on the size and age of the chicks. The sibling hierarchy permits parents to reduce their investment in the last hatched and presumably less fit chick(s), and thereby increases the probability of the remaining chick(s) surviving. That is, when food is scarce, the last hatched chick(s) will be eliminated and the available resources may be more efficiently channeled into the older, presumably more fit chick(s).

From these arguments, several predictions can be made: 1) synchronous hatching of a C-egg, similar in weight to the A- and B-eggs, should increase the probability of survival of the C-chick; 2) however, the elimination of the feeding hierarchy will reduce the probability of survival of the A- and B-chicks, especially in the first five days post-hatch, when the probability of mortality is highest; 3) in the absence of asynchronous hatching, early post-hatch mortality should be random amongst A-, B- and C-chicks; and finally, 4) brood reduction should occur later in synchronous nests since available resources should be distributed more equally amongst siblings.

The results obtained in this study are consistent with all of these predictions, and thus support Lack's (1947, 1954, 1968) hypothesis that asynchronous hatching maximizes parental reproductive success by facilitating the elimination of the younger, less fit chick(s).

Control nests had a mean A-C hatch interval of over two days, compared to less than one for experimental nests. The ASP/D up to five days post-hatch of experimental C-chicks was significantly higher than that of control C-chicks. It would be misleading, however, to attribute the increase in the probability of survival of the experimental C-chick entirely to synchronous hatching, since Parsons (1975a) produced experimental evidence where survival of the C-chick was correlated mainly to hatch weight. However, the observed improvement in the survival of the C-chicks in Parsons study, was significant. Thus asynchronous hatching is an important factor determining the chances of survival of the C-chick, as observed in this study.

It could also be argued that reproductive success could be increased if female Herring Gulls laid C-eggs that weighed about the same as the A- and B-eggs, thereby increasing the survival of the C-chicks. However, several lines of evidence suggest that laying a larger C-egg, which hatches synchronously, reduces parental reproductive success. First, in agreement with prediction 2 above, any attempt to produce a C-chick equal in all aspects to the A- and B-chicks has been found to affect adversely the survivorship probabilities of the latter. In this study, for example, there was a trend for experimental A- and B-chicks to have lower ASP/D values than their control counterparts. Secondly, control A-chicks in this study could, on average,

expect to survive four more days than experimental A-chicks, and this difference approached significance. On the other hand, experimental C-chicks had significantly higher ASP/D for the first five days post-hatch and survived significantly longer than control C-chicks (11.82 vs 4.66 days). Presumably then, there is a negative correlation between the average life span of the C-chick, and the A-chick (and possibly the B-chick to some degree). Thus, the advantage of laying a smaller C-chick appears to be that it has a minimal effect on the survival of the A- and B-chicks, at least in the first days post-hatch. There is also evidence in the literature that the extended presence of the C-chick in the brood has a negative effect on the growth rate of its elder sibs, most notably the B-chick (Graves et al. 1984), and subsequently the A- and B-chicks fledge lighter than in those broods where brood reduction occurs soon after hatching of the last chick (Graves et al. 1984).

There is further evidence that increased investment in the C-chick has a negative effect on its older sibs, in comparing the "asynchronous" and "synchronous" subgroups of the experimental nests. Essentially the situation in the synchronous group is equivalent to that in which parents delayed the onset of incubation until the last egg was laid. That is to say that the C-egg would receive more investment at a cost to the A- and B-egg, since by hatching synchronously the A- and B-chicks will have lost some advantage with re-

spect to the feeding hierarchy. In the "asynchronous" group, the chick hatching first, whether heavier than its brood mates or not, survived significantly longer than the last hatched chick. In the "synchronous" group, there was no difference in the mean life expectancy of chicks assigned to the A, B or C position. Although the sample sizes are small, it appears that there is an advantage in beginning incubation prior to the laying of the last egg, since in doing so, the survival probability of the A-chick increases. This agrees with Parsons (1975a) who showed experimentally that hatching order had a significant effect on chick survival, especially with respect to the A- and C-chicks. The results of this study, however, do not allow me to assess the effect of asynchronous and synchronous hatching on overall reproductive success of the parents.

The third prediction derived from Lack's (1954, 1968) brood reduction hypothesis, is that in the absence of asynchronous hatching, early post-hatch mortality should not be greatest in the C-chick but rather should be distributed equally amongst the A-, B- and C-chicks. As expected from this prediction, A-, B- and C-chicks disappeared first in equal proportions from experimental nests, whereas in control nests, proportionately more C-chicks died first compared to the A- and B-chicks. These results again support Lack's hypothesis that due to asynchronous hatching mortality is greatest in the last hatched chick.

The significance of the brood reduction strategy is apparent when the breeding ecology of the Herring Gull is considered. It has been argued that the optimal brood size in Herring Gulls is two since parents have difficulty adequately feeding three flying young (Nisbet and Drury 1972). It has also been postulated (Graves et al. 1984) that the third egg functions as an insurance egg, and this was supported by the results of my first experiment (see Chapter 1). Thus if the A- and B-eggs produce viable young, the C-egg/chick should be eliminated quickly. In this manner parental investment is efficiently channelled into the remaining chicks which require the least amount of PI to attain fledging. That the A- and B-eggs are the ones most likely to produce a fledgling may be inferred from the fact that they have a higher mean fresh egg weight compared to the C-egg. The reverse pattern holds true for some penguins, where the B-egg is larger than the A-egg, and subsequently enjoys a higher fledging success (Williams 1981). Nevertheless, as mentioned in Chapter 1, these inferences may be confounded by operative sex ratios within a population (Ryder 1983; Trivers 1974). Albeit, the end result appears the same, in that, the offspring with the highest cost/benefit ratio disappears first significantly more often than those with lower cost/benefit ratios.

From the above arguments comes the final prediction- in the absence of asynchronous hatching, available resources

will be evenly, but possibly inefficiently, distributed among brood mates. The feedings observed for complete clutches in this study support this prediction. In five experimental nests observed with complete broods, A-, B- and C-chicks participated equally in all feedings observed, while in three control broods, the C-chick participated in significantly fewer feedings than its older brood mates. These results are similar to those obtained by Hahn (1981) who observed feeding in asynchronously hatching Laughing Gulls. My observations on feedings in experimental synchronously hatching gull broods is apparently the first report in the literature, and they support previous arguments that in the absence of a feeding hierarchy, parents can not control which chicks receive food, and hence all chicks obtain it in equal amounts. This is because adult Herring Gulls regurgitate food for chicks, and hence can not control which chick obtains food, since all chicks in synchronous broods are competitively similar. In control broods, parents can control which chicks obtain food to some degree, by moving about and thus making the chicks chase them. The older and larger chicks will be able to follow the parents more closely than will the younger and smaller chick(s).

One result of equal resource distribution is that it may delay brood reduction. Consequently, until brood reduction occurs, parents are investing in (an) offspring which will eventually be lost, since in a synchronous brood the oppor-

tunity for one chick to dominate its sibs is less easily attained. The first chick in control nests was lost on average 2.1 days after hatching, while in experimental nests the first chick was lost 4.3 days after hatching, supporting the argument that synchronous hatching delays brood reduction, as predicted by O'Connor (1978). Interestingly, the second chick was lost at 5.5 and 6.0 days post-hatch, in control and experimental nests respectively. This is to be expected since the A- and B-chicks in control nests are very similar in size, just as were all the chicks in the experimental nests.

If, all chicks obtained equal feeding opportunities, as was found in the experimental nests, then they should grow at similar rates. All things being equal experimental A-chicks should grow more slowly than control A-chicks since, at least in the first days post-hatch, it is competing with nest mates of similar competitive ability. The observed growth rates of experimental and control A-chicks, however, did not agree with this prediction, since there was a trend for experimental A-chicks to grow faster than their control counterparts. However, one A-chick in the control group disappeared at 5 days post-hatch, and lost 20 g before disappearing, hence reducing the average growth rate of the control A-chicks.

That C-chicks in synchronous broods had significantly faster growth rates compared to control C-chicks was expect-

ed. By hatching synchronously and at a similar weight as its brood mates, the C-chick could expect to obtain, on average, an equal amount of food, and thus a similar growth rate. In control nests, the C-chick hatches lighter and obtains less food, and this is reflected by its slower growth rate.

In addition to facilitating brood reduction, Hahn (1981) hypothesized that asynchronous hatching reduced sibling rivalry. As a result, resources would be used for growth rather than for aggression. The results of my behavioural observations do not agree with Hahn (1981). In fact there was a trend for sib-sib aggression to be more prevalent in control nests compared to experimental nests, albeit at low levels. However, brood reduction may have occurred before competition was severe enough to warrant overt aggression.

In conclusion, Herring Gulls appear to benefit in several ways by hatching their eggs asynchronously: 1) asynchronous hatching provides the A- and B-chick with a competitive advantage over the C-chick (also enhanced by the smaller size of the C-chick relative to its elder sibs); 2) this creates a feeding hierarchy, which allows the A- and B-chicks to obtain the majority of food offered by the parents, and hence; 3) early post-hatch mortality is greatest in the C-chick, which would require the most future investment to fledge, and; 4) the loss of the C-chick occurs soon after it hatches, and thus minimizes the amount of investment it receives.

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Appendix A

SURVEY OF THE KENT ISLAND HERRING GULL POPULATION

A.1 INTRODUCTION

After doubling in size every 12-15 years since the turn of the century (Kadlec and Drury 1968), the western North Atlantic Herring Gull population appears to have stabilized, and even declined in some areas (Drury and Nisbet 1973). It has been hypothesized that these declines may be due to a southward shift in the center of population growth (Drury and Nisbet 1973).

Kent Island, New Brunswick, Canada, once supported a Herring Gull population estimated at 25,000 pairs (Cameron 1945, in Cannell and Maddox 1983). The colony has declined, especially between 1950 to 1965, and has since stabilized between 5000-8000 pairs (Cannell and Maddox 1983). The purpose of this study was to make a detailed census of the Kent Island Herring Gull colony, with a view to toward quantifying the decline of the colony.

A.2 METHODS AND MATERIALS

To estimate the size of the Kent Island Herring Gull breeding population, a nest count was undertaken on 21 June, 1984. Areas covered by the survey are indicated in Figure 1. To avoid counting nests twice, paint was sprayed on an area adjacent to each nest. Data were collected on active nests only, that is nests which contained at least one egg or chick. Data were also collected on the location of the nests which were classified into one of three groups: 1) rock, (nest built on rock or pebbles), raspberry (nest built in raspberry) and meadow (nest is surrounded by not more than 50 % raspberry).

A.3 RESULTS

A total of 1341 nests were found in the area censused. Of these, 28.2 % were found on the shore and rock ledges, 24.7 % in raspberry, and 47.12 % in grassy or meadow areas. Assuming that 20.0 % of the nests in the census area were overlooked (a liberal estimate), then the number of nests in the census area would be 1600. An additional 200 nests may be added as an estimate of the number of nests outside the census area. This brings the total estimate of Herring Gull nests on Kent Island to 1800. Finally, an additional 300 nests may be added to this figure to account for the nests destroyed by eggers (this does not include the resultant predation during the disturbance). Hence, it is estimated

that approximately 2100 pairs nested on Kent Island during the summer of 1984.

A.4 DISCUSSION

The Kent Island Herring Gull population has evidently declined since 1980, and several factors may be involved.

Drury and Nisbet (1973) suggested that the center of population growth of the New England and Maritime Herring Gull populations, was shifting south. Reasons for this may include a decline in human refuse, either at refuse sites (Nisbet 1978b) or a reduction in fish landings (Nisbet 1978b). Extensive analysis of banding records and returns would be required to show that the decline in the size of the more northerly Herring Gull colonies is due to a shift in the center of population growth.

Another possible explanation, for the decline in the Herring Gull population, on Kent Island, is human predation. During the last two week-ends in May, and the first two week-ends in June, the colony was visited by between four to 20 "eggers". Although my presence reduced their area of activity, their actions appeared to have significantly affected the gulls.

First, complete and partial clutches were removed. The actual number of eggs taken on any one visit was not quantified directly but each "visitor" carried either a one gallon

or a five gallon pail. Thus a rough estimate of eggs taken would be between 50-100 eggs/visit. The removal of complete or partial clutches may have released pairs from the nest, and hence increased the number of potential cannibals in the colony. It is well known that Herring Gulls exhibit cannibalistic behaviour (Paynter 1949; Parsons 1975b).

Secondly, the "egggers" arrived at approximately 1300 hrs, and in some cases did not depart until 1800 hrs. While in the colony the egggers travelled in loose groups, often displacing 50-100 gulls at a time. Some egggers were also observed to throw eggs at each other, at gulls, and an array of inanimate objects. Such disturbance likely influenced reproductive success, since Kadlec and Drury (1968) found that the degree to which reproductive success was adversely affected was directly proportional to the proportion of the colony disturbed, and the duration of the disturbance. Such large disturbances have been postulated to be the cause of colony desertions (Buckley and Buckley 1977, in Erwin et al. 1981).

The presence of the egggers, and the removal of eggs may have also affected the synchrony within "sub-colonies", and delayed egg-laying. As a result, egg-sizes may have decreased, as well as the chicks chances of survival (Parsons 1975a; Parsons et al. 1976).

In conclusion, the Kent Island Herring Gull colony has declined in size, from an estimated 5000 pairs in 1980 to an estimated 2100 pairs in 1984. Although this decline is coincidental with a shift in the center of population growth, there is no data as yet to confirm that gulls that once bred at Kent Island now breed elsewhere. The decline of the colony, appears to be at least in part due to "egging" by local residents. The "egging" is not of a subsistence nature for the most part. The disturbance during the egging visits is considerable and may affect up to 100 birds at any given moment. This continued, and persistent egging, is believed to have significantly reduced reproductive success, and also possibly resulted in the emmigration of a large percentage of adults from this colony.

Appendix B

THE EFFECT OF FOG ON CHICK SURVIVAL

B.1 INTRODUCTION

Many studies have documented the high rate of mortality incurred by larid nestlings in the first week post-hatch, as well as the higher reproductive success of those pairs nesting in the early and peak periods of the breeding cycle (McCrimmon 1980, and references therein). Mortality during the early post-hatch period is often associated with starvation, or related factors (see Hunt and McLoon 1975), which is in part the result of a slow transition by the parents from incubating to brooding behaviour (Kadlec and Drury 1968).

Inclement weather has also been found to affect chick survivorship, by reducing parental foraging efficiency in terns (Dunn 1975). Wind and rain have been suggested to be associated with chick mortality in the first week post-hatch (Harris and Plumb 1965).

During this research project, an extended fog period occurred during peak hatching. The purpose of this paper is to document the effects of the fog on chick survival and parental foraging patterns.

B.2 METHODS AND MATERIAL

To examine the possible effects of fog on chick survival to five days post-hatch, data were collected on the number of chicks hatching between 18 June and 20 July. Only chicks hatching in control 3 and 2-chick broods were used in the analysis, so the results would not be confounded by experimental effects. For analysis chicks were classed as either: hatched in fog (29 June-9 July), and did not hatch in fog (18-28 June, and 10-20 July). The data for A-, B- and C-chicks were clumped so as to provide adequate sample sizes for Chi-Square analysis.

B.3 RESULTS

Visibility during the fog period averaged 0.17 km at 0800 h, and 0.5 to 1.0 km at 2000 h (ADT). Average visibility during the non-fog period was between 2 and 3 km at 0800 h and between 2 and 4 km at 2000 h. In addition, during the foggy period, 9/11 nights were foggy compared to 7/22 during the non-fog period. This difference is significant ($\chi^2=7.34$, $df=1$, $P<0.01$). Average daily temperatures were similar between the fog ($x=11.5$ C) and non-fog ($x=11.0$ C) periods. The average speeds of maximum wind gusts were also similar between the fog and non-fog periods (11.8 km/h and 13.6 km/h, respectively)(R. Cunningham, unpubl. data).

Regurgitate contents were recorded to determine if the fog affected adult foraging patterns. During the non-fog period, 50 regurgitates and their contents were recorded. Of these, 90.0% contained fish, 24.0% contained euphasids and crab, and 22.0% contained insects. During the fog period, 38 regurgitates were recorded, of which 36.8% contained fish, 65.8 % contained euphasids, and crab, and 18.4% contained insects.

Overall chick survival to five days post-hatch was markedly lower in the fog period (35/77 chicks surviving to five days post-hatch) compared to the non-fog period (16/22). This difference is significant ($\chi^2 = 5.09$, $df=1$, $P=0.025$).

B.4 DISCUSSION

The fog period severely reduced chick survival, even at a time (i.e., peak hatching) when parental reproductive success is normally highest (Parsons et al. 1976; Erwin 1971). The extended period of fog may have reduced chick survivorship as a result of its effect on parental foraging success, and/or through chilling of the young chicks.

Dunn (1975) observed in Common Terns, that during a rainy period, one parent brooded the chicks while the other foraged, and thus feeding rates declined. In this study, the proportion of chick regurgitates containing fish dropped by almost 60 % in the fog period, while the proportion of re-

gurgitates containing euphasids increased three-fold during the fog-period. It appears then that the fog hindered the location of fish schools but on the other hand, increased the availability of euphasids. One explanation for this may be the fact that euphasids migrate upward in the water column at night, in response to similar movements by their prey. The fog then, may have significantly reduced light levels to a point where the prey of euphasids stayed near the water's surface. As a result, the euphasids may have become more available to the gulls, especially at upwellings (Brown 1980). The increase in the number of chick regurgitates containing euphasids may also be due to the fact that adults switched from foraging for fish to euphasids. Since no data were collected on foraging adults, this last hypothesis can not be examined.

Although parental foraging strategies appear to have been affected by the fog period, the effect, if any, on chick survivorship can only be inferred by the coincidental higher mortality rates in the fog period.

With respect to thermoregulation, Dawson and Bennett (1980) found that hatchling Western Gulls (L. occidentalis livens Audubon) could increase their heat production by 1.8 times their basal metabolic rate. Dawson and Bennett (1980) indicate that they have only "modest capacities" for increasing heat production when they are cold stressed. Thus, if adult foraging efficiency was significantly reduced by

the fog, it may have forced the attending parent to forage as well. Consequently, the young chicks may have suffered cold stress, and eventually died. This is even more plausible if the chicks were not obtaining adequate levels of nutrition to maintain optimal thermoregulatory levels, especially while parents were away foraging, or during investigator visits into the colony, when parents also left their chicks alone.

Finally, it is possible that the fog caused an increase in cannibalistic tendencies, since chicks may have been left alone, and if starving may have begged loudly, thus attracting cannibalistic individuals.

In summary, although the exact mode of action is not known, the results obtained in this study, show that survival was significantly reduced for those chicks hatching during the fog period. The fog affected parental foraging strategies, and may possibly have caused chicks to become cold stressed, both of which may have directly or indirectly negatively affected the chances of survival of chicks hatching during the fog period.

Appendix C

Mayfield (1975) method of comparing survivorship probabilities applied to chicks for up to five days post-hatch. (This example uses the data for A-chicks from asynchronous and synchronous nests.

	Synchronous A (n=28)	Asynchronous A (n=15)
Total Exposure Days	98	68
Number of Chicks Lost	17	5
Average Mortality/Day	0.1734	0.0735
Average Survival/Day	0.8266	0.9265
Estimated Survival (Y^5)	0.3859	0.6826
Estimates Mortality ($1-Y^5$)	0.6141	0.3174
Total Estimated Mortality	17.1949	4.761
Total Estimated Survival	10.8052	10.239

	Mortality	Survival	Total
Synch. A	17.1948	10.8052	28
Asynch A	4.761	10.239	15
	21.9558	21.0442	43

$$\chi^2 = 43 [(17.1498 \times 10.230) - (4.761 \times 10.8052)]^2 / 21.9558 \times 21.0442 \times 15 \times 28$$

$$\chi^2 = 3.44, df = 1, 0.10 > P > 0.05$$