

**SEASONAL VARIATION IN HATCHING PATTERN AND  
CHICK SURVIVAL IN THE RING-BILLED GULL  
(*Larus delawarensis*)**

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## ABSTRACT

The general objective of my study was to monitor proximate causes and seasonal patterns of hatching asynchrony and chick survival in the Ring-billed Gull (*Larus delawarensis*). Two different plots were set up at a Ring-billed Gull colony near Port Colborne, Ontario in the summer of 1992. One group was from 'peak' nesting pairs (clutches initiated between 15 April and 1 May); a second group was from 'late' nesting pairs (clutches initiated between 9 - 22 May). Despite equal intra-clutch egg laying intervals between the peak and late periods, intra-clutch hatching intervals lengthened as the season progressed (ie. hatching became more asynchronous). Clutches from both periods were monitored for nocturnal attendance and brood patch development of parents was monitored during the egg laying period. Late nesters were characterized by an absence of nocturnal desertion, substantial brood patch defeathering at clutch initiation and a reduction in the number of chicks fledged per pair. Chick survival to 25 days (taken as fledging) reflected patterns of chick mass at brood completion and five days post-brood completion, in peak clutches. In late clutches, survival was poor for all chicks and, was partially independent of hatching order, due in part to stochastic events such as Herring Gull predation and adverse weather. In both the peak and late periods, last-hatched C-chicks realized the poorest survival to fledging among brood mates.

An artificial hatching pattern (manipulated synchrony) and an artificial hatching order were created, in three-chick broods, through a series of egg exchanges. In peak and late clutches manipulated to hatch synchronously ( $\leq 24$  h): C-chick survival to fledging did not differ from the survival of A- and B-chicks, in the peak period. In the late period, the survival of C-chicks was significantly lower than that of A-chicks. In peak clutches manipulated such that chicks from last-laid eggs (C-chicks) hatched 24 h - 48 h ahead of the A- and B- chicks, C-chick survival was greater than in controls. Within those broods, C-chicks survived better on average than both A- and B- chicks.

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## INTRODUCTION AND LITERATURE REVIEW

The phenomenon of brood reduction (# of chicks surviving to fledging per brood < # chicks hatched per brood, Lack 1966) has been reported for many seabird species including the Herring Gull (*L. argentatus*, Parsons 1970, 1975a, 1975b), Black-headed Gull (*L. ridibundus*, Lundberg and Väisänen 1979), Laughing Gull (*L. atricilla*, Hahn 1981), Western Gull (*L. occidentalis*, Pierotti and Bellrose 1986, Sydeman and Emslie 1992) Common Tern (*Sterna hirundo*, Morris 1988, Bollinger et al. 1990) and the Heermann's Gull (*L. heermanni*, Urrutia and Drummond 1990). This phenomenon, in which parents often produce broods larger than the number of offspring reared to fledging, has also been reported for other birds such as, the Common Grackle (*Quiscalus quiscula*, Howe 1976, 1978), the Osprey (*Pandion haliaetus*, Hagan 1986, Steidl and Griffin 1991), the Pied-billed Grebe (*Podilymbus podiceps* Forbes and Ankney 1987), the Blackbird (*Turdus merula*, Magrath 1989, 1992), and the House Sparrow (*Passer domesticus*, Veiga 1992). Reduction of brood size is usually non-random, as chicks hatching from last-laid eggs realize poorer survival than their older siblings: chicks hatching from eggs earlier in the clutch (O'Connor 1978, Braun and Hunt Jr. 1983, Pierotti and Bellrose 1986, Forbes and Ankney 1987, Skagen 1988, Forbes 1991).

The modal clutch size of some temperate nesting seabirds including Ring-billed Gulls is three-eggs (Emlen et al. 1966, Emlen and Miller 1969, Kirkham and Morris 1979, Chardine and Morris 1983). In a typical three-egg clutch, third-laid eggs are smaller in size than first- and second-laid eggs (Herring Gulls, Parsons 1976, and Black-headed Gulls, Lundberg and Väisänen 1979) and significantly lighter (Herring Gulls, Hébert and Barclay 1988). Lundberg and Väisänen (1979) found a correlation between lower egg size and higher chick mortality, in natural clutches. When clutches of Ring-billed Gulls were manipulated to hatch synchronously, Killoran (1991) found



that, despite a smaller mass and volume of third-laid eggs, an equal probability of survival resulted amongst brood mates

An asynchronous hatch results in the formation of a size hierarchy amongst brood mates in which third-hatching chicks are smaller and at a competitive and developmental disadvantage to older siblings. When such a hierarchy is present, last-hatched chicks often realize poorer survival than older brood mates (Harris 1964, Bollinger et al. 1990, Killoran 1991). Killoran (1991) manipulated clutches to hatch asynchronously with a separation of 48 hours between the hatching of each chick. All first-hatched chicks of those experimental broods fledged, while only 13 % of last-hatched survived to fledging. Sydeman and Emslie (1992) observed that fledging success of third-hatched Western Gull chicks decreased significantly with increasing hatching asynchrony. How asynchronously a brood hatches may therefore have a greater effect on third-chick survival than size hierarchies within the brood that result from differences in egg size.

Seasonal variation in the degree of intra-clutch hatching synchrony has been observed in some seabirds (Nisbet and Cohen 1975, Courtney 1979, Chardine and Morris 1983, Shaw 1985, Morris 1988, Bollinger et al. 1990). Despite equal intra-clutch egg-laying intervals throughout a breeding season (defined as the time interval between the laying of the first and third eggs within a brood of three), the intra-clutch hatching intervals (the time between the hatching of the first and third chicks) lengthen as a given breeding season progresses (Morris 1988). Nisbet and Cohen (1975) recorded seasonal changes in hatching intervals and hatching asynchrony for Common Terns and Roseate Terns (*S. dougalii*); both increased across the breeding season. Courtney (1979) found the same trend for Common Terns at Port Colborne. Chardine and Morris (1983) monitored the hatching intervals of Ring-billed Gulls and observed that 76 % of clutches initiated early in the breeding season

hatched relatively synchronously ( $\leq 1$  day), while 89 % of clutches initiated late in the season hatched asynchronously ( $\geq 2$  days).

In Ring-billed Gulls, early season intra-clutch hatching intervals average around 24 - 48 hours while late breeders average around 96 hours (Chardine 1978). Such a pattern may be caused by nocturnal desertion resulting in a delay of effective incubation until clutch completion by early nesting broods, and the onset of partial or complete incubation prior to clutch completion in late breeders within a breeding season (Parsons 1972, Courtney 1977, 1979, Hahn 1981, Chardine and Morris 1983, Inoue 1985, Atwood 1986, Gaston and Powell 1989). Nisbet and Cohen (1975) suggested that one cause of the lengthening hatching intervals during a breeding season was a tendency for the birds to start incubating A-eggs progressively earlier as the season advances. Fetterolf (1979) noted that Ring-billed gulls nesting at a Lake Ontario colony spent seven evenings away from the colony after the onset of egg laying. Courtney (1979) monitored the incubation attentiveness of Common Terns and found nocturnal nest attendance was particularly poor in early clutches but increased steadily through egg laying. Chardine and Morris (1983) reported a similar trend for Ring-billed Gull clutches. In such cases, it was argued that the desertion slowed the initial development of A-and B-eggs until the laying of C-eggs, and as a result, chicks of early clutches hatched more synchronously than clutches initiated late in the breeding season.

The incomplete vascularization and defeathering of the brood patches (the abdomen areas used to incubate eggs) may also be a mechanism for hatching synchronization in early clutches (Courtney 1979). Brood patches are often free of feathers and have highly vascularized skin that enhances heat transfer to the eggs. Brood patch development involves both defeatherization and vascularization, which are regulated by prolactin working with other hormones (Hébert and Sealy 1992). Brood patches are believed to play an

important role in the incubation rhythm in addition to facilitating heat transfer to the eggs (Beer 1962, Hébert and Sealy 1992). Beer (Beer 1962) measured brood patch lengths and widths of Black-headed Gulls trapped at the two and three-egg stages. Significant trends for the lengths and widths to increase were found between the two trapping periods. Pierotti (1981) showed similar trends, for incubation patch area to increase during incubation, in peak nesting Western Gulls. Courtney (1979) monitored the seasonal differences in total brood patch area development between peak and late nesting Common Terns and found that at clutch initiation, incubation patch defeathering was more advanced in late nesting birds than in peak nesting birds. Thus, late nesters had more area available for heat transfer to the eggs in addition to spending more time incubating.

The proximate mechanisms just reviewed produce the circumstance of asynchronous hatching, and so, predispose the last hatched chick to a disadvantage when compared to earlier hatched siblings. Among theories postulated to explain the asynchrony of hatching observed in seabirds, two have received the strongest support. The first, the "insurance egg hypothesis," considers the last-hatched chick to function as a form of insurance against the loss of an earlier laid egg or an older sibling (Graves et al. 1984, Anderson 1990, Forbes 1991). This hypothesis assumes that the amount of parental investment required to fledge a complete brood exceeds a parent's ability to do so. The insurance hypothesis predicts an optimal fledging number lower than the number of eggs laid and therefore, the fledging of an entire brood of three chicks would be a rare event (Graves et al. 1984, Bollinger et al. 1990).

The second major hypothesis to explain the observed pattern of chick loss was Lack's "brood reduction hypothesis" (Lack 1966). The brood reduction hypothesis suggests patterns of hatching asynchrony to be a parental adaptation that allows for potential adjustment of brood size in response to an

unpredictable food supply. Because an asynchronous hatch normally creates a size hierarchy amongst the chicks in a brood favouring A- and B-chicks, the C-chicks would therefore have an increased likelihood of starvation when conditions are poor. A more synchronous hatch would reduce the size discrepancies amongst chicks created by an asynchronously hatched brood. Thus, C-chicks would be more effective in competition for food resources (Bollinger et al. 1990).

The brood reduction hypothesis has been tested to explain the patterns of hatching synchrony occurring in many seabirds including Common Terns (Morris 1988), Laughing Gulls (Hahn 1981) and Herring Gulls (Hébert and Barclay 1986) but not in Ring-billed Gulls. According to the brood reduction hypothesis, the mechanism of brood reduction is only required to act under conditions of food limitation or a similar stress (Chardine and Morris 1983). As food availability is difficult to determine, I tested the brood reduction hypothesis using an experimentally induced hatching extreme, synchronous hatching. Individual clutches can be made to hatch synchronously by grouping eggs whose stage of pipping are similar (Hébert and Barclay 1986). A more synchronous hatching ( $\leq 24$  h) would give all chicks a more equal ability to compete for food resources as well as eliminate any ability parents may have to provide selective attention to larger chicks. Thus, in broods manipulated to have their chicks hatching synchronously, all chicks might expect to realize comparable survival (Shaw 1985, Morris 1988). Shaw (1985) found the age at which C-chicks (chicks hatching from third-laid eggs in a brood of three) died was inversely related to the length of the A- to C-chick hatching interval.

I also considered the relative importance of relative egg size versus relative hatching order. Parsons (1970) found that in Herring Gulls, post-hatching chick mortality was inversely related to egg size and independent of hatching order. Bolton (1991) found that larger eggs of the Lesser Black-

backed Gull (*L. fuscus*) produced chicks of larger mass and tarsus length, than chicks from smaller eggs. As these qualities could contribute to increased chances of chick survival, I designed the experimental protocol to consider the question of relative egg size versus relative hatching order by manipulating hatching order such that chicks hatching from smaller, third-laid eggs (C-chicks) hatching 24 h - 48 h ahead of the A- and B-chicks.

The general objective of the my study was to determine proximate causes of seasonal variations in hatching synchrony and to comment on ultimate explanations for the phenomena. Proximate causes and seasonal patterns of hatching synchrony and chick survival in the Ring-billed Gull were studied in two different plots at a Ring-billed Gull colony near Port Colborne, Ontario to address the following questions:

- (1) What trends were there in the egg-laying and chick hatching patterns of three-egg clutches initiated in peak and late periods of the 1992 season?
- (2) What differences existed in the nocturnal incubation patterns, recorded from laying to five days after clutch completion, between clutches initiated in the peak and late nesting periods?
- (3) Were there any differences in the total brood patch areas among birds trapped at various stages of egg laying during the peak and late periods?
- (4) What was the body mass of each chick at hatching, brood completion and five days post-brood completion?; and what was their survival post hatching?

(5) For peak and late clutches manipulated to hatch synchronously (hatching interval  $\leq 24$  h):

- was the probability of survival for experimental C-chicks increased when compared to control C-chicks?
- what was the body mass of those chicks at hatching, brood completion and five days post-brood completion?; and what was their survival post hatching?

(6) For broods in which the C-chick was manipulated to hatch ahead of the A- and B-chicks by 24 h - 48 h:

- was the probability of survival for experimental C-chicks increased when compared to control C-chicks?
- what was the body mass of those chicks at hatching, brood completion and five days post-brood completion?; and what was their survival post hatching?

## METHODS

### Study Site

This study was conducted on a breakwall colony off the north shore of Lake Erie near Port Colborne, Ontario (42° 53'N, 79° 16'W). Approximately 2500 pairs of Ring-billed Gulls and 150 pairs of Herring Gulls nested across a sparsely vegetated, limestone rock pile adjacent to the central and west arms of the concrete breakwall. Approximately 800 pairs of Common Terns nested on the east arm of the breakwall. The substratum varied from loose gravel and pebbles to larger rocks and broken concrete pieces. Nesting material primarily consisted of aquatic vegetation and small twigs that had washed onto the rock pile.

Two study plots were marked out on 30 March 1992 (see Appendix I & II). Plot I, or the 'peak' plot (8 m x 10 m), was located on the northern tip of the rock pile. A blind was erected approximately five metres in from the shore-line, which faced south over-looking the plot. Plot II, the 'late' plot (7 m x 9 m), was located on the central part of the west arm of the rock pile. A blind was erected that faced west overlooking the plot. Plot II was covered with 6 ml plastic sheeting on 30 March, 1992 and later (10 April) with a heavier 15 ml plastic to provide an unused area to concentrate the late nesting birds when the plastic was removed later in the season (8 May).

### Clutch Initiation

Clutches initiated within each plot during their respective periods were individually marked with numbered, metal, nest markers within 24 h of the laying of the first egg. Nests were inspected daily for the presence of new eggs throughout the egg laying period. Eggs were weighed to  $\pm 0.5$  g using a 100 g Pesola scale and measured to  $\pm 0.05$  mm with Vernier calipers within 24 h of

laying. Each egg within a nest was identified with a felt-tipped marker according to its position in the laying sequence of that clutch.

### **Nest Attentiveness**

Beginning 15 April (Plot I) and 9 May (Plot II) the amount of time parents spent incubating was monitored using nest-monitoring devices placed on available clutches at the one-egg stage. Nest-monitoring devices consisted of a monel-wire ring attached to a microswitch connected by a 16-gauge lampcord to a 20-pen Esterline Angus Event Recorder (Model A620X). This particular model was portable, clock driven and powered in the field by a 12-V marine battery (for detailed description see Morris and Hunter 1976). Clutches were monitored continuously from the one-egg stage through a minimum of five days post clutch completion on all nests.

Event recorders were run at a chart speed of 3.98 cm / hour and the marine battery power source was exchanged frequently, as required, with a second, fully charged, marine battery. All monitored nests were inspected every 24 hours for complications arising from incorporation of the metal ring into the nesting material. The attendance data for nests in which the wire was found incorporated into the nest material were discarded from the previous evening's data set. Sample sizes for nocturnal nest attendance analysis and exclusions due to incorporation are given in Appendix III. Nest monitoring activities were terminated on 30 April in the peak plot and on 31 May in the late.

### **Brood Patches**

Brood patch measurements were obtained from incubating adults at the one, two, and three-egg stage during peak period; and the one and three-egg stage for birds nesting in the late period. Birds were trapped using a walk-in trap, constructed from one inch mesh wire fencing. Trapped birds were brought back to the blind, where length and width measurements of the three brood



patches and head-bill measurements were taken with Vernier calipers. Each bird was banded with a U.S.F.W.S. aluminum band and released. Brood patch areas for each of the three brood patches were calculated using the formula for an oval ( $\text{area} = 0.25 \cdot \text{length} \cdot \text{width} \cdot \pi$ ). Total brood patch areas for each individual were obtained by adding each of the three brood patches for that individual.

### **Hatching and Experimental Manipulations**

A sample of control clutches ( $n = 20$  clutches initially) was chosen by random draw from the available pool of three-egg clutches in the peak and late plots. The only condition put on these nests was that they were three-egg clutches in which all chicks hatched.

Two artificial hatching patterns of manipulated synchrony (ESYN.; within 24 h;  $n = 19$ ) and manipulated hatching order (EC-1st.; chick from third-laid egg, C-chick, hatched first;  $n = 16$ ) were created from the remaining three-egg clutches in the peak nesting period. Three egg clutches not selected as controls in the late sample ( $n = 3$ ) were supplemented with one-egg ( $n = 2$ ) and two-egg ( $n = 7$ ) clutches artificially increased to three-egg clutches, and used in the creation of the manipulated hatching synchrony clutches in the late period. Hard boiled Ring-billed gull eggs were added to these clutches during incubation and later substituted with pipped eggs to create the synchronous hatching pattern. In all cases of clutch supplementation parents were monitored for their acceptance of new eggs to their nest.

Synchronously hatched broods were created when the A-egg showed signs of pipping. Peak broods were formed by exchanging third eggs (C-eggs) with donor C-eggs at a stage of pipping similar to A- and B-eggs. Synchronous broods in the late period were created in a similar fashion to the peak with the addition of exchanges of B-eggs with pipped donor B-eggs when necessary.

Individual clutches of the second experimental group (EC-1st) had their hatching order manipulated such that chicks from C-eggs hatched 24 h - 48 h ahead of chicks hatching from A- and B-eggs. This pattern was created by exchanging C-eggs in clutches where the A-eggs showed early stages of pipping with holed C-eggs from donor clutches. Chicks hatched from holed eggs within 12 h - 24 h, whereas chicks normally took at least 36 h - 48 h to hatch from eggs which showed early stages of pipping. Thus, a pattern was created where a chick hatched from a C-egg 24 h - 48 h ahead of chicks hatching from A- and B-eggs.

In the peak period replacement eggs were third-eggs from monitored clutches within the study plot and an additional monitored area that extended five metres east of the original plot. In the late period, replacement eggs came from another area at the colony which was at a similar stage of development to birds nesting in the late plot. To control for egg size during manipulations, replacement eggs were required to be within a range of  $\pm 2$  mm length and  $\pm 2$  mm width of the original egg. If the fresh laying mass of the replacement egg was known, then an additional condition was applied in which the fresh laying mass of those eggs was less than  $\pm 2$  g of the original egg.

All chicks were dyed with Rhodamine B, usually within 12 h of hatching, weather permitting. Chicks were dyed in accordance to normal hatching order: chicks hatching from A-eggs on the head, chicks from B-eggs on the throat / breast area, and chicks hatching from C-eggs on the rump. Chicks from control and synchronous ESYN. nests in which two or three chicks hatched on the same day were assigned a brood rank determined by a variety of factors including relative dryness of the chicks, their proximity to shell fragments and size differences amongst the chicks.

Chicks from different study groups were differentiated by the application of a red leg band to all peak ESYN. chicks, a white leg band to all EC-1st.

chicks and all late ESYN. chicks. Chicks from control broods in both periods were not banded, however the degree of handling for chicks in all groups was similar.

Individual chick mass measurements were recorded at the hatching of each chick within a brood, for all broods. Individual mass measurements were taken again at brood completion (the hatching of last chick within a brood); and five days post-brood completion for broods that still contained three surviving chicks. When the mass of a chick exceeded 100 g, a 1 Kg Pesola scale was used.

On all occasions, the time spent in the plot per visit was noted and never exceeded 1 hour. Survival of chicks in the three study groups was recorded daily from the blind until all surviving chicks were considered fledged (taken as 25 days of age).

### **Statistical Analysis**

After testing the appropriate data sets for normality and homogeneity of variance, non-parametric statistical methods of analysis were chosen. For example, egg volumes were tested for normality using a Kolmogorov-Smirnov Lilliefors test (Zar 1984). The distribution of peak C-egg volumes was found to be significantly different from a normal distribution (two-tail,  $n = 94$ ,  $P = 0.001$ ). Variances between A-, B- and C-eggs in the peak period were significantly heterogeneous (Bartlett  $X^2 = 19.6$ ,  $df = 2$ ,  $P < 0.0001$ ). Because these and other data sets collected did not meet the criteria for a parametric test, non-parametric tests were used. It is recognized that mean values reported with standard deviations and standard errors are parametric measures. These values are used for graphing purposes only and not for any statistical inference.

When comparing chick survival among groups of chicks (ie. first-hatched chicks to last-hatched chicks) Chi-square 2 x 2 contingency tables were used whenever possible. The alternative test used to the Chi-square was the Fisher

exact probability test, used when greater than 20 % of expected frequencies from the contingency table were less than 5.0 (Zar 1984).

## Results

### Investigator Disturbance

Visits into the plots were terminated on 1 June (peak) and 25 June (late). Termination of visits into the plots were before the majority of chicks had reached five to seven days post-hatching, at which time the chicks become increasingly mobile and are more likely to run off their territory if disturbed (Brown 1992). Any chicks observed running or wandering while the investigator was present, were placed back in their natal territory.

### Clutch Initiation

The number of new clutches initiated was recorded daily in the peak (plot I) study plot from 12 April to 2 May (day 103 - 123). The plastic sheeting covering the late plot was removed on 8 May (day 129). The number of new clutches initiated in the late (plot II) study plot was recorded daily from 9 May to 2 June (day 130 - 154). A total of 89 clutches were initiated in the peak plot and 33 clutches in the late. The number of clutches initiated in four day time blocks across the breeding season in the peak and late study plots is reported in Fig. 1.

The final clutch size of each nest was recorded. The distribution of one, two, three and four egg clutches laid in the peak and late plots is presented in Table 1. Among the peak clutches, 81 % ( $n = 72$  clutches) of the clutches were three-egg clutches. Fifty-two percent ( $n = 17$  clutches) of clutches initiated in the late period were three-egg clutches. The occurrence of three-egg clutches was higher in the peak period than in the late period ( $\chi^2 = 15.2$ ,  $df = 1$ ,  $P < 0.001$ , occurrence of one- and two egg clutches pooled versus occurrence of three-egg clutches).

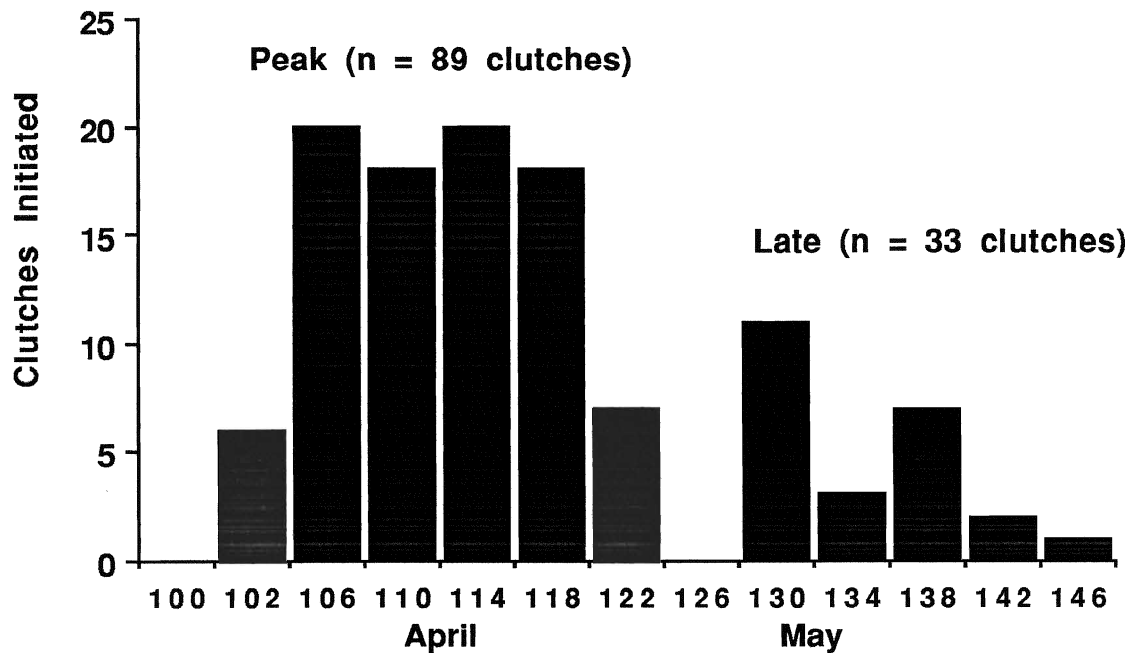


Fig. 1. Distribution of Ring-billed Gull clutches initiated in the peak and late study plots. Peak clutch initiation was monitored from 9 April to 4 May 1992 (day 100 to day 125, 1 January = day 1). Late clutch initiation was monitored from 9 May to 2 June (day 130 to day 154). A total of 89 clutches were initiated in the 8 m x 10 m peak study plot and a total of 33 clutches were initiated in the 7 m x 9 m late study plot. Numbers of clutches initiated have been grouped into four-day blocks.

Table 1. Numbers of one-, two-, three- and four-egg clutches completed in the peak and late study plots. Percent of total is indicated in parenthesis.

Group	Clutch Size				Total
	One	Two	Three	Four	
Peak	7 (8 %)	5 (6 %)	72 (81 %)	5 (6 %)	89
Late	8 (24 %)	8 (24 %)	17 (52%)	0 (0%)	33

### **Egg Laying Intervals**

Mean egg laying intervals (days  $\pm$  1 s.d.) for 17 peak and 10 late control three-egg clutches are reported in Fig.2. No significant difference was found in the laying interval of the A- and B-eggs, between the peak and late periods (Mann-Whitney  $U = 84$ ,  $n_1 = 17$ ,  $n_2 = 10$ ,  $P > 0.05$ ). Likewise, no significant difference was found in the laying intervals of the B- and C-eggs, between peak and late nesting periods ( $U = 63$ ,  $n_1 = 17$ ,  $n_2 = 10$ ,  $P > 0.05$ ). The total egg laying interval, the interval between the laying of the A- and C-egg, did not differ significantly, between the peak and late nesting periods ( $U = 71.5$ ,  $n_1 = 17$ ,  $n_2 = 10$ ,  $P > 0.05$ ).

### **Hatching Intervals**

Mean chick hatching intervals (hours  $\pm$  1 s.d.) for control three-egg clutches initiated in the peak and late study plots are reported in Fig. 3. Hatching was more synchronous in clutches initiated in the peak period than clutches initiated in the late period. The interval between the hatching of A- and C-chicks, during the peak period, was significantly shorter than the corresponding interval during the late period ( $U = 41.0$ ,  $n_1 = 17$ ,  $n_2 = 10$ ,  $P < 0.05$ ). The hatching interval between A- and B-chicks was significantly shorter in the peak, than in the late period ( $U = 47.0$ ,  $n_1 = 17$ ,  $n_2 = 10$ ,  $P < 0.05$ ). The interval between B-chicks and C-chicks did not differ significantly between the peak and late periods ( $U = 68.5$ ,  $n_1 = 17$ ,  $n_2 = 10$ ,  $P > 0.05$ ).

Within the peak period, chick hatching in three-egg clutches was more synchronous than egg laying. The interval between the laying of A- and B-eggs was significantly longer than the interval between the hatching of A-and B-chicks ( $U = 3$ ,  $n_1 = 17$ ,  $n_2 = 17$ ,  $P < 0.001$ ). Within the late period, chick hatching in three-egg clutches was also more synchronous than egg laying. The interval between the hatching of A- and C-chicks was however, significantly shorter than



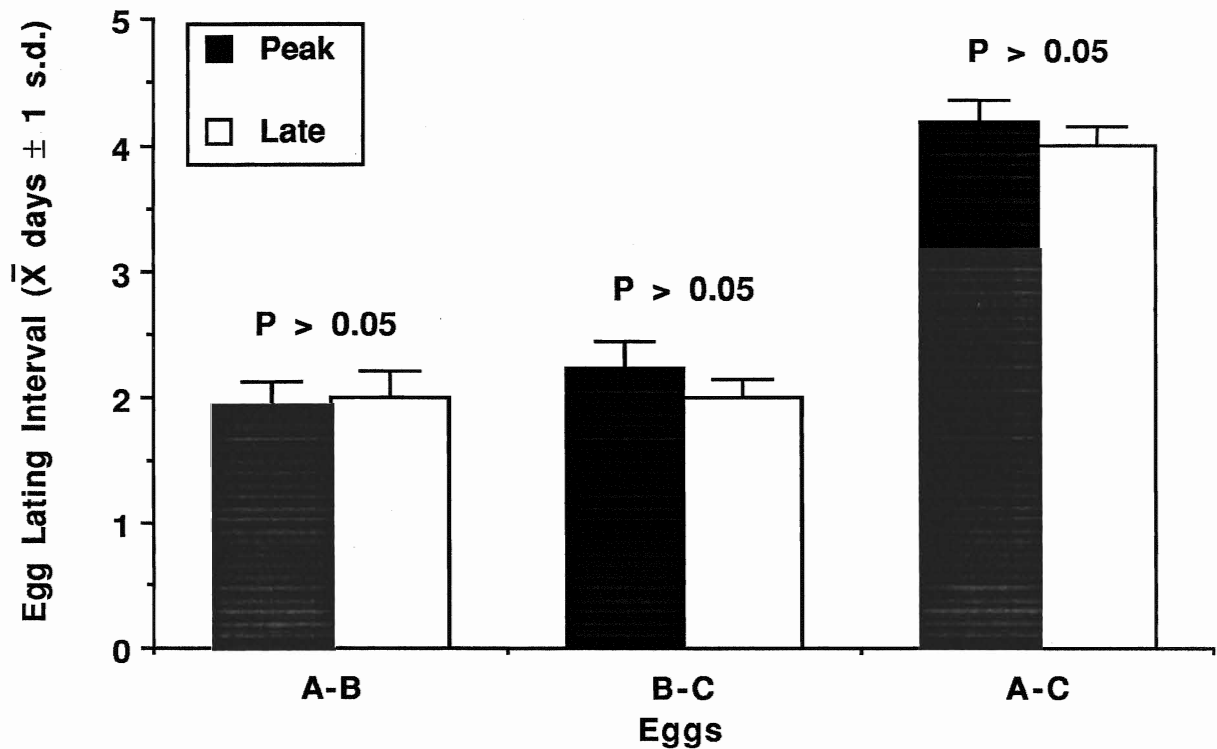


Fig. 2. Mean egg laying intervals ( $\pm 1$  s.d.) for three-egg clutches initiated in the peak ( $n = 17$  clutches) and late ( $n = 10$  clutches) study plots. Total egg laying interval is represented as the interval between the laying of A- to C-eggs. P-values were generated from Mann-Whitney U-tests comparing between the peak and late periods at the respective stages.

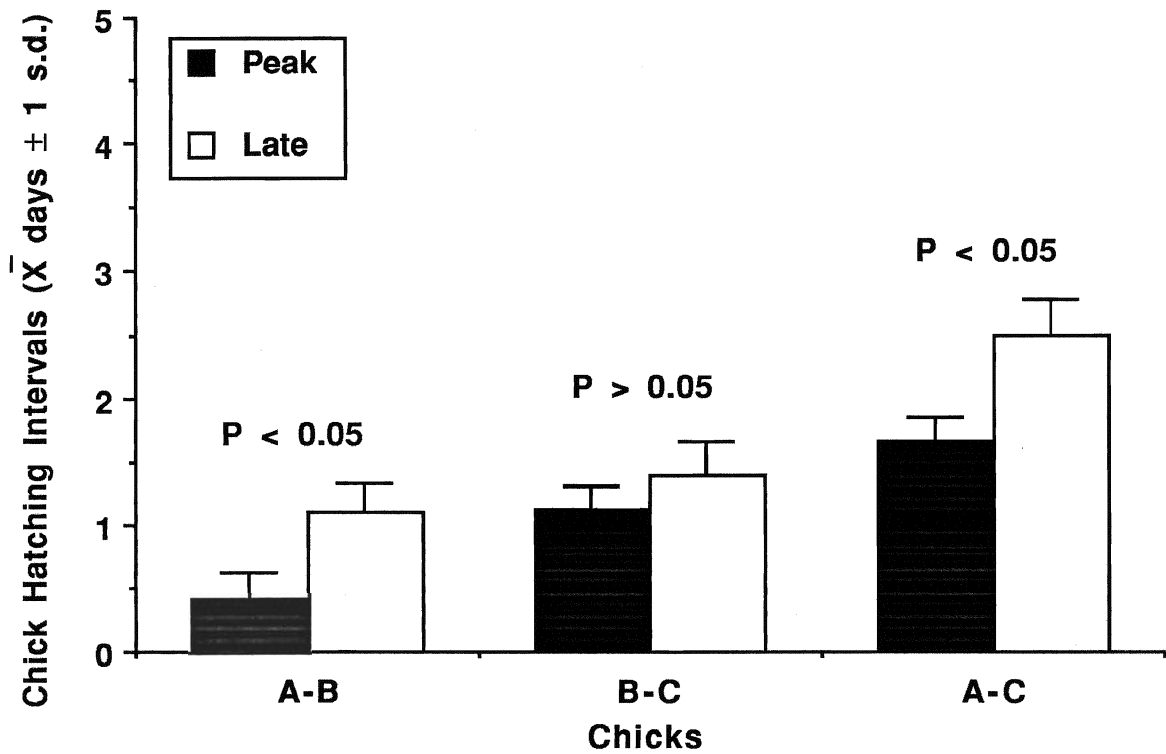


Fig. 3. Mean chick hatching intervals ( $\pm$  1 s.d.) for three-egg clutches initiated in the peak and late study plots. Total chick hatching interval is represented as the interval between the hatching of chicks one to three. P-values were generated from Mann-Whitney U-tests comparing between the peak and late periods at the respective stages.

the interval between the laying of A- and C-eggs, in the late period ( $\bar{x}$  laying  $\pm$  1 s.d. = 96.0h  $\pm$  11.3h;  $\bar{x}$  hatching  $\pm$  1 s.d. = 60.0h  $\pm$  20.4h; U = 7,  $n_1$  = 10,  $n_2$  = 10,  $P$  < 0.01).

### Brood Patch Development

In the peak period, 36 incubating Ring-billed Gull adults were trapped at the one-egg stage ( $n$  = 12), two-egg stage ( $n$  = 12) and the three-egg stage ( $n$  = 12). In the late period, 19 incubating adult birds were trapped at the one-egg stage ( $n$  = 9) and the three-egg stage ( $n$  = 10). Length and width measurements were taken for all three brood patches on all trapped birds. In addition head-bill measurements were taken for all trapped birds as an index of body size.

The mean areas ( $\pm$  1 s.d.) of right, left and lower brood patches of birds trapped at the various stages in the peak and late periods are listed in Appendix IV. There were no differences among the three brood patch areas of birds at a given stage. In the peak period, no significant difference was found among the three brood patches of birds incubating either the one-egg stage (Friedman ANOVA  $X^2$  = 1.17,  $df$  = 2,  $n$  = 12,  $P$  > 0.05), the two-egg stage (Friedman  $X^2$  = 3.17,  $df$  = 2,  $n$  = 12,  $P$  > 0.05) or the three-egg stage (Friedman  $X^2$  = 4.50,  $df$  = 2,  $n$  = 12,  $P$  > 0.05). Similarly, in the late period, no significant difference was found among the three brood patches of birds incubating either the one-egg stage (Friedman  $X^2$  = 2.89,  $df$  = 2,  $n$  = 9,  $P$  > 0.05) or the three-egg stage (Friedman  $X^2$  = 5.40,  $df$  = 2,  $n$  = 10,  $P$  > 0.05).

The mean total (summed areas of three brood patches per bird  $\pm$  1 s.d.) brood patch area for birds trapped at various stages in the peak and late period are reported in Fig. 4. In the peak period, brood patch areas became progressively more defeathered (larger) as egg laying progressed. The total brood patch areas of birds trapped at the three-egg stage were significantly larger than that of birds trapped at the one-egg stage (U = 1,  $n_1$  = 12,  $n_2$  = 12,  $P$

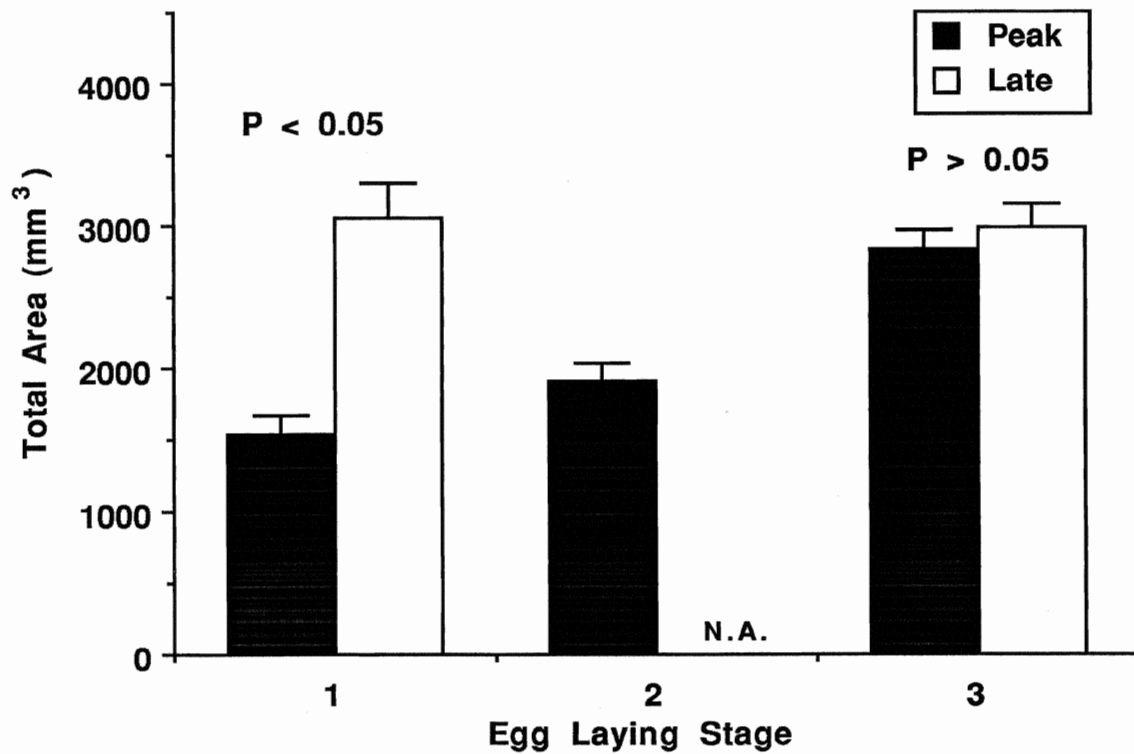


Fig. 4. Mean brood patch areas ( $\pm 1$  s.d.) for peak Ring-billed Gulls trapped at the one-, two- and three-egg stage and for late birds trapped at the one- and three-egg stage. Mean areas were calculated from summed areas of the three individual patch areas on a given bird. P-values were generated from Mann-Whitney U-tests comparing peak and late periods at the one- and three-egg stages.

< 0.0005) and the two-egg stage ( $U = 12$ ,  $n_1 = 12$ ,  $n_2 = 12$ ,  $P < 0.001$ ). The difference in total brood patch areas between birds trapped at the one and two-egg stage approached significance ( $U = 39$ ,  $n_1 = 12$ ,  $n_2 = 12$ ,  $0.10 > P > 0.05$ ).

In the late period, defeathering of brood patches was effectively complete at clutch initiation (Fig 4.), as total brood patch areas of birds trapped at the one-egg stage did not differ significantly from birds trapped at the three-egg stage ( $U = 34$ ,  $n_1 = 9$ ,  $n_2 = 10$ ,  $P > 0.05$ ). The brood patch defeathering of birds trapped at the one-egg stage in the late, was also comparable to that of birds trapped at the three-egg stage in the peak ( $U = 36$ ,  $n_1 = 12$ ,  $n_2 = 9$ ,  $P > 0.05$ ). The total brood patch areas of birds trapped at the one-egg stage in the peak period were significantly smaller than that of birds trapped at the one-egg stage in the late period ( $U = 9$ ,  $n_1 = 12$ ,  $n_2 = 9$ ,  $P < 0.005$ ). The total brood patch areas of birds trapped at the third egg stage in the peak and late period did not differ significantly ( $U = 44$ ,  $n_1 = 12$ ,  $n_2 = 10$ ,  $P > 0.05$ ).

In total, 55 birds were trapped (36 peak and 19 late) for brood patch measurement across the various stages. By using differences in head-bill measurements (back of skull to tip of beak), it was determined that 41 males (head-bill  $\geq 96.0$  mm) and 14 females were trapped. To test for differences in brood patch area between males and females, the brood patch areas of birds from the peak three-egg stage, late one-egg stage and late three egg stage were pooled, as no significant differences were found among these stages (see above). Differences observed in brood patch areas, were not likely the result of different sexes, with differing size brood patches, incubating at a particular stage. No significant difference was observed between males and females of the pooled sample ( $U = 89$ ,  $n_1 = 22$ ,  $n_2 = 9$ ,  $P > 0.05$ ).

## Nocturnal Desertion

Nocturnal nest attendance (incubation) was recorded for 20 nests initiated in the peak period and for 19 nests initiated in the late period. Nocturnal nest attendance was recorded as the time spent on the nest in a given night, defined as the interval between one half hour after sunset until one half hour before sunrise the next morning. Nocturnal attendance was standardized for differences in nighttime duration by expressing attendance in minutes spent on the nest per hour.

The mean nocturnal attendance ( $\pm 1$  s.e.) of peak birds at the one-egg stage, two-egg stage, clutch completion (three-egg stage) and for five days post-clutch completion are presented in Fig. 5. The mean nocturnal attendance ( $\pm 1$  s.e.) of late birds at the one-egg stage, two-egg stage, clutch completion (three-egg stage) and for five days post-clutch completion are presented in Fig. 6.

The nest attendance was lower in the peak period than in the late period at both the one-egg stage ( $U = 0$ ,  $n_1 = 19$ ,  $n_2 = 19$ ,  $P < 0.0001$ ) and the two-egg stage ( $U = 73$ ,  $n_1 = 20$ ,  $n_2 = 18$ ,  $P < 0.005$ ). Birds spent an average of less than one minute (0.33 min.) on the nest per hour, at the one-egg stage, in the peak period, and an average of 49.16 minutes on the nest per hour in the late period. At the two-egg stage birds incubating in the peak period spent an average of 24.08 minutes on the nest per hour compared to an average of 56.25 mins. on nest / hour, in the late period. Departures from the colony were usually more synchronous than returns. The longest absences from the colony averaged up to eight hours at the one-egg stage.

At clutch completion the nocturnal nest attendance did not differ significantly ( $U = 172$ ,  $n_1 = 19$ ,  $n_2 = 19$ ,  $P > 0.05$ ) between birds incubating during the peak and late periods. Later into incubation (days four and five post-

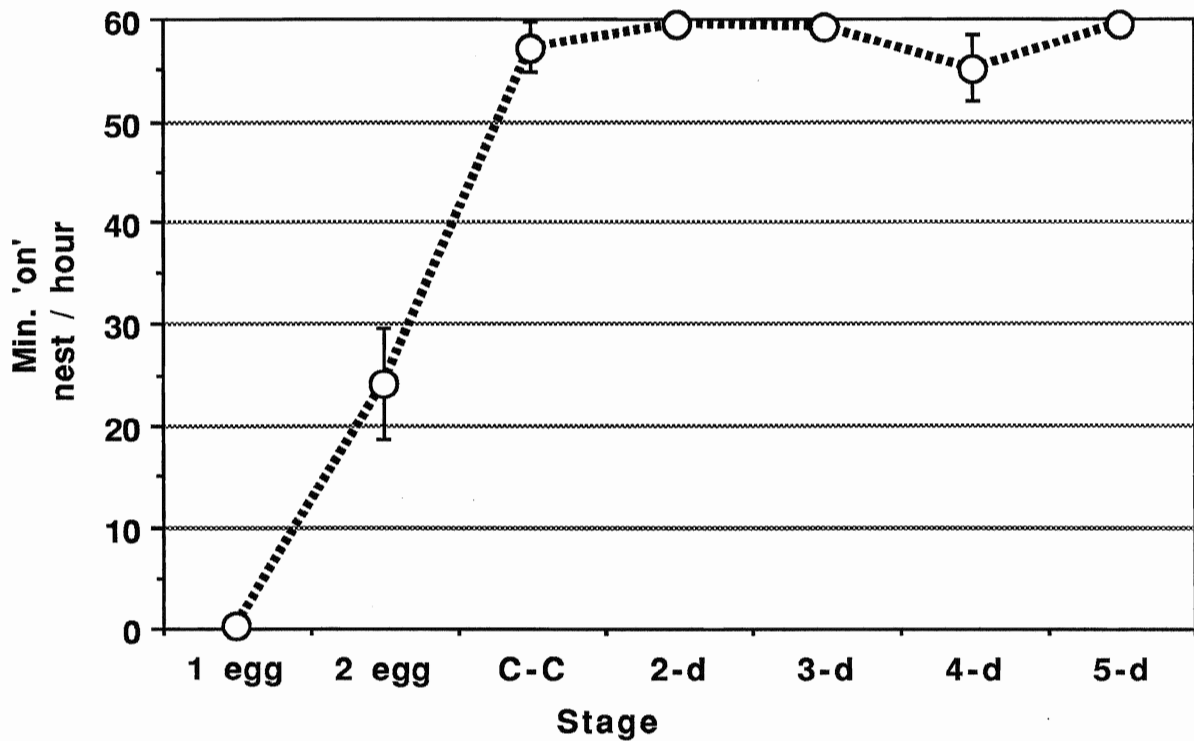


Fig. 5. Mean ( $\pm 1$  s.e.) time spent on the nest / hour for Ring-billed Gulls attending 20 nests during the peak period. Stages are reported with respect to number of eggs in nest: one-egg, two-egg and clutch completion (C.C.= clutch completion: three-egg stage), and five days post-clutch completion. Attendance is standardized to minutes on the nest / hour to accommodate for differences in nighttime periods, defined as one-half hour after sunset through to one-half hour before sunrise the following morning.

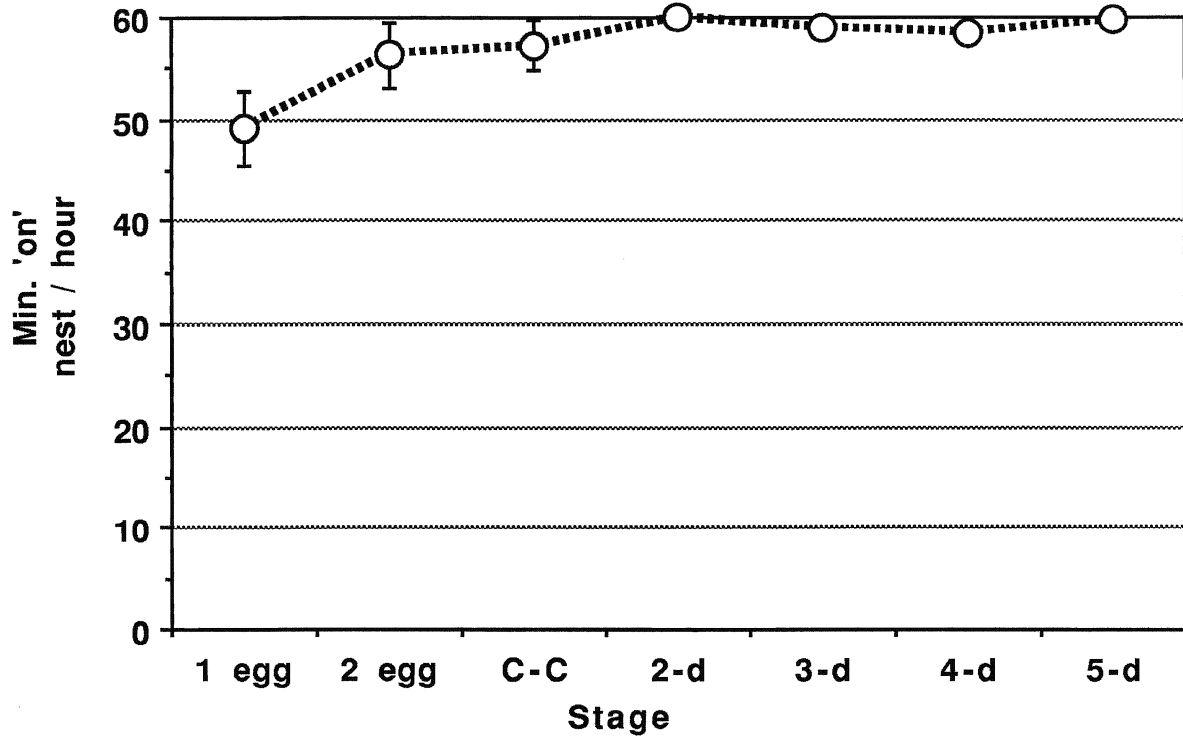


Fig. 6. Mean ( $\pm 1$  s.e.) time spent on the nest / hour for Ring-billed Gulls attending 19 clutches during the late period. Stages are reported with respect to number of eggs in nest: one-egg, two-egg and clutch completion (C.C. = clutch completion: three-egg stage), and five days post-clutch completion. Attendance is standardized to minutes on the nest / hour to accommodate for differences in nighttime periods, defined as one-half hour after sun set through to one-half hour before sun rise the following morning.



clutch completion), the nocturnal attendance of peak nest and late birds did not differ significantly (Fig. 5 and Fig. 6;  $U = 116$ ,  $n_1 = 20$ ,  $n_2 = 16$ ,  $P > 0.05$ ).

There were dramatic differences in the nocturnal nest attendance pattern within the peak period (Friedman  $X^2 = 61.8$ ,  $df = 6$ ,  $P < 0.0001$ ). Attendance on the nest was lowest at the one-egg stage (peak one-egg stage < peak two-egg stage,  $U = 17.0$ ,  $n_1 = 17$ ,  $n_2 = 20$ ,  $P < 0.0001$ ; peak one-egg stage < peak clutch completion,  $U = 0$ ,  $n_1 = 17$ ,  $n_2 = 19$ ,  $P < 0.0001$ ; peak two-egg stage < peak clutch completion,  $U = 57.5$ ,  $n_1 = 20$ ,  $n_2 = 19$ ,  $P < 0.0005$ ; peak one-egg stage < peak 4 - 5 d post-clutch completion,  $U = 0$ ,  $n_1 = 19$ ,  $n_2 = 19$ ,  $P < 0.0001$ ).

There were some trends in the nocturnal nest attendance within the late period (Friedman  $X^2 = 21.2$ ,  $df = 6$ ,  $P < 0.005$ ). Attendance on the nest was lowest at the one- and two-egg stage (late one-egg stage  $\approx$  late two-egg stage,  $U = 112.0$ ,  $n_1 = 19$ ,  $n_2 = 18$ ,  $P > 0.05$ ; late one-egg stage < late clutch completion,  $U = 86$ ,  $n_1 = 16$ ,  $n_2 = 19$ ,  $P < 0.01$ ; late one-egg stage  $\leq$  late 4 - 5 d post-clutch completion,  $U = 129.0$ ,  $n_1 = 18$ ,  $n_2 = 16$ ,  $0.1 > P > 0.05$ ). In the five days post-brood completion, incubation was high and did not differ, in both the peak and late periods (peak post-clutch completion days 1 - 5, Friedman  $X^2 = 4.0$ ,  $df = 4$ ,  $P > 0.05$ ; late post-clutch completion days 1 - 5, Friedman  $X^2 = 7.1$ ,  $df = 4$ ,  $P > 0.05$ ).

### **Egg Volume and Mass**

Egg volumes were calculated from length and width measurements using the formula:  $volume = k \cdot l \cdot w^2$ , where  $k = 0.502$  for Ring-billed Gull eggs (Morris and Chardine 1986). Mean egg volumes ( $\pm 1$  s.d.) taken for a sample of 94 peak and 15 late three-egg clutches are reported in Fig. 7. In the peak period there was a significant difference among eggs of a clutch (Friedman  $X^2 = 76.4$ ,  $df = 2$ ,  $P < 0.0001$ ). The volume of A- and B-eggs did not differ

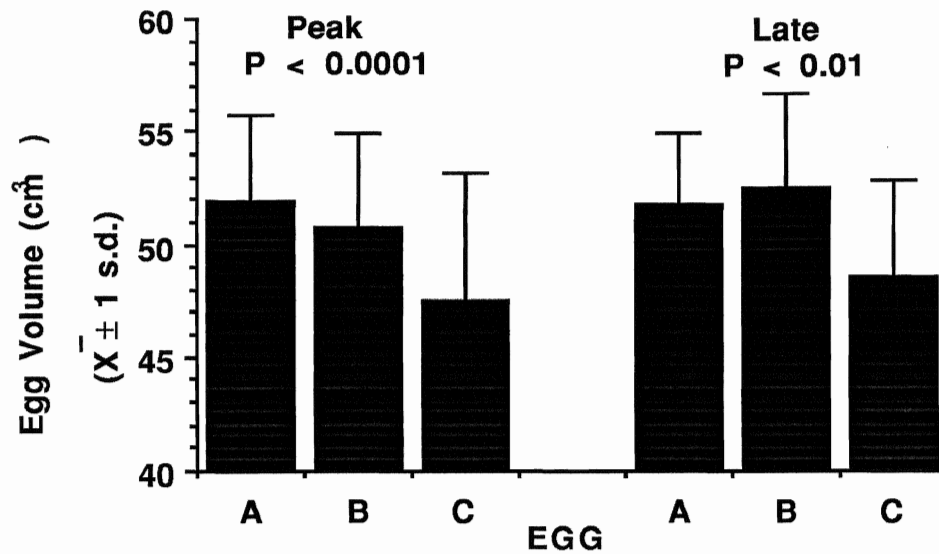


Fig. 7. Mean egg volumes ( $\pm 1$  s.d.) for A-, B- and C-eggs in the peak and late plots. P-values were generated from Friedman ANOVA's testing for differences among egg volumes within the peak and late periods.

significantly ( $U = 3815.5$ ,  $n_1 = 94$ ,  $n_2 = 94$ ,  $P > 0.05$ ). C-eggs were smaller than both A- and B-eggs (A-eggs & C-eggs,  $U = 2061.0$ ,  $n_1 = 94$ ,  $n_2 = 94$ ,  $P < 0.005$ ; B-eggs & C-eggs,  $U = 2643.0$ ,  $n_1 = 94$ ,  $n_2 = 94$ ,  $P < 0.005$ ).

In the late period, there was also a significant difference found among the volumes of eggs in a clutch (Fig. 7; Friedman  $\chi^2 = 14.5$ ,  $df = 2$ ,  $P < 0.01$ ). As in the peak period, C-eggs were smaller than A- and B-eggs in the late period (A-eggs & B-eggs,  $U = 107.0$ ,  $n_1 = 15$ ,  $n_2 = 15$ ,  $P > 0.05$ ; A-eggs & C-eggs,  $U = 49.0$ ,  $n_1 = 15$ ,  $n_2 = 15$ ,  $P < 0.01$ ; B-eggs & C-eggs,  $U = 42.0$ ,  $n_1 = 15$ ,  $n_2 = 15$ ,  $P < 0.005$ ).

No significant difference was found between the volumes of A-eggs between the peak and late periods (Fig. 7;  $U = 683$ ,  $n_1 = 94$ ,  $n_2 = 15$ ,  $P > 0.05$ ). Similarly, no significant differences were found between the volumes of B-eggs ( $U = 578$ ,  $n_1 = 94$ ,  $n_2 = 15$ ,  $P > 0.05$ ), or C-eggs ( $U = 704$ ,  $n_1 = 94$ ,  $n_2 = 15$ ,  $P > 0.05$ ), in the peak and late periods.

Egg mass measurements were recorded for each egg in a clutch within 24 h of laying for eggs of 94 peak and 15 late clutches. The mean values ( $\pm 1$  s.d.) of those eggs are reported in Fig. 8. There were significant differences among the fresh egg masses in both the peak (Friedman  $\chi^2 = 97.6$ ,  $df = 2$ ,  $P < 0.0001$ ) and late (Friedman  $\chi^2 = 10.1$ ,  $df = 2$ ,  $P < 0.01$ ) nesting periods. In the peak period, egg mass formed a graded series where A-eggs were heavier than both B-eggs ( $U = 3547$ ,  $n_1 = 94$ ,  $n_2 = 94$ ,  $P < 0.05$ ) and C-eggs ( $U = 1809$ ,  $n_1 = 94$ ,  $n_2 = 94$ ,  $P < 0.0001$ ). In addition, B-eggs had a larger mass than C-eggs, in the peak period ( $U = 2514$ ,  $n_1 = 94$ ,  $n_2 = 94$ ,  $P < 0.0001$ ).

In the late period, eggs formed a mass hierarchy in which C-eggs were smaller than both A-eggs ( $U = 63.0$ ,  $n_1 = 15$ ,  $n_2 = 15$ ,  $P < 0.05$ ) and B-eggs

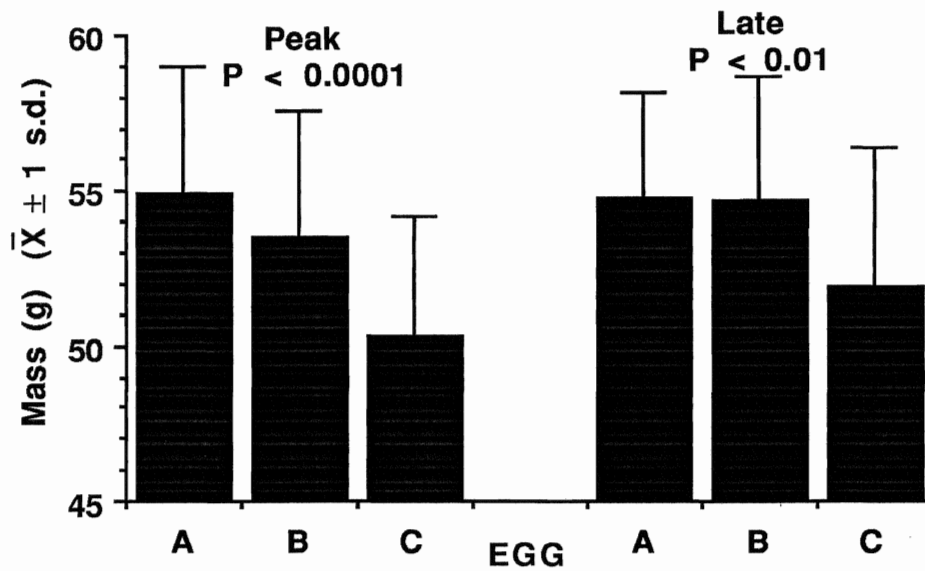


Fig. 8. Mean egg masses ( $\pm 1$  s.d.) for A-, B- and C-eggs in the peak and late plots. P-values were generated from Friedman ANOVA's testing for differences among egg volumes within the peak and late periods.

( $U = 61.5$ ,  $n_1 = 15$ ,  $n_2 = 15$ ,  $P < 0.05$ ). The masses of A- and B-eggs did not differ significantly ( $U = 111.0$ ,  $n_1 = 15$ ,  $n_2 = 15$ ,  $P > 0.05$ ).

No significant difference was found in the mass of A-, B- or C-eggs between the peak and late periods (Fig. 8; A-eggs,  $U = 673$ ,  $n_1 = 94$ ,  $n_2 = 15$ ,  $P > 0.05$ ; B-eggs  $U = 599$ ,  $n_1 = 94$ ,  $n_2 = 15$ ,  $P > 0.05$ ; C-eggs  $U = 580$ ,  $n_1 = 94$ ,  $n_2 = 15$ ,  $P > 0.05$ ).

### **Chick mass**

In both the peak and late periods, chick mass measurements were taken for each chick of a brood at hatching, and again at brood completion (usually the hatching of the chick from the third-laid egg; the C-chick). An additional mass measurement was taken for each chick at five days post-brood completion (P.B.C.) in broods in which all three chicks survived to that age. The mean mass measurements ( $\pm 1$  s.d.) at hatching, brood completion and five days post-brood completion for chicks of peak and late broods are reported in Fig. 9 and Fig. 10 respectively.

There were significant differences among the mass of brood mates hatching in the peak period (Fig.9; Friedman  $X^2 = 15.3$ ,  $df = 2$ ,  $P < 0.001$ ). The mass, at hatching, of A-chicks was not significantly different from that of B-chicks ( $U = 98.5$ ,  $n_1 = 17$ ,  $n_2 = 17$ ,  $P > 0.05$ ), however the hatching mass of A-chicks was greater than the hatching mass of C-chicks ( $U = 73.0$ ,  $n_1 = 17$ ,  $n_2 = 17$ ,  $P < 0.05$ ). The mass at hatching of B-chicks did not differ significantly from the the hatching mass of C-chicks ( $U = 107.0$ ,  $n_1 = 17$ ,  $n_2 = 17$ ,  $P > 0.05$ ).

At brood completion, there were significant differences among the masses of brood mates (Fig.9 Friedman  $X^2 = 21.2$ ,  $df = 2$ ,  $P < 0.0005$ ). The mass of A-chicks

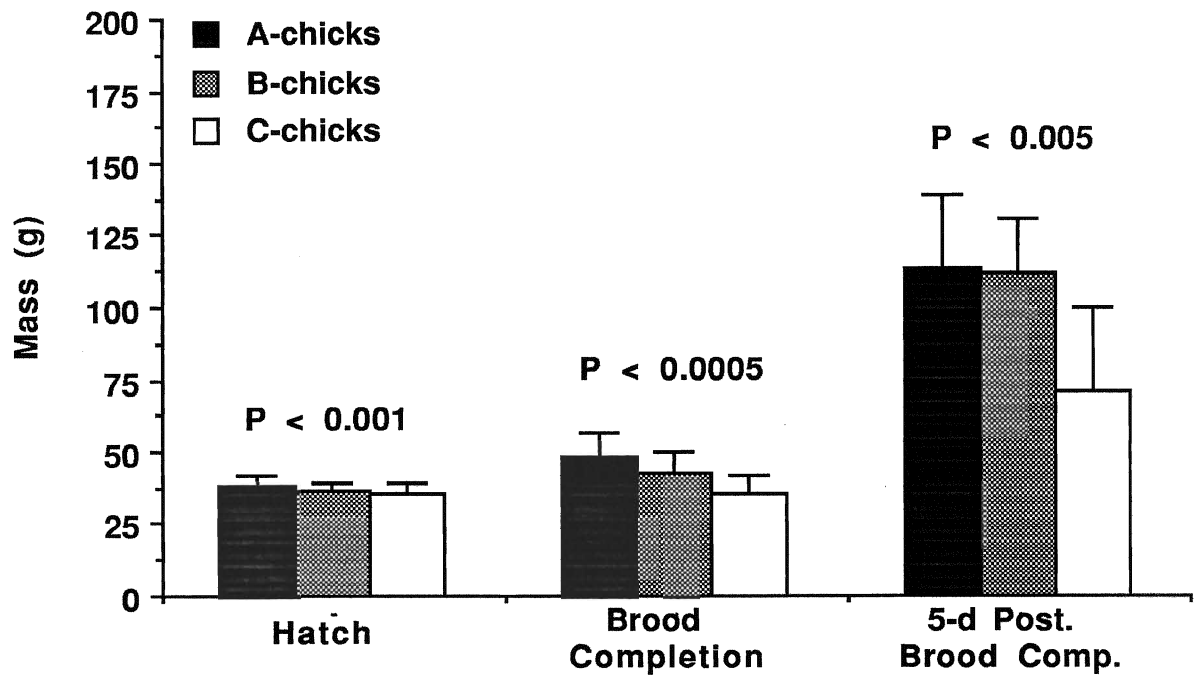


Fig. 9. Mean chick masses ( $\pm 1$  s.d.) for chicks in the peak period. Values are reported for chicks of 17 broods at hatching and brood completion and for chicks of nine broods in which all three chicks survived to five days post-brood completion. P-values were generated from Friedman ANOVA's testing for differences among chick mass at the respective stages.

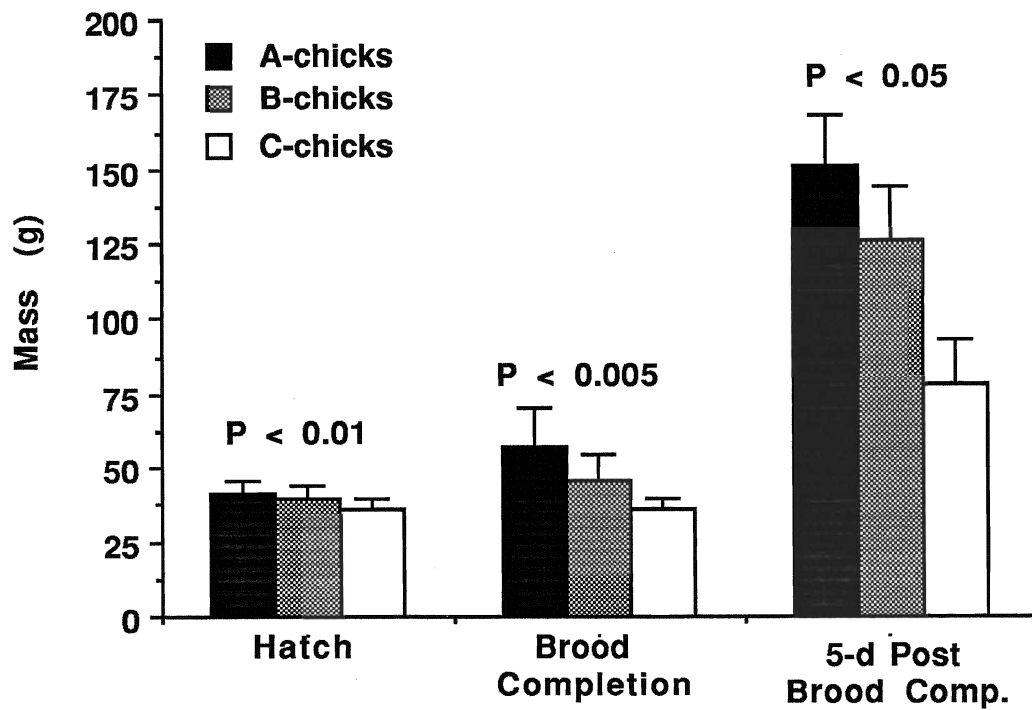


Fig. 10. Mean chick masses ( $\pm 1$  s.d.) for chicks hatching in the late period. Values are reported for chicks of nine broods at hatching, eight at brood completion and for chicks of three broods in which all three chicks survived to five days post-brood completion. P-values were generated from Friedman ANOVA's testing for differences among chick mass at the respective stages.

and B-chicks did not differ significantly ( $U = 92.0$ ,  $n_1 = 17$ ,  $n_2 = 17$ ,  $P > 0.05$ ). C-chicks were significantly lighter than both A-chicks ( $U = 35$ ,  $n_1 = 17$ ,  $n_2 = 17$ ,  $P < 0.0005$ ) and B-chicks ( $U = 52.5$ ,  $n_1 = 17$ ,  $n_2 = 17$ ,  $P < 0.005$ ).

In the nine peak broods where all three chicks survived to five days post-brood completion, there were significant differences among the chicks in a brood (Fig. 9; Friedman  $X^2 = 11.0$ ,  $df = 2$ ,  $P < 0.005$ ). Again the mass of A-chicks and B-chicks did not differ significantly ( $U = 38.5$ ,  $n_1 = 9$ ,  $n_2 = 9$ ,  $P > 0.05$ ). C-chicks were smaller than both A-chicks ( $U = 12$ ,  $n_1 = 9$ ,  $n_2 = 9$ ,  $P < 0.05$ ) and B-chicks ( $U = 10$ ,  $n_1 = 9$ ,  $n_2 = 9$ ,  $P < 0.01$ ).

In the late period, there were significant differences among the mass of brood mates at hatching (Fig. 10; Friedman  $X^2 = 10.1$ ,  $df = 2$ ,  $P < 0.01$ ). The mass of first hatched, A-chicks, was not significantly different from that of second hatched, B-chicks ( $U = 34.5$ ,  $n_1 = 9$ ,  $n_2 = 9$ ,  $P > 0.05$ ), however the hatching mass of A-chicks was greater than the hatching mass of last hatched, C-chicks ( $U = 14.5$ ,  $n_1 = 9$ ,  $n_2 = 9$ ,  $P < 0.05$ ). The difference in hatching mass between B-chicks and C-chicks approached significance ( $U = 23.5$ ,  $n_1 = 9$ ,  $n_2 = 9$ ,  $0.1 > P > 0.05$ ), with C-chicks being lighter than B-chicks.

At brood completion in the late period, there were significant differences among the masses of brood mates (Fig. 10; Friedman  $X^2 = 12.3$ ,  $df = 2$ ,  $P < 0.005$ ). The mass of A-chicks and B-chicks differed significantly ( $U = 13$ ,  $n_1 = 8$ ,  $n_2 = 8$ ,  $P < 0.05$ ). C-chicks were smaller than A-chicks ( $U = 2$ ,  $n_1 = 8$ ,  $n_2 = 8$ ,  $P < 0.005$ ). The extent to which C-chicks were smaller than B-chicks at brood completion approached significance ( $U = 13.5$ ,  $n_1 = 8$ ,  $n_2 = 8$ ,  $0.1 > P > 0.05$ ).

In the three late broods where all three chicks survived to five days post-brood completion, there were significant differences among the chicks in a brood (Fig. 10; Friedman  $X^2 = 6.0$ ,  $df = 2$ ,  $P < 0.05$ ). The mass of A-chicks and B-chicks did not differ significantly ( $U = 2.0$ ,  $n_1 = 3$ ,  $n_2 = 3$ ,  $P > 0.05$ ). C-chicks



were significantly smaller than both A-chicks ( $U = 0.0$ ,  $n_1 = 3$ ,  $n_2 = 3$ ,  $P < 0.05$ ) and B-chicks ( $U = 0.0$ ,  $n_1 = 3$ ,  $n_2 = 3$ ,  $P < 0.05$ ).

### **Chick Survival**

The survival to fledging (taken as 25 days post-brood completion) for chicks of unmanipulated broods in the peak ( $n = 17$ ) and late period ( $n = 10$ ) is reported in Table 2. Within the peak period, there were significant differences among the chicks that survived to 25 days of age. The number of C-chicks that survived ( $n = 4$  chicks) was significantly lower than the number of A-chicks ( $n = 13$ ;  $X^2 = 9.5$ ,  $df = 1$ ,  $P < 0.005$ ), or B-chicks fledging ( $n = 15$ ;  $X^2 = 14.4$ ,  $df = 1$ ,  $P < 0.001$ ). The number of A-chicks and B-chicks surviving to fledging did not differ significantly (Fisher exact  $P = 0.33$ ).

In the late period, chick survival was generally poor (Table 2). No C-chicks ( $n = 0$  chicks) survived to fledging, this was significantly lower than the number of A-chicks surviving to fledging (Fisher exact  $P = 0.04$ ). The number of A-chicks ( $n = 4$  chicks) and B-chicks surviving to fledging ( $n = 3$  chicks) in the late period did not differ significantly (Fisher exact  $P = 0.5$ ) nor did the number of B-chicks and C-chicks fledging in the late period (Fisher, exact  $P = 0.11$ ).

The number of C-chicks that survived to fledging, in the peak period, did not differ from the number of C-chicks that survived to fledging in the late period (Table 2; Fisher exact  $P = 0.14$ ). The difference in survival to fledging of peak A-chicks and late A-chicks approached significance (Fisher exact  $P = 0.07$ ), and survival to fledging of peak B-chicks was significantly greater than that of late B-chicks (Fisher exact  $P = 0.004$ ).

The percent survival by age of individual chicks from unmanipulated, peak and late three chick broods is reported in Fig.'s 11 and 12. The most dramatic drop in the percent of chicks alive occurred in the late period, between days two and six. During this time, a series of harsh storms often left chicks cold, wet and frequently unprotected by their parents. Herring Gull predation

Table 2. Chick survival to fledging (25 days post-brood completion) in unmanipulated broods from the peak and late nesting periods. Percent survival is indicated in parenthesis.

Group	# of Chicks Fledged			# of Broods	Av. # flgd. / Brood
	A	B	C		
Peak	13 (76 %)	15 (88 %)	4 (24 %)	17	1.9
Late	4 (40 %)	3 (30 %)	0 (0 %)	10	0.7

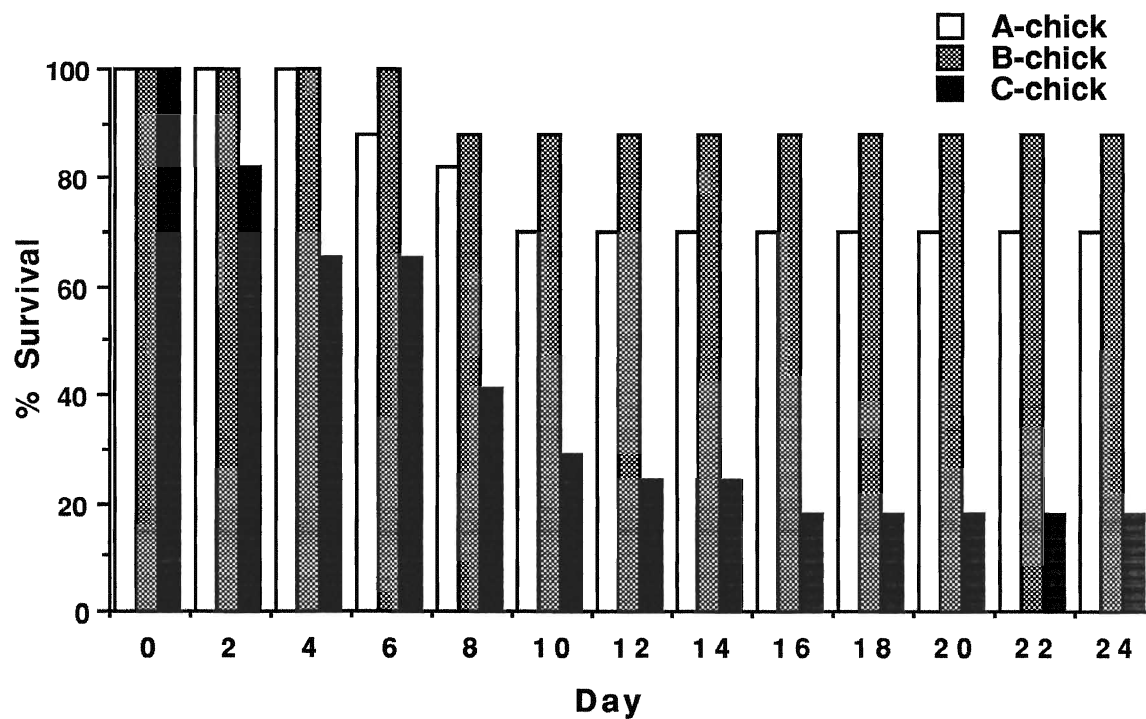


Fig. 11. Percent survival of individual chicks from unmanipulated peak broods. A total of 17 three-chick broods were available during the peak period. Day 0 = brood completion (hatching of the C-chick).

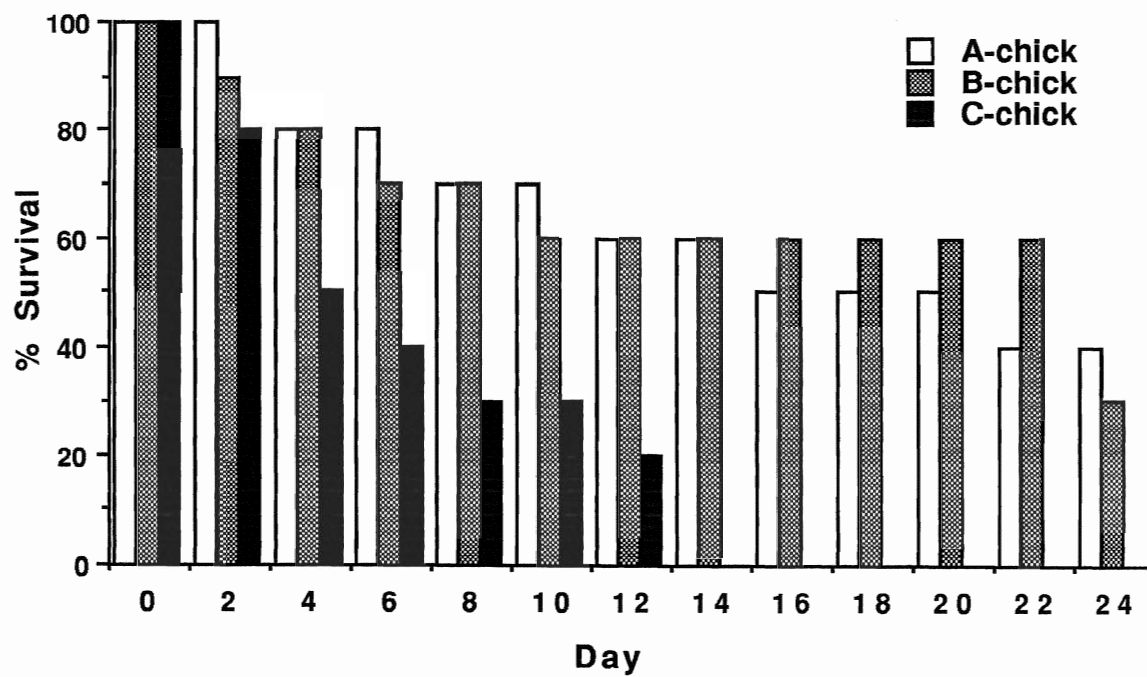


Fig. 12. Percent survival of individual chicks from unmanipulated late broods. A total of 10 three-chick broods were available during the late period. Day 0 = brood completion (hatching of the C-chick).

was also a suspected source of chick mortality, as several aggressive Herring Gull pairs nesting directly adjacent to the late plot were observed attacking and sometimes killing young chicks. Predation did not appear to be a significant cause of chick mortality in the peak plot.

### **Hatching Synchrony Manipulations**

In both the peak and late periods, selected broods were manipulated through a series of third-egg exchanges to have all chicks of a brood hatching synchronously ( $\leq 24$  h). The mean mass ( $\pm 1$  s.d.) of chicks from synchronously hatching broods in the peak period are given in Fig. 13. The mean mass ( $\pm 1$  s.d.) of chicks from synchronously hatching broods in the late period are presented in Fig. 14.

In the peak period, there were no differences among the masses of  $E_{\text{SYN}}$  chicks at hatching (Fig. 13; Friedman  $X^2 = 4.5$ ,  $df = 2$ ,  $P > 0.05$ ), or at brood completion (Friedman  $X^2 = 3.1$ ,  $df = 2$ ,  $P > 0.05$ ). At five days post-brood completion, differences among brood mates approached significance (Friedman  $X^2 = 5.6$ ,  $df = 2$ ,  $0.1 > P > 0.05$ ). There were no differences between the masses of C-chicks from synchronous broods and the masses of C-chicks from unmanipulated broods at hatching (see Fig. 9 and 13,  $U = 124.0$ ,  $n_1 = 17$ ,  $n_2 = 19$ ,  $P > 0.05$ ) or at brood completion ( $U = 116.0$ ,  $n_1 = 17$ ,  $n_2 = 19$ ,  $P > 0.05$ ). Differences between C-chicks of control and  $E_{\text{SYN}}$  broods in the peak period at five days post-brood completion approached significance ( $U = 22.0$ ,  $n_1 = 9$ ,  $n_2 = 10$ ,  $0.1 > P > 0.05$ ).

In the late period, significant differences amongst the hatching masses of brood mates were indicated using a Friedman ANOVA ( $X^2 = 6.78$ ,  $df = 2$ ,  $P < 0.05$ ). Paired tests between the chicks found differences amongst chicks approached significance (Fig. 14; Late A-chicks  $\geq$  C-chicks,  $U = 32.5$ ,  $n_1 = 11$ ,

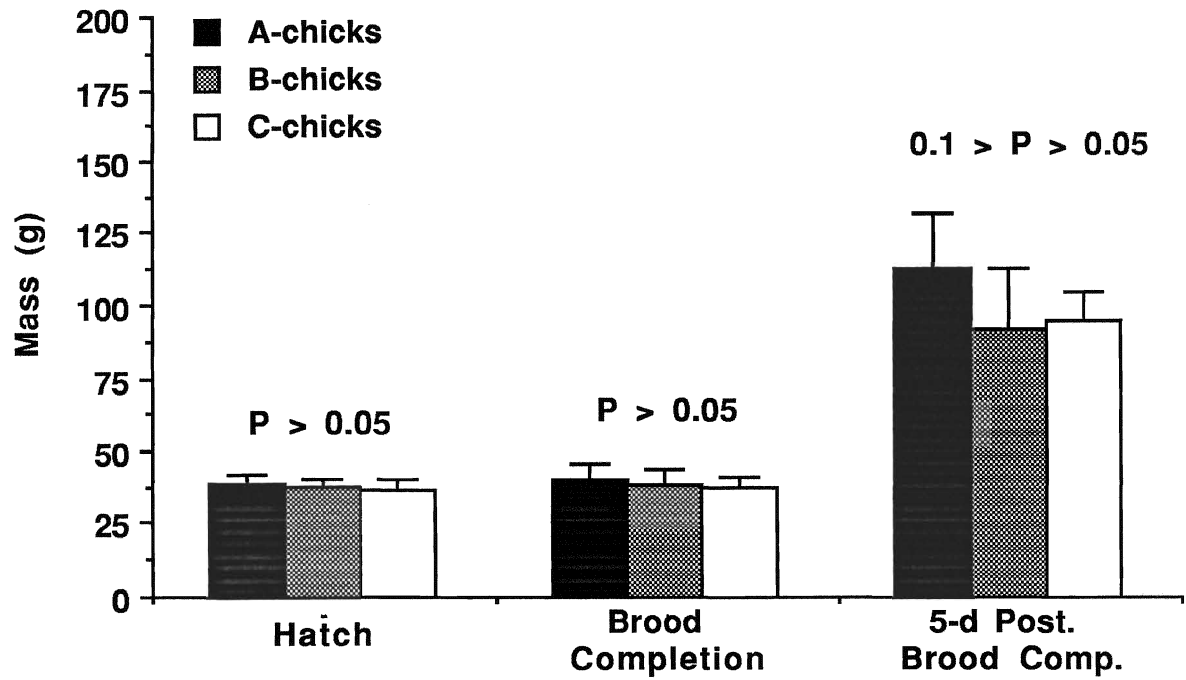


Fig. 13. Mean chick masses ( $\pm 1$  s.d.) for chicks of broods in the peak period where chicks were manipulated to hatch synchronously within 24 h of each other ( $E_{SYN}$ ). Values are reported for chicks of 19 broods at hatching and brood completion and for chicks of ten broods in which all three chicks survived to five days post-brood completion. P-values were generated from Friedman ANOVA's testing for differences among chick mass at the respective stages.

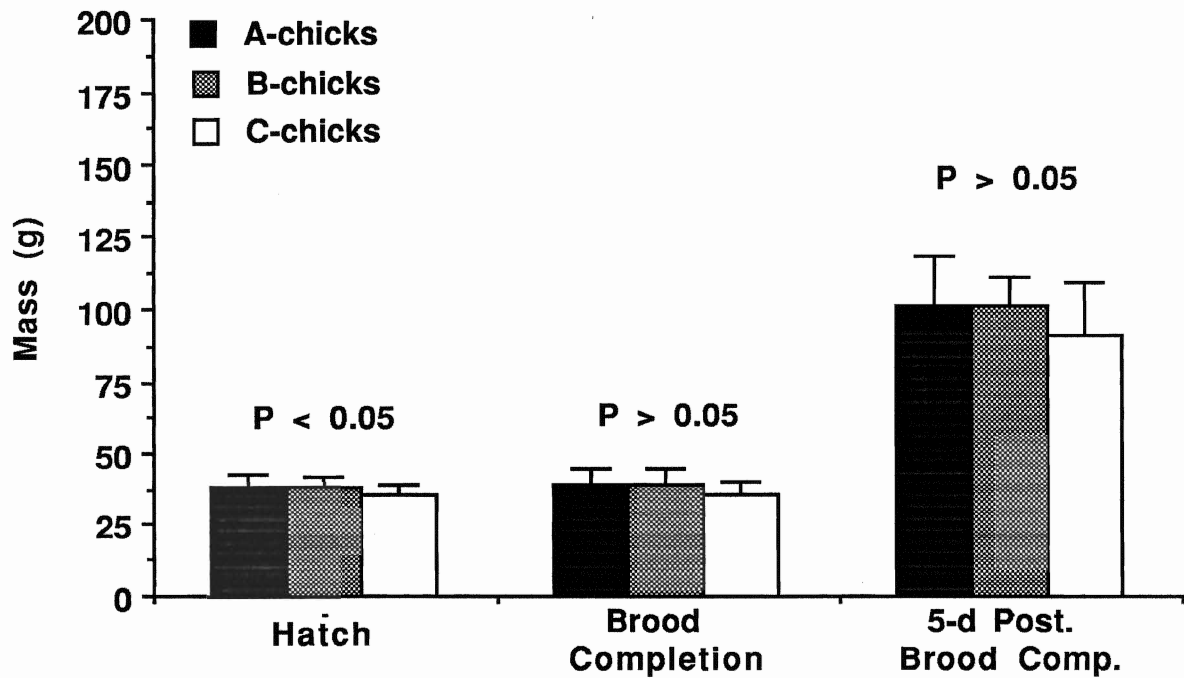


Fig. 14. Mean chick masses ( $\pm 1$  s.d.) for chicks of broods in the late period where chicks were manipulated to hatch synchronously within 24 h of each other ( $E_{SYN.}$ ). Values are reported for chicks of 11 broods at hatching and brood completion and for chicks of six broods in which all three chicks survived to five days post brood completion. P-values were generated from Friedman ANOVA's testing for differences among chick mass at the respective stages.

$n_2 = 11$ ,  $0.1 > P > 0.05$ ; Late B-chicks  $\geq$  C-chicks,  $U = 31.5$ ,  $n_1 = 11$ ,  $n_2 = 11$ ,  $0.1 > P > 0.05$ ). In late broods manipulated to hatch synchronously, there were no differences in mass amongst brood mates at brood completion (Friedman  $\chi^2 = 4.0$ ,  $df = 2$ ,  $P > 0.05$ ) or at five days post-brood completion (Friedman  $\chi^2 = 1.0$ ,  $df = 1$ ,  $P > 0.05$ ).

No significant differences were found between C-chicks of  $E_{SYN}$  broods and C-chicks of unmanipulated, control broods at hatching (see Fig. 9 and 14,  $U = 47.5$ ,  $n_1 = 8$ ,  $n_2 = 11$ ,  $P > 0.05$ ), at brood completion ( $U = 37.5$ ,  $n_1 = 8$ ,  $n_2 = 11$ ,  $P > 0.05$ ) or at five days post-brood completion ( $U = 6.5$ ,  $n_1 = 3$ ,  $n_2 = 6$ ,  $P > 0.05$ ).

The survival to fledging of chicks from the experimental, synchronously hatched broods from the peak and late periods is contrasted with the survival to fledging of chicks from unmanipulated, control broods in those periods (Table 3). In the peak period, C-chick survival from  $E_{SYN}$  broods was not significantly different from  $E_{SYN}$  A-chicks ( $\chi^2 = 2.92$ ,  $df = 1$ ,  $P > 0.05$ ) and B-chicks ( $\chi^2 = 0.42$ ,  $df = 1$ ,  $P > 0.05$ ). The survival to fledging of  $E_{SYN}$  A-chicks in the peak period was greater than  $E_{SYN}$  B-chicks ( $\chi^2 = 5.40$ ,  $df = 1$ ,  $P < 0.05$ ).

In the late period, the survival to fledging of C-chicks from synchronously hatched broods was lower than that of  $E_{SYN}$  A-chicks (Fisher exact  $P = 0.03$ ), and not significantly different from the number of  $E_{SYN}$  B-chicks that fledged (Fisher exact  $P = 0.16$ ). The survival to fledging of late  $E_{SYN}$  A-chicks from synchronous broods did not differ from the survival of synchronous late  $E_{SYN}$  B-chicks ( $\chi^2 = 0.73$ ,  $df = 1$ ,  $P < 0.05$ ).

The percent survival of individual chicks from peak and late broods manipulated to hatch synchronously ( $E_{SYN}$ ) are reported in Fig.'s 15 and 16. In synchronous broods of both periods most chick mortality had occurred by the second week after brood completion.



Table 3. Chick survival to fledging (25 days post-brood completion) of control (unmanipulated) and experimental broods from the peak and late nesting periods. Chicks from E<sub>SYN</sub> broods were manipulated to hatch synchronously ( $\leq$  24 h). Percent survival is indicated in parenthesis.

Group	Chicks Fledged			# of Broods	Av. # flgd. / Brood
	A	B	C		
Peak Cont.	13 (76 %)	15 (88 %)	4 (24 %)	17	1.9
Peak E <sub>SYN</sub> .	15 (80 %)	8 (42 %)	10 (53 %)	19	1.7
Late Cont.	4 (40 %)	3 (30 %)	0 (0 %)	10	0.7
Late E <sub>SYN</sub> .	6 (55 %)	4 (36 %)	1 (9 %)	11	1.0

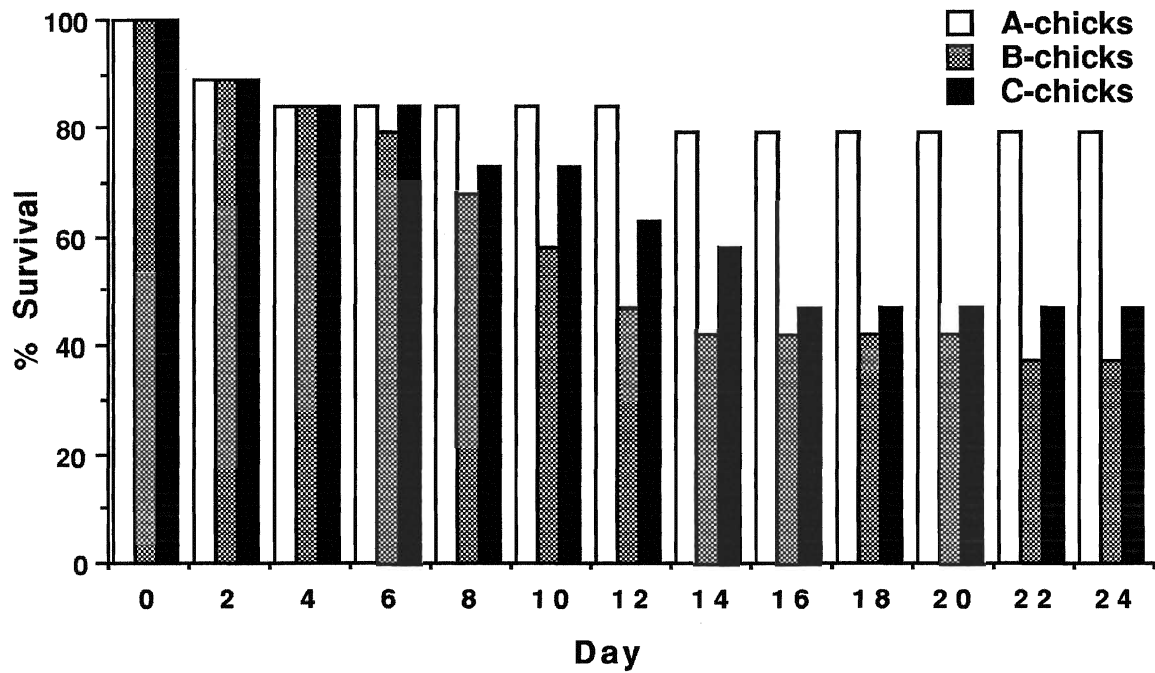


Fig. 15. Percent survival of individual chicks from peak broods manipulated to hatch synchronously ( $E_{SYN.}$ ). Nineteen peak broods were manipulated to hatch in the synchronous experimental pattern. Day 0 = brood completion (hatching of the C-chick).

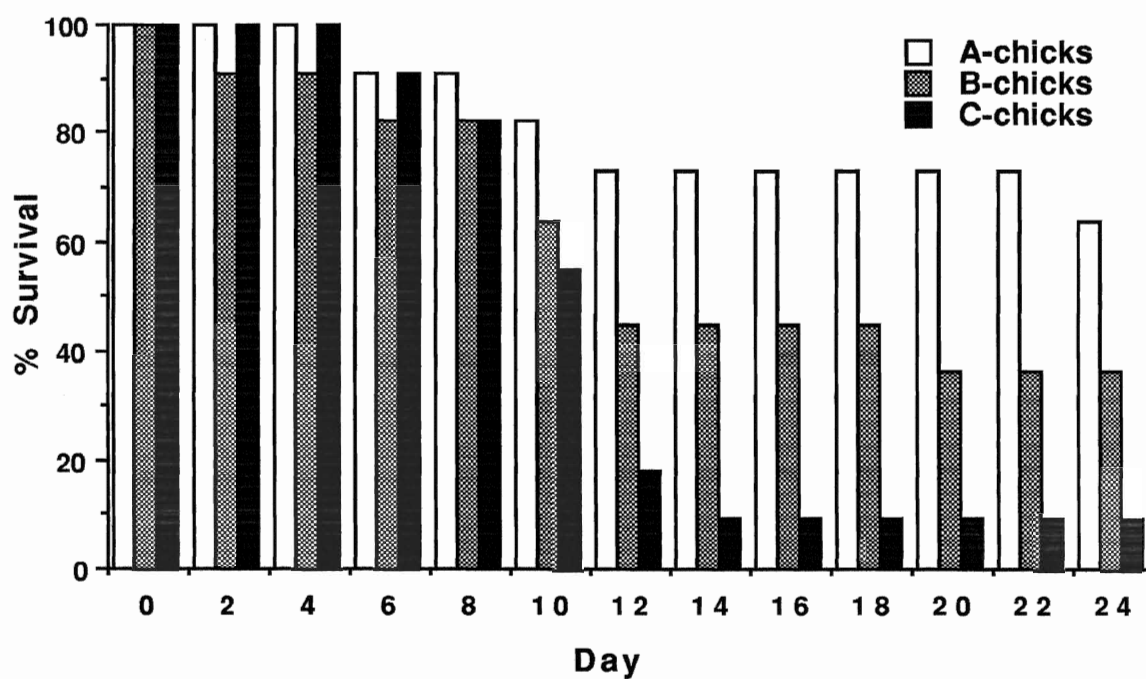


Fig. 16. Percent survival of individual chicks from late broods manipulated to hatch synchronously ( $E_{\text{SYN}}$ ). Eleven late broods were manipulated to hatch in the synchronous experimental pattern. Day 0 = brood completion (hatching of the C-chick).

### Hatching Order Manipulations

In the peak period, a manipulation of hatching order was performed on selected three-egg clutches (designated EC-1st.). These clutches were manipulated to have chicks from third-laid eggs (C-chicks) hatching 24 h - 48 h ahead of the A- and B- chicks to test the importance of relative egg size versus relative hatching order. The mean mass ( $\pm 1$  s.d.) of chicks from these broods at hatching, brood completion and five days post-brood completion is reported in Fig. 17. There were significant differences amongst brood mates at hatching (Friedman  $X^2 = 9.7$ ,  $df = 2$ ,  $P < 0.01$ ). The hatching mass of C-chicks was significantly lower than A-chicks ( $U = 43.5$ ,  $n_1 = 16$ ,  $n_2 = 16$ ,  $P < 0.005$ ) and differences between B-chicks approached significance ( $U = 82$ ,  $n_1 = 16$ ,  $n_2 = 16$ ,  $0.1 > P > 0.05$ ).

There were significant differences amongst the mass of chicks of a brood at brood completion (Fig. 17; Friedman  $X^2 = 21.7$ ,  $df = 2$ ,  $P < 0.0005$ ). The mass of A-chicks and B-chicks did not differ significantly at brood completion in EC-1st. clutches ( $U = 99.0$ ,  $n_1 = 16$ ,  $n_2 = 16$ ,  $P > 0.05$ ). C-chicks were significantly heavier than both A-chicks ( $U = 22.5$ ,  $n_1 = 16$ ,  $n_2 = 16$ ,  $P < 0.0005$ ) and B-chicks ( $U = 22.5$ ,  $n_1 = 16$ ,  $n_2 = 16$ ,  $P < 0.0005$ ) at brood completion. At five days post-brood completion there were no significant differences among brood mates in EC-1st. broods (Fig. 17; Friedman  $X^2 = 1.7$ ,  $df = 2$ ,  $P > 0.05$ ).

The survival to fledging of chicks from 16 EC-1st. broods from the peak period is reported in Table 4 with the survival to fledging of chicks from unmanipulated broods in that period. The number of A-chicks and B-chicks surviving to fledging in EC-1st. broods did not differ significantly [ $n(\text{A-chicks}) = 8$ ;  $n(\text{B-chicks}) = 8$ ;  $X^2 = 0$ ,  $df = 1$ ,  $P > 0.05$ ]. C-chick survival to fledging ( $n = 14$  chicks) was greater than A-chicks ( $X^2 = 5.2$ ,  $df = 1$ ,  $P < 0.05$ ) and B-chicks ( $X^2 = 5.2$ ,  $df = 1$ ,  $P < 0.05$ ). The survival to fledging of C-chicks in experimental

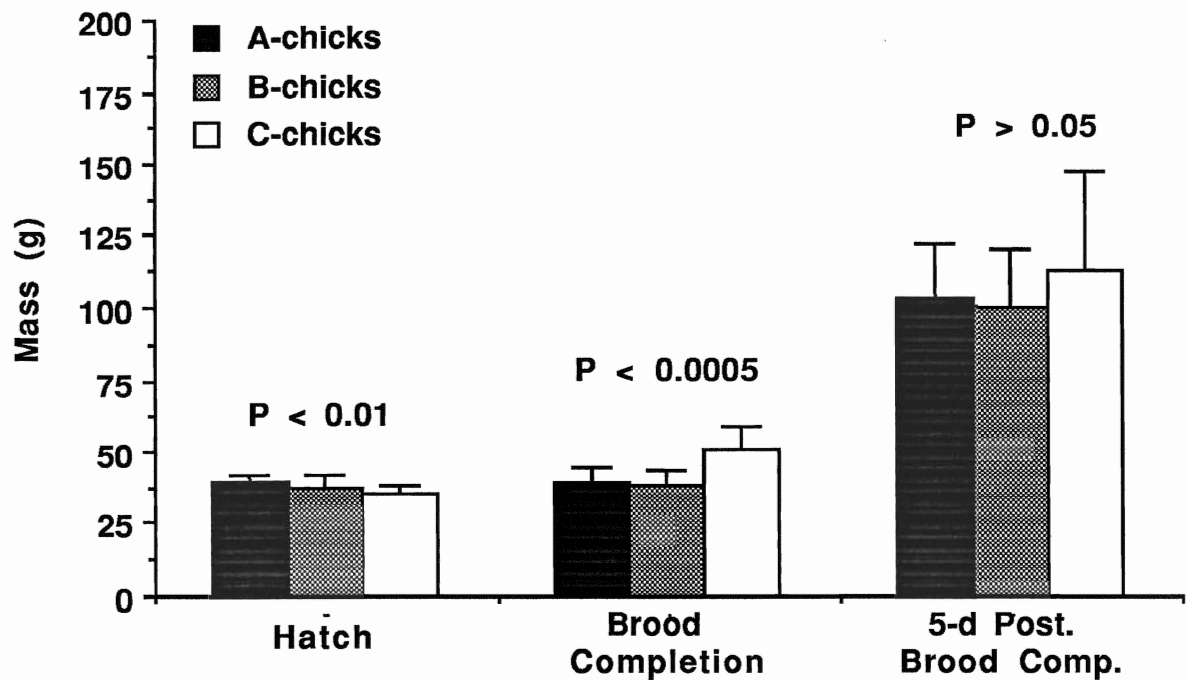


Fig. 17. Mean chick masses ( $\pm 1$  s.d.) for chicks of broods in the peak period where C-chicks were manipulated to hatch 24 h - 48 h ahead of the A- and B-chicks ( $E_{C-1st.}$ ). Values are reported for chicks of 16 broods at hatching and brood completion and for chicks of eight broods in which all three chicks survived to five days post-brood completion. P-values were generated from Friedman ANOVA's testing for differences among chick mass at the respective stages.

Table 4. Chick survival to fledging (25 days post-brood completion) of control (unmanipulated) and experimental EC-1st. broods from the peak nesting period. Chicks from EC-1st. broods were manipulated to hatch such that chicks hatching from third-laid eggs (C-chicks) hatched 24 h - 48 h ahead of chicks hatching from first and second-laid eggs (A- and B-chicks). Percent survival is indicated in parenthesis.

Group	Chicks Fledged			# of Broods	Av. # flgd. / Brood
	A	B	C		
Peak Cont.	13 (76 %)	15 (88 %)	4 (24 %)	17	1.9
EC-1st.	8 (50 %)	8 (50 %)	14 (88 %)	16	1.9

broods was significantly greater than the survival to fledging of C-chicks from control broods ( $\chi^2 = 13.6$ ,  $df = 1$ ,  $P < 0.001$ ).

The percent survival of individual chicks from manipulated hatching order broods in which C-chicks hatched ahead of A- and B-chicks ( $E_{C-1st.}$ ) is presented in Fig. 18. As in unmanipulated broods (Fig. 11), the majority of chick mortality in  $E_{C-1st.}$  broods occurred in the first two weeks post-brood completion.

### **Whole Brood Success and Failure**

Whole brood success is defined as any brood in which all three chicks survived to the fledging age (25 days post-brood completion). Whole brood failure is defined as any brood where no chick survived to the age of fledging. Whole brood success and failure are reported in Table 5 for control and all experimental conditions in the peak and late periods. Complete brood failure was high during the late period. The occurrence of whole brood success was marginal in the peak and non-existent in the late period.

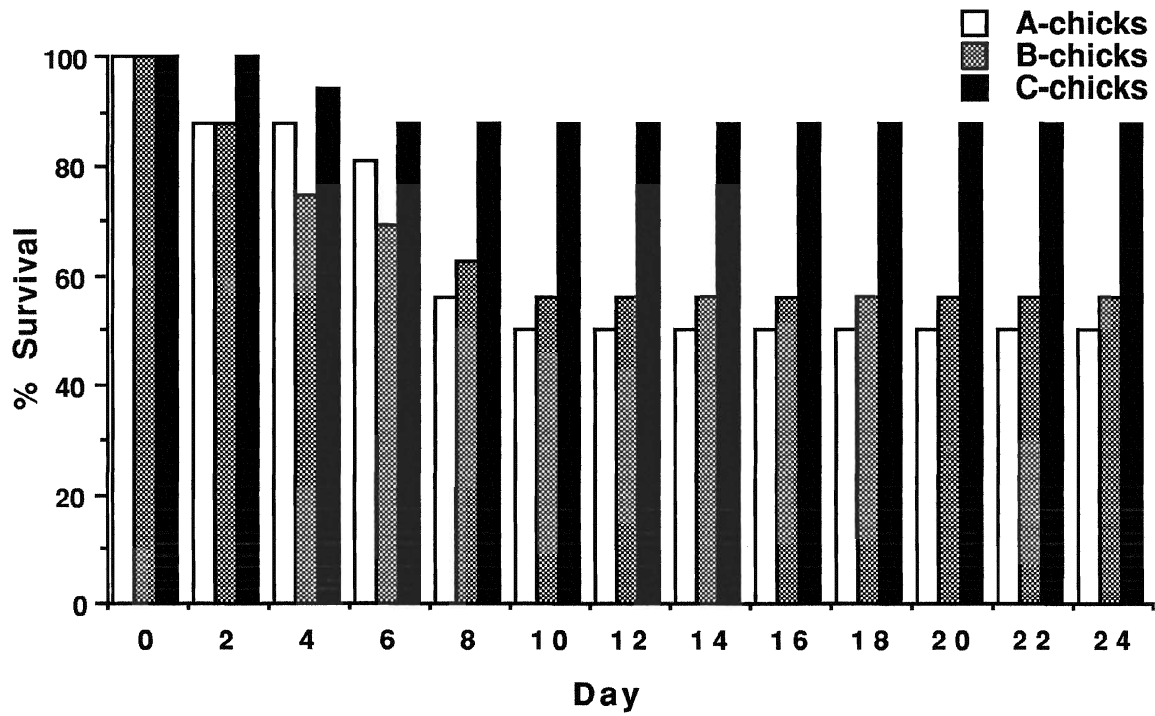


Fig. 18. Percent survival of individual chicks from manipulated hatching order broods in which C-chicks hatched ahead of A- and B-chicks ( $E_{C-1st.}$ ). Sixteen peak broods were manipulated to hatch in this experimental pattern. Day 0 = brood completion (hatching of last-hatched B-chick).



Table 5. Whole brood success (# of broods fledging all three chicks) and whole brood failure (# of broods where no chicks fledged) for control and experimental conditions in the peak and late periods.

<b>Group</b>	<b>W.B.S.</b>	<b>W.B.F.</b>
<b>(# of broods)</b>	<b>(# of broods)</b>	<b>(# of broods)</b>
<b>Peak</b>		
Control (n = 17)	2	1
ESYN. (n = 19)	0	1
EC-1st. (n = 16)	3	1
<b>Late</b>		
Control (n = 10)	0	5
ESYN. (n = 11)	0	3

## Discussion

The modal clutch size for many temperate nesting Gulls and Terns is three eggs. Third-laid eggs are typically smaller than the first two. Furthermore, asynchronous hatching within a brood results in a size hierarchy among siblings, creating the potential for brood reduction. Thus third hatched chicks are younger, smaller and at a competitive disadvantage to older siblings, and so, often suffer reduced survival (Parsons 1970, Parsons 1975a, Nisbet and Cohen 1976, Hébert and Barclay 1986, Bollinger et al 1990, Bolton 1991, Killoran 1991). In the summer of 1991 (Killoran 1991), I examined the influence of hatching synchrony patterns on the survival of Ring-billed Gull chicks. A sample of peak broods manipulated to hatch synchronously (A- to C-chick hatching interval  $\leq 24$ h), had the highest incidence of whole brood success (50 %) and the highest number of C-chicks surviving to fledging (ten or 77 %). A second experiment set up broods to hatch asynchronously (48h between the hatching of each chick), chick mass hierarchies favoured A-chicks whose survival was 100%, while only 13 % of C-chicks reached the age of fledging. This suggested that asynchronous hatching was an important determinant of differential chick survival in the Ring-billed Gull.

Chardine and Morris (1983) reported a seasonal shift in hatching asynchrony between the peak and late breeding season, similar to patterns investigated in the 1991 season. The intentions of this study were to: 1) look at patterns of egg laying and chick hatching in the peak and late breeding seasons; 2) measure seasonal patterns of nocturnal nest attendance and brood patch defeathering as proximate mechanisms of a seasonal increase in hatching asynchrony; 3) measure mass discrepancies among the eggs of a clutch, among brood mates at hatching, brood completion and five days post-brood completion, and to monitor the post hatching survival of chicks; 4) monitor mass differences and chick survival in broods where chicks were manipulated

to hatch synchronously ( $\leq 24$  h); 5) monitor mass differences and chick survival in broods where chicks from third-laid eggs (C-chicks) were manipulated to hatch 24h - 48h ahead of their siblings (the A- and B-chicks). Using a format that will reflect the order of these intentions, I will discuss and review the results obtained, in context with the literature.

### **Seasonal Hatching Patterns**

Intra-clutch hatching intervals of Ring-billed Gulls nesting at Port Colborne increased and became more asynchronous during the breeding season, while laying intervals remained constant. In the peak period, intra-clutch hatching intervals were shorter than intra-clutch egg laying intervals, particularly between the hatching of A- and B-chicks (Fig. 3). In the late period, intra-clutch hatching intervals were more reflective of intra-clutch egg laying intervals. Chardine and Morris (1983) also observed constant laying intervals across the breeding season in Ring-billed Gulls. In that study, hatching was completed in 24 hours or less for the majority of peak clutches. Most late clutches hatched asynchronously, with two or more days between the hatching of the A- and C-chicks. A seasonal increase in hatching asynchrony despite constant egg laying intervals has also been reported in Herring Gulls and Lesser Black-backed Gulls (MacRoberts and MacRoberts 1972), Common Terns (Nisbet and Cohen 1975, Courtney 1979, Morris 1988), and Roseate Terns (Nisbet and Cohen 1975).

The consistency across several seabird species, suggests the typical hatching pattern in the peak period is similar to the experimental synchronous condition created in 1991 (Killoran 1991), where whole brood success was high and an equal probability of survival resulted amongst brood mates. Whereas, a typical hatching pattern in the late period is similar to the asynchronous manipulation where mass disparities among the chicks lead to brood reduction directed mainly at last hatched chicks.

## **Proximate Causes?**

A major focus of my study was to investigate seasonal patterns of two phenomena suspected to cause a seasonal variation in intra-clutch hatching synchrony in Larids, seasonal changes in: 1) nocturnal nest attendance and 2) brood patch defeathering during the egg laying period.

## **Nocturnal Desertion**

Nocturnal nest desertion early in the breeding season, and the resulting delay in effective incubation until clutch completion, has been suggested to increase intra-clutch hatching synchrony, in peak Ring-billed Gull clutches (Chardine and Morris 1983). Conversely, increased nest attentiveness by late nesting birds was suggested to produce a more asynchronous hatching in late clutches. Nisbet and Cohen (1975) suggested that one cause for hatching intervals to lengthen across a breeding season, in Common and Roseate Terns, was a tendency for parents to begin effective incubation earlier as the season progressed.

In this study, event recorders revealed a decrease in nocturnal desertion of clutches by Ring-billed Gull adults during the late breeding season (Fig. 6). In the peak nesting period, nocturnal nest attentiveness increased from total absence to constant attendance as egg laying progressed (Fig. 5). In contrast, during the late period, parents incubated first and second eggs for longer durations than peak nesting birds. The lengthy desertions seen in the peak appeared to be absent in the late period, where brief 'upflights' or localized 'panics' were more common than lengthy desertions.

Nocturnal desertion may be a behavioural response to avoid nocturnal predation (Emlen et al. 1966, MacRoberts and MacRoberts 1972, Hunter et al. 1976, King 1977, Atwood 1986). Chardine and Morris (1983) suggested that the appearance of a predator may be an immediate stimulus for the behaviour.

In my study, predators were seen at the colony during both periods, a Snowy Owl (*Nyctea scandiaca*) during the peak and a Mink (*Mustela vison*) later in the season. However, neither seemed to cause more than a localized disturbance. Similar, almost identical patterns of season shifts in incubation attentiveness to those seen in Ring-billed Gulls in 1992 were documented in Common Terns (Courtney 1979) and Ring-billed Gulls, nesting at a Lake Ontario colony (Chardine and Morris 1983). The systematic decrease in nocturnal desertion with egg laying suggests desertion may play a more ultimate role as a mechanism of achieving greater hatching synchrony in early nests. In addition, selection pressures to achieve asynchronous hatching, in the late period, may be stronger than pressures to avoid predation.

### **Brood Patch Development**

Differences in brood patch development, between peak and late nesting birds, may have been an additional cause of seasonal increase in hatching asynchrony. Brood patches are believed to play an important role in the incubation rhythm, in addition to facilitating heat transfer to the eggs (Beer 1962, Hébert and Sealy 1992). Incubation and brood patch defeathering are, in part, mediated by the action of steroid hormones, in combination with prolactin (regulating defeathering and vascularization) and progesterone (regulating epidermal thickening and sensitivity). Therefore large, more developed brood patches, may be an indicator that the parent is in a hormonal state that is more conducive to prolonged incubation. As well, large brood patches at clutch initiation, are likely to produce a greater and more efficient heat transfer to the eggs, early into incubation.

In my study, differences in brood patch development of Ring-billed Gulls were investigated by trapping incubating adults at various stages of the egg laying period, in both peak and late seasons. In the peak period, brood patch areas became progressively larger at the one, two and three-egg stages

respectively (Fig. 4). Consequently, incubation may have been only partially effective during the early stages of egg laying. Parsons (1972) measured the effectiveness of incubation in Herring Gulls by examining development of embryos and found that incubation was only partially effective during egg laying. Brood patch areas of late nesting birds were large at clutch initiation, comparable in size to those completing clutches in the peak period, and did not increase in size by clutch completion (Fig. 4). Similarly, Beer (1962) measured brood patches in peak nesting Black-headed Gulls trapped at the two and three-egg stages, and found the lengths and widths were greater at the three-egg stage. Courtney (1979) also found seasonal differences in total brood patch area development between peak and late nesting Common Terns with incubation patch defeathering more advanced in late nesting birds.

Selection pressures for a synchronous hatching in the peak and / or a more asynchronous hatching in the late period, may have lead to more substantial brood patch defeathering at clutch initiation, as the breeding season progressed. A second possibility exists that the late nesting group composed of parents attempting to renest after an initial failure. The incubation patches of those birds are likely to be more defeathered initially, than birds nesting for the first time. Immature Ring-billed Gulls, determined by wing and tail plumage (Blokpoel et al. 1985), were observed initiating nests during the late period at Port Colborne, although none were observed nesting in the late plot. Among the Ring-billed Gulls trapped at the one-egg stage in the late period, 44 % ( $n = 4$ ) had refeathered brood patches; an indication that these birds were attempting to renest after an initial failure. This suggests the late group is a composite of younger birds nesting for the first time, and birds renesting after an initial nest failure; both of which show a greater tendency for prolonged incubation, and substantial brood patch defeathering during the early stages of egg laying.

### **Egg Mass, Chick Mass and Chick Survival**

Intra-clutch differences in egg size have been suggested as an explanation for the higher mortality of chicks from smaller, last-laid eggs (Parsons 1970, 1972, Nisbet and Cohen 1975, Lundberg and Väisänen 1979, Hébert and Barclay 1988, Anderson 1990, Custer and Frederick 1990, Bolton 1991). In the present study, third-laid eggs were significantly smaller in mass and volume than A- and B-eggs in both the peak and late periods. However, this pattern of mass difference was not reflected among the hatching mass of chicks in a brood, as the hatching mass of B-chicks from control broods did not differ significantly from that of C-chicks, in both the peak and late periods.

Mass differences among brood mates at brood completion and five days post-brood completion, were an effective measure of the mass hierarchies among siblings. These hierarchies were accurate predictors of survival patterns in both peak and late broods (Fig 9 and Fig. 10). Chick mortality in the peak period was specific to third-hatched chicks in most cases (Table 2). In the late period, while survival to fledging was low for all chicks, mortality was highest in C-chicks as none survived to the fledging age.

Similar non-random patterns of brood reduction have been observed in many bird species including temperate nesting seabirds such as Common Terns (Nisbet and Cohen 1975, Bollinger et al. 1990), Black-headed Gulls (Lundberg and Väisänen 1979), Herring Gulls (Parsons 1970, 1975a, Hébert and Barclay 1986) and Ring-billed Gulls (Killoran 1991). Lundberg and Väisänen (1979) correlated the dimensions of Black-headed Gull eggs with chick mortality and found that C-chicks hatched from eggs 4 % lighter in mass but had a 20 % higher mortality. Parsons (1970) found that, survival of chicks from third-laid eggs was 10 % lower than that of chicks hatching from first and second-laid eggs when differences in egg size were corrected for. However

Ring-billed Gull chicks from C-eggs have survived as well as chicks from A-and B-eggs in broods manipulated to hatch synchronously (Killoran 1991). Thus differential patterns of chick survival may also depend on differential egg size within a nest (Parsons 1970, Lundberg and Väisänen 1979, Anderson 1990, Bolton 1991) in addition to the degree of asynchronous hatching (Lack 1966, Nisbet and Cohen 1975, Zach 1982, Graves et al. 1984, Shaw 1985, Mock and Ploger 1987, Killoran 1991, Magrath 1992).

The patterns of nocturnal nest attendance, and brood patch defeathering, suggests some parental control in the establishment of chick mass hierarchies and the differential survival of first- and second-hatched chicks. Many hypotheses have been put forth to explain the adaptive significance of asynchronous hatching and differential patterns of chick survival, including: the brood reduction hypothesis (Lack 1966); the insurance hypothesis (Dorwood 1962, Graves et al. 1984, Anderson 1990); the nest failure hypothesis (Hussell 1972, Clark and Wilson 1981); and the sibling rivalry reduction hypothesis (Hahn 1981, Mock and Ploger 1987). In addition, several non-adaptive arguments have also been put forth such as the egg protection hypothesis (Parsons 1976), and the hormonal-constraint hypothesis (Mead and Morton 1985). Among these, the brood reduction hypothesis offers the most plausible explanation for the patterns observed in this study. The brood reduction hypothesis suggests that hatching asynchrony is an adaptation which facilitates the reduction of brood size in response to an unpredictable food supply. A more synchronous hatching during the peak season may have resulted from an adaptation that minimized competitive disparities among siblings and maximized the number of offspring fledged, during a period of expected high food availability (abundance, locatability &/or predictability). Conversely, asynchronous hatching during the late period may have resulted from an adaptation that lead to competitive hierarchies among the chicks and



the ability for parents to focus parental investment, when food may have been less abundant or locatable.

### **Hatching Manipulations**

To test the brood reduction hypothesis and the importance of hatching synchrony, in establishing mass hierarchies and differential chick survival, broods were manipulated to hatch synchronously ( $\leq 24$  h; designated  $E_{SYN.}$ ), in both periods. If arguments of the brood reduction hypothesis hold, C-chicks of experimental broods during the peak period should have survived as well as their siblings.

To test the importance of relative egg size versus relative hatching order, an additional manipulation was performed where C-chicks hatched ahead of the A- and B-chicks (designated  $E_{C-1st.}$ ). The purpose of this manipulation was to answer the question: can chicks hatching from smaller, third-laid eggs survive as well or better than their siblings, when given the advantage of hatching order?

### **Artificial Hatching Synchrony**

In broods hatched synchronously in the peak period, C-chick survival to fledging was not different from that of the A- and B-chicks (Table 3). There were no significant differences among the mass of brood mates at hatching, brood completion or at five days post-brood completion (Fig.13). Reducing asymmetries caused by asynchronous hatching resulted in a more equal probability of survival amongst brood mates. This supports the arguments of the brood reduction hypothesis and suggests asynchronous hatching is an important determinant in establishing differential chick survival.

In the late period, A-, B- and C-chicks of  $E_{SYN.}$  broods remained similar in mass (Fig. 14). Although C-chicks survived to fledging as well as B-chicks, A-chicks experienced higher fledging success (Table 3). One explanation why a

synchronous hatching did not result in an equal probability of survival, is that differences in egg size were important in establishing differential survival among chicks. Lundberg and Väisänen (1979) and Parsons (1970) argue differences in egg size within a clutch are important determinants of chick survival. However, other studies have found when all chicks hatched synchronously an equal survival probability resulted amongst brood mates (Fujioka 1985a, Hébert and Barclay 1986, Morris 1988, Bollinger et al. 1990, Killoran 1991). A second explanation is that the harsh storms and predation that occurred during the late period (18 - 23 June) influenced survival patterns. Burness (1992) and Moore (1993) also found that stochastic factors such as predation and adverse weather were, at times, overriding determinants of breeding success in the Common Tern.

### **Artificial Hatching Order**

In this study, the results of the EC-1st. manipulations suggest relative hatching order was more important than relative egg size. Chicks from smaller, third-laid eggs were larger at brood completion and five days post-brood completion than A- and B-chicks when given the advantage of asynchronous hatching. Furthermore, C-chicks had greater survival to fledging, than A- and B-chicks, when hatched first. The finding that hatching order is more important than relative egg size is supported by Parsons (1975a) who manipulated Herring Gull clutches, such that C-chicks hatched first and A-chicks last, and found that C-chicks realized better survival than control C-chicks. Conversely, A-chicks hatched last suffered higher mortality than A-chicks from control broods.

## Synthesis

Intra-clutch hatching asynchrony has been viewed as a parental adaptation facilitating brood reduction during periods of food stress or similar environmental uncertainties (Lack 1966). The proximate mechanisms that I studied in Ring-billed Gulls yielded greater hatching synchrony during the early (peak) breeding season, and hatching asynchrony in late broods. Hatching asynchrony facilitated brood reduction, directed primarily at last hatched chicks. The seasonal shift towards asynchronous hatching may be an adaptation related to seasonal declines in food availability and perhaps, differences in the age and foraging abilities of parents breeding in the two periods.

Differences in age and experience between peak and late nesting groups have been well documented. Haymes and Blokpoel (1980) determined the age composition of peak and late nesting Ring-billed Gulls. The majority of peak birds (89 %) were older ( $\geq$  four years) and the majority of late breeders (64 %) were younger ( $\leq$  three years). Massey and Atwood (1981) characterized differences in age composition and clutch size between first and second-wave nesting California Least Terns and found that 95 % of first-wave (peak) nesting Terns were older birds ( $\geq$  three years of age), while second-wave (late) nesting birds were composed mainly of younger, inexperienced birds (76 %  $\leq$  two years). The remaining pairs nesting in the late period were observed to be renesting after an initial failure. A similar trend of renesting birds was reported for the Common Tern (Nisbet and Cohen 1975). Pyle et al. (1991) and Sydeman et al. (1991) have shown that older, more experienced, Western Gulls tended to lay larger clutches and initiated breeding earlier in the breeding season. In my study, the occurrence of one- and two egg clutches was 16 % and 18 % higher in the late period respectively, suggesting that the majority of Ring-billed Gulls from the peak sample were older and more experienced.

There is good evidence that peak and late nesters are under different selective pressures for asynchronous hatching. Kirkham and Morris (1979) noted that peak hatching coincided with the peak abundance of aerial insects which were commonly present in the diet of young Ring-billed Gull chicks. Haymes and Blokpoel (1978), and Kirkham and Morris (1979) both reported seasonal decline in the proportion of insects parents fed to young Ring-billed Gulls. Burness (1992) noted that Common Terns nesting at Port Colborne foraged at consistent and predictable locations, with low inter-individual variability, during the peak period. Conversely, during the late period inter-individual variability was high and foraging locations were scattered and less predictable. Therefore seasonal declines in prey locatability, predictability and abundance may all contribute to seasonal fluctuations that lead to greater food availability during the peak period for Ring-billed Gulls.

An abundance of food would favour parents that reduce feeding hierarchies within broods (ie. increase hatching synchrony) to fledge more chicks by providing all chicks with an equal competitive ability to obtain food. Hatching asynchrony and the resulting hierarchies, which facilitate brood reduction, may be favored later in the season when food abundance is likely to have declined. Although I was unable to measure food locatability, abundance or predictability, indirect indicators can be used. In the peak of this study and in 1991 (Killoran 1991), synchronously hatched broods did extremely well, suggesting high food availability to Ring-billed Gulls during those periods. In the present study, two cases (12 %) of whole brood success was observed in control peak broods and three (19 %) in EC-1st. broods (Table 5). Killoran (1991) had whole brood success in five of 17 (29 %) unmanipulated peak nesting Ring-billed Gull clutches, and in eight of 16 (50 %) of clutches manipulated to hatch synchronously. Graves et al. supplemented food to Herring Gull broods and found supplemented pairs fledged more chicks than

controls, due mostly to the increased success of third-hatched chicks. No whole brood success occurred in the late period of my study, conversely, whole brood failure was high among control and experimental broods.

The brood reduction hypothesis allows for the occurrence of whole brood success in situations of adequate food availability and sufficient parental foraging abilities. Although of these factors were not measured in the present study, good evidence has been presented to suggest seasonal fluctuations in prey abundance, locatability and predictability may place birds nesting in the peak period are under a strong selection pressure for synchronous hatching. In addition, the brood reduction hypothesis predicts that patterns of chick survival reflect chick mass hierarchies. This prediction was supported in control and  $E_{C-1st}$  broods, in addition, absence of a chick mass hierarchy in  $E_{SYN}$  broods produced a more equal probability of survival amongst brood mates.

## Summary and Conclusions

Seasonal patterns of clutch initiation, nocturnal nest attendance, brood patch development and chick survival were observed in Ring-billed Gulls (*Larus delawarensis*). Despite equal intra-clutch egg laying intervals between the peak and late periods, intra-clutch chick hatching intervals lengthened as the season progressed. Peak nesters showed nocturnal desertion of the nesting colony, and a progressive increase in brood patch area, during the egg laying period. Late nesters were characterized by an absence of nocturnal desertion, increased incubation patch defeathering at clutch initiation, and a reduction of the number of chicks fledged per pair. For both periods, patterns of chick survival strongly reflected trends in chick mass at brood completion and five days post-brood completion. Among chicks of a brood, last-hatched, C-chicks realized poorest survival to the age of fledging. In late clutches, survival was poor for all chicks and, was partially independent of hatching order, due in part to stochastic events such as Herring Gull predation and adverse weather.

In the E<sub>SYN</sub> peak broods manipulated to hatch synchronously, the absence of a chick mass hierarchy at brood completion was reflected in patterns of chick survival to fledging; C-chick survival did not differ from the survival of A- and B-chicks. Survival of peak, E<sub>SYN</sub> C-chicks was also not significantly different from that of control C-chicks, for that period. In the late period, the survival of E<sub>SYN</sub> C-chicks was significantly lower than that of A-chicks, and did not differ significantly from control C-chicks. In peak E<sub>C-1st</sub> clutches C-chick survival to fledging was greater than in controls. Within those broods, C-chicks were heavier at brood completion and survived better on average than both A- and B- chicks.

In both experimental synchronous and unmanipulated clutches, chick survival closely reflected patterns of hatching asynchrony. In control peak and

late clutches that hatched with different degrees of asynchrony, C-chick survival was lower than that of the A- and B-chicks, but was not entirely absent in peak clutches. This provides support for an argument like the brood reduction hypothesis, which suggests patterns of hatching asynchrony are a parental adaptation that allows for potential reduction of brood size. The non-random behaviours of nocturnal desertion and brood patch defeathering patterns are the likely mechanisms of that adaptation, whereby greater or lesser degrees of asynchrony are achieved.

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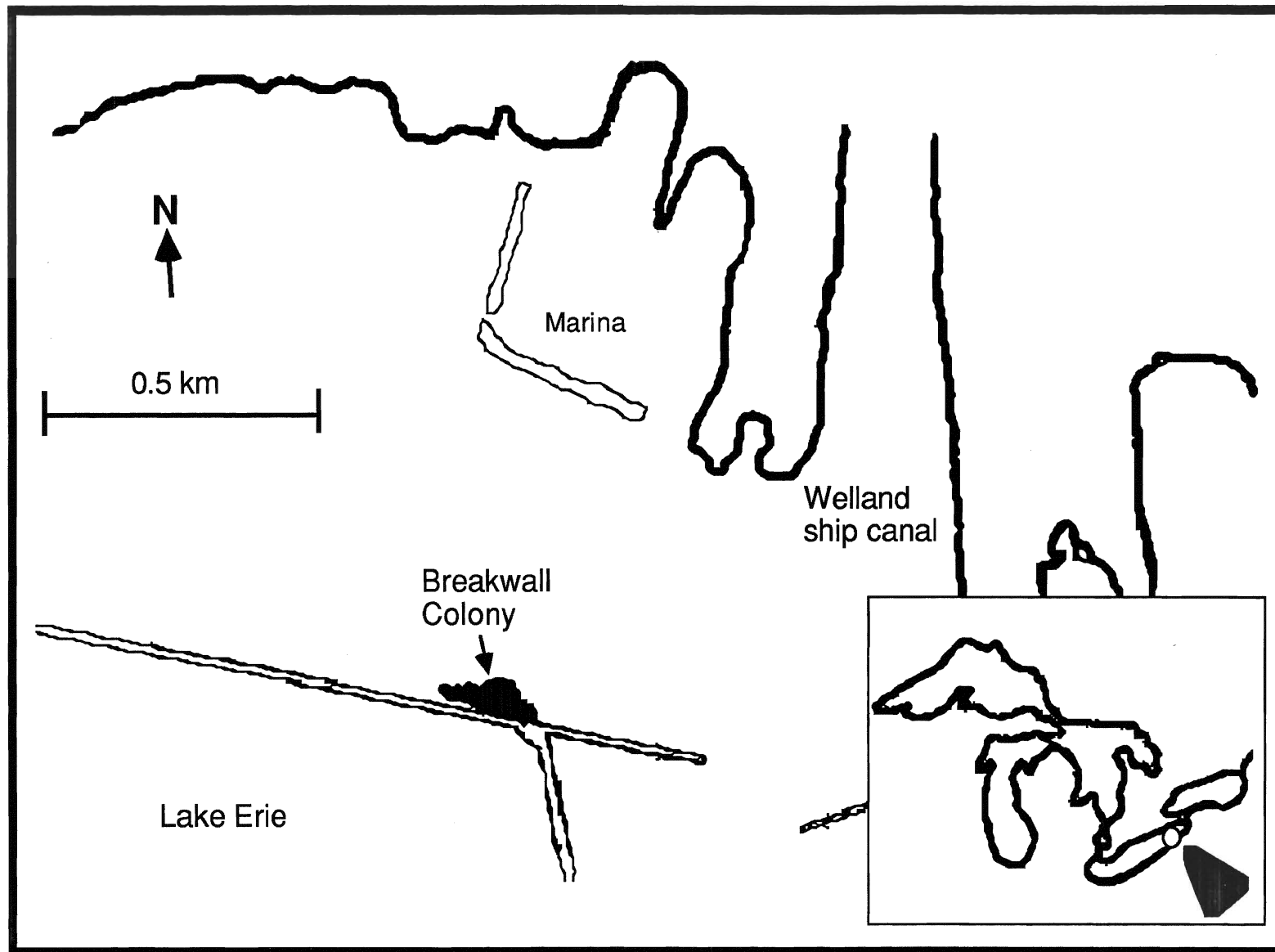
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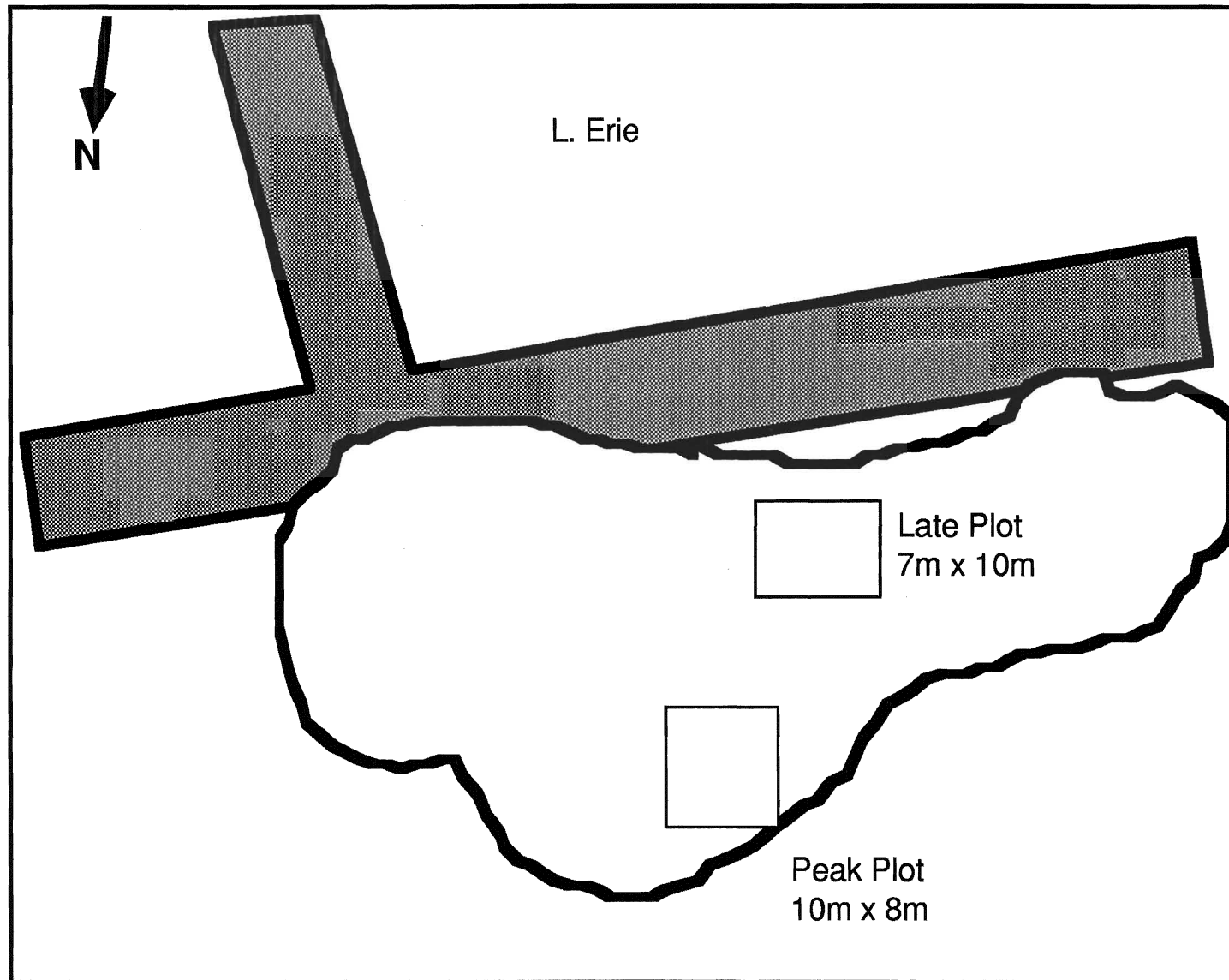
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## Appendix II. Location of peak and late study plots at breakwall colony.



Appendix III. Daily sample sizes for nocturnal nest attendance analysis in the peak and late periods; also reported are number of nests discarded from daily analysis caused by incorporation of the wire ring into the nesting material.

<b>Stage</b>	<b>Number of Nests Used in Analysis</b>	<b>Number of Nests Discarded due to Incorporation</b>	<b>Total</b>
<b>Peak</b>			
1 egg stage	19	1	20
2 egg stage	20	0	20
Clutch Comp.	19	1	20
2-d P.C.C.	20	0	20
3-d P.C.C.	20	0	20
4-d P.C.C.	19	1	20
5-d P.C.C.	15	5	20
<b>Late</b>			
1 egg stage	19	0	19
2 egg stage	18	1	19
Clutch Comp.	19	0	19
2-d P.C.C.	19	0	19
3-d P.C.C.	16	2	18
4-d P.C.C.	16	2	18
5-d P.C.C.	17	1	18



Appendix IV. Mean areas ( $\pm 1$  s.d.) of right, left and lower brood patches of birds trapped and the one- ( $n = 12$ ), two- ( $n = 12$ ) and three-egg stage ( $n = 12$ ) in the peak and from the one ( $n = 9$ ) and three-egg stage ( $n = 10$ ) in the late period. Values are expressed in  $\text{cm}^2$ .

Stage	Mean area of left brood patch ( $\text{cm}^2$ )	Mean area of right brood patch ( $\text{cm}^2$ )	Mean area of lower brood patch ( $\text{cm}^2$ )
<b>Peak</b>			
1 egg stage	5.60 $\pm$ 2.63	5.13 $\pm$ 2.14	4.67 $\pm$ 1.58
2 egg stage	7.20 $\pm$ 1.60	6.82 $\pm$ 2.26	5.11 $\pm$ 2.04
3 egg stage	9.56 $\pm$ 2.27	10.16 $\pm$ 2.05	8.52 $\pm$ 2.13
<b>Late</b>			
1 egg stage	11.83 $\pm$ 4.34	9.09 $\pm$ 2.73	9.56 $\pm$ 2.27
3 egg stage	10.82 $\pm$ 2.92	10.59 $\pm$ 2.35	8.42 $\pm$ 1.95