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Biology of "peak" and "late" nesting Ring-billed gulls, Granite Island, Lake Superior

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Biology of "peak"- and "late"-nesting Ring-billed Gulls, Granite Island, Lake Superior.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in the Department of Biology.

by

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Declaration

The research presented in this thesis was carried out by the author, and has not been previously submitted for credit toward any degree or diploma.

The work of others, where included in this thesis, has been appropriately cited.

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Abstract

Late-nesting Ring-billed Gulls in this study laid fewer and smaller eggs and hatched fewer young than earlier nesting pairs. Birds nesting late in the season appeared to lack sufficient stimuli for incubation, as indicated by their increased restlessness on the nest and higher desertion rates. Factors affecting their behavior include physical condition and social and environmental stimuli. Late-nesting gulls had a lower body weight and condition index than peak-nesting gulls. Their smaller egg size was attributable to decreased amounts of albumen. Analyses of blood metabolites and hormones were inconclusive. It is suggested that the low reproductive success experienced by "late"-nesting Ring-billed Gulls in this study results predominantly from factors during the incubation period.

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1. Introduction

Birds that start nesting later in the season tend to have lower reproductive success than earlier nesting conspecifics. The observable effects of late breeding are well known, as both clutch size and egg size decrease (Coulson and White 1961, Parsons 1970, 1975) and there is a higher proportion of hatching failures later in the season (Brown 1967a, Kadlec and Drury 1968, Vermeer 1970, Hunt 1972, Ryder 1975, Somppi 1978).

Several hypotheses have been put forward to explain the seasonal decline of clutch and egg size. Age of the female and courtship feeding ability of the male (Mills 1979) are two possible parameters. It is possible that females with young, inexperienced mates suffer frequently from lack of food before egg-laying. These differences could at least partly be caused by differing abilities of males to select the nutritionally best items to carry back to the female (Taylor 1979). The lack of food for females may retard ovary development and result in production of a smaller size and number of eggs (Mills 1973, Nisbet 1977). In the Shag (*Phalacrocorax aristotelis*) Coulson *et al*. (1969) noticed that both young and late-laying birds experience a shorter interval of egg development in the oviduct. This is clearly correlated with egg size and may indicate insufficient time for the maximum development and functioning of the reproductive system (Coulson *et al*. 1969).

Factors such as food availability would tend to vary with the location and with the species involved. Parsons (1976) suggested that the availability of food has no effect on clutch size since the cessation of laying occurs at a time when there is sufficient food for adults to feed young as well as themselves. However, Mills (1979) did notice a decline in the abundance of food and also observed that birds nesting later in the season may be less efficient foragers for food and consequently lay fewer and smaller eggs.

A seasonal decline in hatching success could result from several factors: Synchronization of nesting is important for both hatching (Section 4.1.4) and fledging success. Parsons (1975) maintains that Herring Gull (*Larus argentatus*) chicks hatching early or late relative to the rest of the group are more likely to die before fledging that those that hatch at the peak. This seems to be a generally consistent phenomenon in larids (c.f. Patterson 1965, Brown 1967a, Kadlec and Drury 1968, Chardine 1978), and may have an anti-predator function (Parsons 1975).

Nest location has also been shown to affect breeding success. Most studies show optimal breeding success at central locations within the colony (for review see Burger 1974). Those nesting outside the main cluster of the colony may either be less aggressive birds unable to secure a place in the colony (Patterson 1965, Black-headed Gulls (*Larus ridibundus*)), of a lighter weight (Coulson 1971, Black-legged Kittiwakes (*Rissa tridactyla*)), or young birds (Patterson 1965, Black-headed Gulls, Ryder 1975, Ring-billed Gulls

(*Larus delawarensis*)). Carrick and Murray (1964) noted in the Silver Gull (*Larus novaehollandiae*) that some individuals dominate others during competition for food and feeding rights in all but the most opportunistic situations. Adults in better condition would presumably be able to defend larger territories, to nest in the most dense part of the colony and to produce the largest eggs. Thus age, with associated behavioral changes, as well as social status, strongly affects reproductive success.

Chick survival is another important aspect of reproductive success. Early mortality has been reported in "late"-hatched chicks and could result from small egg size, as noted in the Herring Gull (Parsons 1970), Common Tern (*Sterna hirundo*) (Nisbet 1973), and Black-headed Gull (Lundberg and Väisänen 1979), or from an inadequate parental behavioral transition from incubation to care of the young (Vermeer 1963, Kadlec *et al*. 1969, Parsons 1970). Additionally, Nisbet (1973) noticed that the performance of male Common Terns in courtship-feeding may be a predictor of their future performance in feeding the chicks in the period just after hatching when they are usually most critically dependant on him.

Variations in available food supply may influence chick survival more than the foraging ability of the parents (Hunt and Hunt 1976). This would affect the growth patterns of the surviving young (Ricklefs 1968). Vermeer (1970) found that Ring-billed Gull chicks which hatched late in the season survived as well and grew as rapidly as those hatched early in the season. Kirkham and Morris (1979) obtained similar results and noted changes in food type from insects to fish as the season progressed. Perhaps factors before hatch, those occurring during the incubation period or in the eggs themselves, more strongly determine the overall reproductive success of "late"-nesting birds than actual survival of chicks.

In addition to observing the effects of late-breeding, one may also note factors which influence the timing of nesting. Late clutch initiation may reflect the younger age and/or inexperience of one or both members of a pair as compared with earlier nesters (see Ryder 1980 for review), or characteristics of the pair bond (Coulson 1966, Mills 1973). It has been documented that later breeding by young birds may partly result from their lower efficiency in feeding (Orians 1969, Brown Pelican, *Pelecanus occidentalis*, Recher and Recher 1969, Little Blue Heron, *Florida caerulea*, Dunn 1972, Sandwich Tern, *Sterna sandvicensis*, Verbeek 1977, Herring Gull, Searcy 1978, Glaucous-winged Gull, *Larus glaucescens*, Ingolfsson and Estrella 1978, Herring Gull, Burger and Gochfeld 1979, Ring-billed Gull, Ulfstrand 1979, Black-headed Gull, Quinney and Smith 1980, Great Blue Heron, *Ardea herodias*). Thus the seasonal decline in clutch and egg size may also be a direct result of the variation in the physiology and quality of the individuals (Coulson 1968).

The nutritional plane of females during the previous winter (Cavé 1968) or the food supply for the breeding females immediately prior to the breeding season (Perrins 1970) may also determine the date of laying. It is known that nutritional efficiency strongly affects the endocrine stimulus of gonadal growth, as well as the level of productivity (King 1972). If courtship stimulates the final growth phase of the ovary, as suggested by Lehrman (1964) and Brown (1967b), females mated with young males or males inefficient at courtship feeding (Nisbet 1977), would be less stimulated and thus would take longer to prepare for breeding.

Both Chardine (1978) and Somppi (1978) found a higher incidence of egg loss in late Ring-billed Gull nests compared to earlier nests. Chardine (1978) thought this could be attributed to poorer incubation attentiveness, while Somppi (1978) found they were attentive over 90% of the time until they simply stopped incubating. Chardine (1978) found no birds in immature plumage amongst late-nesting Ring-billed Gulls. He suggested that late nesters could nevertheless be on average younger than earlier breeders but not young enough to exhibit immature plumage. He proposed that seasonally varying environmental factors, independant of the gulls themselves could also have been responsible for the decrease in total reproductive success later in the season. In addition to monitoring seasonal variation in clutch size and hatching success I decided to examine physical condition and incubation behavior of the adults to see if these features varied with the timing of breeding.

2. Materials and Methods

2.1 Definitions

The following definitions are used throughout:

Clutch: the number of eggs in a nest that are attended by a mated pair.

Clutch initiation: the day the first egg is laid in each nest (Burger 1979).

Peak breeding pairs: those that initiated their clutches during five days centered around the median of clutch initiation.

Late breeding pairs: the last 10% of all pairs to initiate clutches on the colony.

Incubation period: the interval between the laying of an egg and the emergence of the chick from that egg (MacRoberts and MacRoberts 1972).

Hatching success: the percent of eggs which hatched from one or more nests (Ryder 1976).

Nesting success: the percent of nests in which at least one egg hatched (Burger 1979).

Fledging success: the percent of all chicks hatched that survived to 21 days of age (Gilman *et al*. 1977).

Breeding success: the proportion of chicks reaching 21 days of age from the total number of eggs laid (Gilman *et al*. 1977).

Reproductive success: the number of chicks per breeding pair that survived to 21 days of age (Gilman *et al*. 1977).

Condition Index: Body weight (g)/bill length (cm) plus keel length (cm) (Fox, pers. comm.).

Egg Shape Index: 100 times the breadth of the egg divided by length (Coulson 1963).

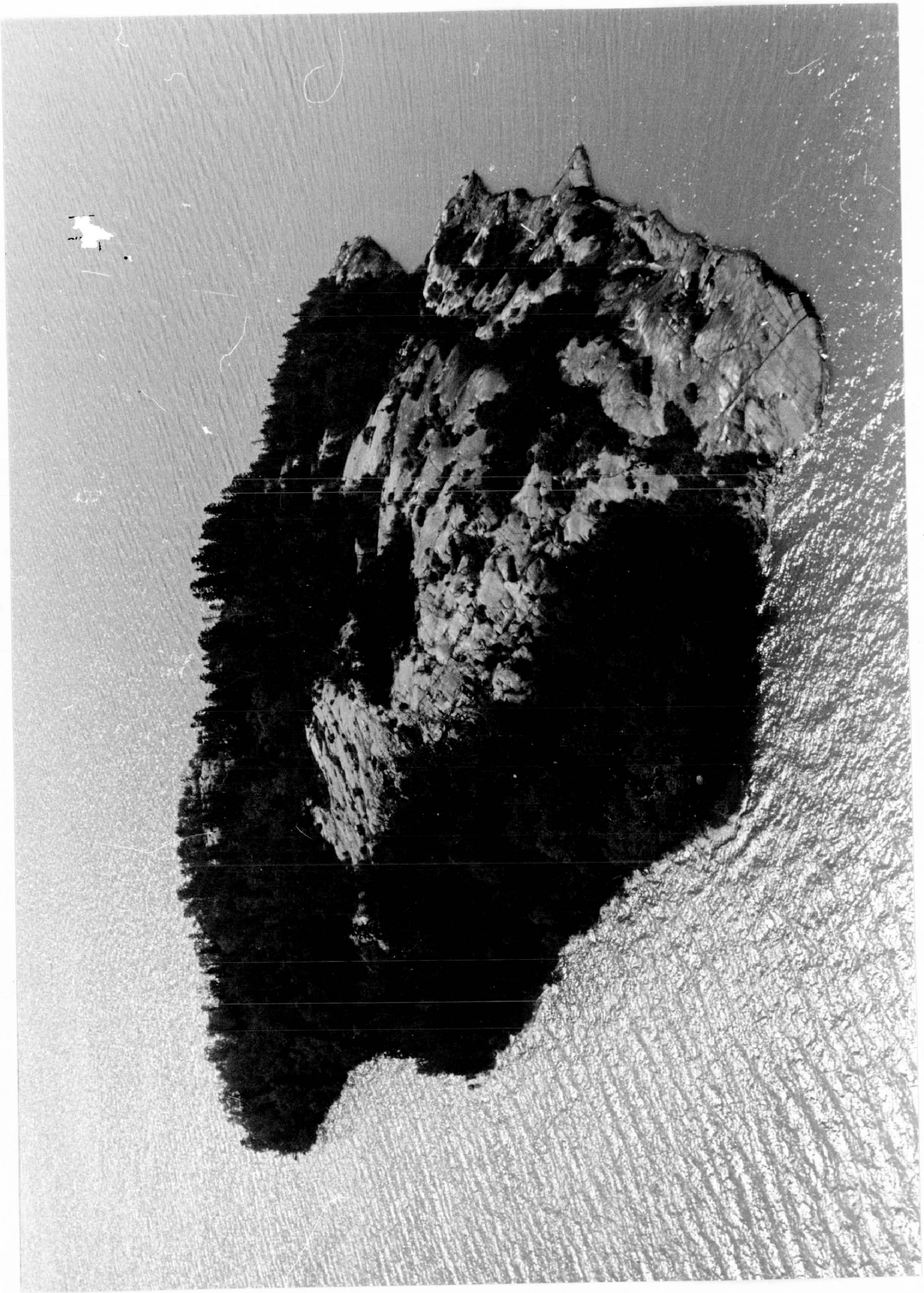
2.2. Study area

Granite Island is located in Black Bay, on northern Lake Superior (48°43'N, 88°29'W) (Figure 1). The island is approximately 60 ha and is dominated by steeply inclined granite slopes rising to an approximate height of 30 m above the surrounding water (Ryder and Carroll 1978). White cedar (*Thuja occidentalis*) occupies the south, southeast and northeast portions of the island, with clumps of mountain ash (*Sorbus decora*), pin cherry (*Prunus pensylvanica*), red osier dogwood (*Cornus stolonifera*) and red-berried elder (*Sambucus pubens*) on the more exposed north and northeast slopes (Figure 2). The summit of the island and the exposed northeast slope consist mostly of bare granite rock (64%) interspersed with shallow soil-filled depressions (36%) in which the dominant vegetation is rough cinquefoil (*Potentilla norvegica*) and Kentucky blue-grass (*Poa pratensis*), interspersed amongst the Ring-billed Gull nests.

The Ring-billed Gull colony was located on the summit and exposed northeast slope of the island. The colony consisted of 1900 pairs in 1978 and 2400 pairs in 1979. Approximately 150-200 pairs of Herring Gulls nested on the north and northwest side of the island, with five to ten nests interspersed amongst the Ring-billed nests. An additional 30 species of birds have been observed nesting on the island (Chamberlain 1973).

Figure 1. Location of Granite Island in northern Lake Superior (from Ryder 1974).

Figure 2. Aerial photograph of Granite Island (Chamberlain 1973).



The relatively flat surface on the summit of the island, 43 by 83 m, was occupied by approximately 350 pairs of Ring-billed Gulls during each year of my study. This area was selected as a study area for "peak"-nesting gulls and will be referred to as the summit study area (Figure 3). The second study area included the entire Ring-billed Gull nesting area (Area 1-3, Figure 3) and was used for "late"-nesting gulls. This provided a larger sample as "late"-nesters were widely spaced throughout the colony.

2.3. Statistical procedure

Statistical treatment followed Nie *et al.* (1970). Student's t-tests were used only if the variances, tested by Oneway ANOVA, were not significantly different ($p > 0.05$). Non-parametric tests, in particular the Mann-Whitney U Test were used where appropriate (Siegel 1956). Medians were used with small, unequal sample sizes since they are not affected by extreme values (Zar 1974). Significance is assumed at $p < 0.05$ unless otherwise stated.

2.4. Nesting data

2.4.1. Nest histories of "peak"- and "late"-nesting gulls

On 17 May 1978 I arrived on Granite Island and marked all one-egg and two-egg nests in the summit study area with numbered wooden blocks. In 1979 I arrived on Granite Island on 14 May. The island still had large patches of snow and

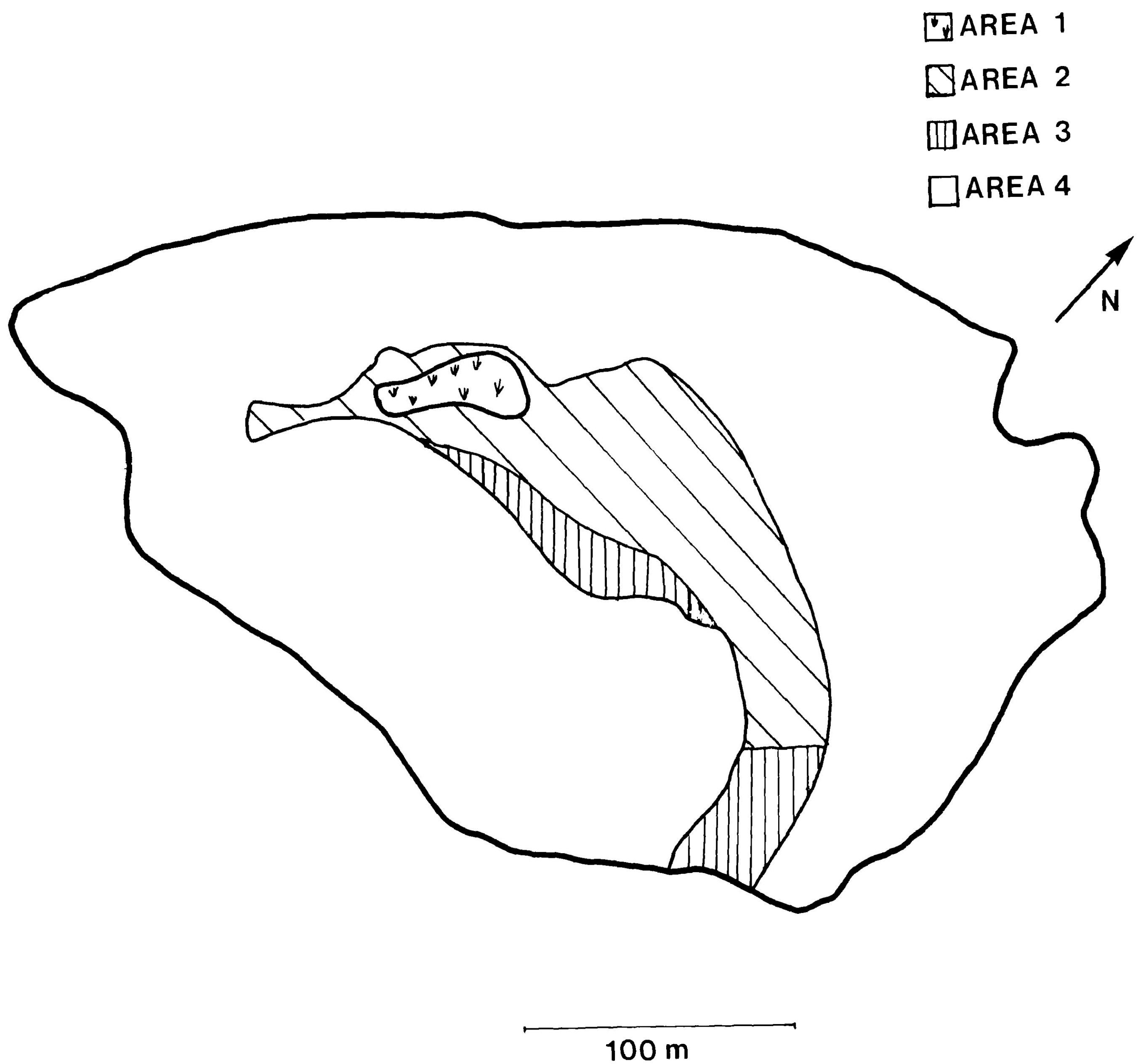
Figure 3. Study areas on Granite Island, 1978 and 1979.

Area 1: "peak" 1978 and 1979; summit study area

Area 2: "late" 1978 and 1979

Area 3: "late" 1979

Area 4: unoccupied by Ring-billed Gulls


AREA 1
AREA 2
AREA 3
AREA 4
N
100 m

ice and an estimated 30 nests were seen on the entire colony. An exact count of nests was not made as I was concerned about disturbance during this early stage of clutch initiation. I left the island and returned on 20 May. I placed numbered wooden blocks next to one-egg clutches in the summit study area. Clutches were marked daily until I had a sample of 150 clutches in 1978 and 75 clutches in 1979. Data from these clutches were used to represent those of "peak"-nesting gulls. Judging by the number of nests present in the study area upon my arrival each year (48 three-egg clutches in 1978, between 40-50 two- and three-egg clutches in 1979), it is very likely that the "peak" sample in both 1978 and 1979 were within the same 5-day period. After the majority of clutches was completed I kept histories of all nests by visiting the colony once a day in 1978 and every second or third day in 1979. The sample of "peak"-nesters and frequency of nest checks were decreased in 1979 to reduce disturbance to the nesting birds.

In each year "late" nests were marked in the following manner: a week after peak clutch initiation was over (this being measured by a sharp reduction in the number of clutches initiated), I searched the colony for one-egg clutches. Beside these I placed a dated wooden block. These nests were visited daily in each year and new eggs were recorded. In addition all new one-egg clutches were marked. Nests marked in the first three or four days were eventually not included for analysis because I wanted to selectively include only the last 10% of the clutches that were initiated on the island for the late sample. This ensured a sufficient timing difference between "peak" and "late" nests so that any differences existing between these two groups would be apparent. The larger sample of late clutches in 1979 reflects an increase in the size of the area searched to include a cliff area not searched in 1978 as well as an area close to the water on the north-east slope (Figure 3). The extent to which this influenced the sampling effectiveness cannot be completely assessed. In both years I did not enter the colony in very hot or wet weather as such disturbance was assumed to be detrimental to the developing embryos (Somppi 1978).

I marked eggs in each clutch a, b, or c according to the order laid, the a-egg being the first egg laid. To determine if there were any differences in size between "peak" and "late" eggs, egg length and width were measured with vernier calipers to the nearest 0.1 mm. In 1978 eggs were weighed to the nearest 0.5 g using a 50 g Pesola spring balance.

For efficiency in locating chicks, groups of nests (maximum of 14) in the summit study area (1978) were enclosed with a 1.8 cm hexagonal mesh wire fence, 30.5 cm in height with a 10 cm inside skirt. In 1979 four large enclosures of 2.5 cm mesh were constructed in the summit study area rather than many smaller enclosed areas. Less time was spent erecting these fences thus reducing disturbance to the gulls. In addition, the larger mesh and larger enclosure proved less injurious to the chicks. In 1978 "late"-nesters were only fenced if the adults remained attentive late into incubation when there was a good possibility of their hatching at least one egg. In 1979 no "late" nests were fenced. This was done primarily to reduce disturbance (see discussion).

In 1978 I measured a sample of 33 and 35 "peak"-chicks and 21 "late" chicks on alternate days. I weighed chicks with a 500 g Pesola spring scale (± 5.0 g) and measured culmen, gonys, gape and tarsus (Baldwin et al. 1931) with vernier calipers (± 0.1 mm). To minimize the amount of time spent in the colony I measured only chick weight in 1979. I weighed all chicks captured in 35-40 minutes beginning at opposite ends of the study area on alternate days. Thus my sample size varied daily. I weighed all "late"-hatched chicks I was able to capture until they fledged or until I left the colony for the season (17 July 1978 and 19 July 1979). If the "late"-hatched chicks were not yet 21 days of age on my last return visit they were recorded as missing since I could not determine which chicks subsequently fledged.

2.4.2. Artificially incubated eggs

To eliminate the effects of differential parental behavior and environmental variables which affect hatching success, 10 3-egg clutches were collected 20 May 1978 and 23 May 1979. The eggs were wrapped securely in clothing, placed in a box and transported the same day to a Humidaire Egg Incubator at Lakehead University. The incubator was maintained at 38°C and 55% relative humidity and turned once per hour.

Twenty-nine "late" eggs were gathered on 4 June 1978 and put in the incubator within three hours of collection. The eggs included five three-egg clutches, three two-egg clutches and eight one-egg clutches. In 1979 22 late eggs including four three-egg clutches, four two-egg clutches and two one-egg clutches were collected. Eggs gathered for this experiment were replaced with eggs from nearby nests so the adults would not desert. Eggs from recently completed "late" clutches were brought to the laboratory on 17 June within three hours of collection.

2.4.3. Incubation behavior

In 1978 I used a point sampling technique (see Dunbar 1976) to measure the attentiveness of 33 pairs of gulls in the summit study area. Dunbar (1976) found that estimates of behavior obtained from the point sampling method did not differ significantly from the true function. I used two 35 mm cameras capable of 250 exposures each (Figure 4). The cameras were timed for one exposure per hour. "Late"-nesting gulls were distributed throughout the colony making it difficult to get a large sample within view of the camera. The largest sample I could obtain was three pairs. The camera was timed to go off every three minutes. Each frame of the developed film was examined for the presence or absence of a gull on its nest by running it through a Kodak Ecktagraphic Filmstrip Adapter and projecting it onto a large sheet of paper with an outline of the area (Somppi 1978).

In 1979 behavior of gulls on all nests, as well as their presence or absence was recorded from a blind situated on the edge of the summit study area. Thirty-six "peak" nests and two "late" nests were visible from the blind. Upon hatching, when my study of attentiveness of "peak"-nesting gulls was completed, I moved the blind to a location on the top of the north-east slope where five "late" nests were visible. The

Figure 4. Camera equipment used for monitoring incubation attentiveness in 1978.

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blind was left for three days so the gulls in the area could habituate to it. The behavior of each incubating gull was recorded as settling, waggling or sideways building (Beer 1961, 1963). These were lumped together as "restless" for the purpose of analysis as the number of observations for each individual behavior per week of incubation was small (5-13). Observation sessions occurred in the morning, afternoon and evening and averaged two hours in length. Daily observations were grouped together as week one, two and three of incubation, this being timed from the day of clutch completion for ease of data collection.

2.5. Aging of gulls

Gulls that were trapped but not previously banded were aged as either adult or subadult on the basis of plumage. Ring-billed gulls vary considerably in the age at which they acquire adult plumage, with vestiges of immature plumage occasionally continuing into a gull's fifth year (Ludwig 1974). Pigment deposition and vascularization of soft parts in gulls is under hormonal control (Boss 1943, Johnston 1956). Species with a subadult period between the juvenile and adult stages usually show a concomitant transition in plumage and eye color (Bent 1921, 1937 in Trauger 1974), no doubt depending on the age at which the bird first breeds, which, in Ring-billed gulls, varies from two to five years of age. I considered a gull as being subadult if the plumage exhibited one or more of the following characteristics:

1. buffy coverts on the primaries
2. complete or partial subterminal tail band
3. lack of windows or one small window on the primaries

(based on Ludwig 1974 and personal observation). For reasons stated above, I assumed that such birds had relatively less breeding experience than gulls in adult plumage (Ryder 1975).

2.6. Egg quality

In 1979 33 "peak" eggs and 21 "late" eggs were collected for measurements of egg quality. I determined the relative amounts of lipid and nitrogen (a measure of protein content) in the yolk to determine if any differences in these components existed between "peak" and "late" eggs. Eleven a-eggs from "peak" clutches were marked on 21 May. When the c-egg was laid the complete clutches were collected and egg length and width measured with vernier calipers to the nearest 0.1 mm. The eggs were hard-boiled for 10 minutes so that yolk and albumen could easily be separated. This treatment has no effect on the water fraction of yolk and albumen (Ricklefs and Montevecchi 1979). Eggs were then frozen until analysis. This procedure was also followed for "late" eggs. Two three-egg clutches, four two-egg clutches and seven one-egg clutches were collected between 11-26 June, shortly after the clutch was completed. Again, removed eggs were replaced with eggs from nearby nests so the adults would not desert.

In the laboratory each egg was thawed and separated into yolk, albumen and shell, and each component was subsequently weighed. Wet weights for albumen were not recorded because of the possibility of water loss through cracks in the shell. Albumen and shell were dried for at least 48 h at 50°C and weighed. All yolks were dried in vacuo at 50 - 55°C for 48 h (until constant weight) and then weighed (Ricklefs 1977b). Eggshell thickness was determined with a Starret No. 1010 dial indicator metric pocket gauge. Thickness was measured on both ends and the middle of each egg shell, then averaged. Egg volume was calculated as 0.489 x breadth^2 (max) x length (Ryder 1975). The Ratcliffe Index, which is also an index of eggshell thickness and density, was calculated as eggshell weight (mg) /length (mm) x breadth (mm) (Ratcliffe 1970).

To each dried yolk, approximately 90 ml of chloroform: methanol (2:1) was added and stirred for 2 h. The mixture was then centrifuged and the supernatant collected. Chloroform : methanol (2:1) was added to the precipitate and stirred overnight. The mixture was filtered and the solid material washed with chloroform : methanol (2:1) dried, weighed and frozen for nitrogen determination. All supernatants were combined, washed with water (0.2% of the combined volume), and placed in a separatory funnel. After standing for a minimum of 2 h the aqueous layer was removed and the organic phase evaporated to dryness on a rotary evaporator, then weighed.

The non-lipid fraction was dried for at least 48 h at 50°C and weighed. Samples from 10 "peak" and 10 "late" yolks were then analyzed on a Perkin-Elmer Model 240

Elemental Analyzer to obtain the amount of nitrogen which was used as an index of the amount of protein present.

2.7. Condition of the adults

2.7.1. Weights and measurements

In 1978 gulls were captured using a drop trap (Mills and Ryder 1979). All trapped birds were weighed on a 1000 g Pesola spring scale (± 5 g). Sex was determined by external measurements (Ryder 1978).

In 1979 I trapped 13 "peak"- and 23 "late"-nesting gulls for determination of body condition, age (by plumage and/or previous leg band if banded as a chick) and hormonal status. Body weight was taken with a 1000 g Pesola spring scale (± 5 g). Bill and body measurements were taken with vernier calipers to the nearest 0.1 mm. Tarsus, wing length (Baldwin et al. 1931) and keel (Harris 1970) were measured and the condition index was calculated. Brood patch development was subjectively assessed according to size (large or small), amount of vascularization and amount of refeathering (see Figure 5).

2.7.2. Blood analysis

In 1979 blood was collected from the brachial artery of 10 "peak"- and 10 "late"-nesters into 10 ml heparinized vacuum tubes (Figure 6). The blood was centrifuged at approximately 2500 rpm for 20 minutes within a half hour of collection; this prevented breakdown of the glucose fraction by bacterial action (Bennett and Bolen 1978). The plasma was immediately frozen

Figure 5. Brood patch of a Ring-billed Gull, Granite Island, week 1 of incubation. Note the feather sheaths on the edges.

Figure 6. Method of removing blood from the brachial artery of a Ring-billed Gull, Granite Island, 1979.

in liquid nitrogen and transported to the Wildlife Toxicology Division, Canadian Wildlife Service, Ottawa, where levels of metabolites were determined using the following methods (G. Fox pers. comm.): levels of uric acid were determined colorimetrically using the difference in phosphotungstate reduction before and after treatment with the specific enzyme uricase (Sigma Kit No. 680 or American Monitor Colorimetric Uricase Uric Acid reagent system No. 1017). Urea Nitrogen was determined colorimetrically using the Urease-Berthelot reaction (Sigma Kit No. 640). Total protein was determined colorimetrically using the Biuret method of Henry et al. (1974). Alpha-amino nitrogen was determined using the colorimetric ninhydrin method of Mathews et al. (1964). Cholesterol was determined colorimetrically by enzymatic hydrolysis by cholesterol esterase, oxidation by cholesterol oxidase and reaction of the liberated peroxide with 4-aminoantipyrene in the presence of phenol to form a colored quinoeimine dye (Bio-Rad's Quanta-Zyme Cholesterol Kit). Triglycerides were determined colorimetrically by enzymatic hydrolysis and quantification of NADH using p-isdonitrotetrazolium violet (Bio-Rad's Quanta-Zyme Triglycerides Kit). Calcium was determined colorimetrically using O-cresolphthaline complexone (American Monitor's "60 second calcium" Cat. No. 1032). Glucose was determined colorimetrically using the ortho-toluidine reaction (American Monitor's "Trucose" Cat. No. 1054). Thyroxine (T_4) was determined by specific radioimmunoassay, as were progersterone, total estrogens, total androgens and corticosterone.

3. Results

3.1. Nest histories of "peak"- and "late"-nesting gulls

3.1.1. Egg laying

Egg laying extended from 11 May to 13 June 1978 and 14 May to 9 July, 1979.

Nests representing the peak of laying were selected from those initiated 17-19 May 1978 and 20-22 May 1979. Those representing "late"-nesting gulls were selected from those initiated 29 May - 13 June, 1978 and 4 June - 9 July 1979.

3.1.2. Clutch size

"Peak"-initiated clutches were significantly larger than "late"-initiated clutches in both years ($t_{189} = 6.97$, $p < 0.001$, 1978, $t_{179} = 10.26$, $p < 0.001$, 1979). The mean clutch size and standard deviation (S.D.) for "peak"-nesting gulls was 3.27 ± 0.95 ($n = 135$) in 1978 and 3.06 ± 0.82 ($n = 72$) in 1979. "Late"-nesting females produced a mean of 2.25 ± 0.86 ($n = 56$) eggs in 1978 and 1.76 ± 0.84 ($n = 109$) eggs in 1979. Fourteen "peak" clutches in 1978 and five "peak" clutches in 1979 contained five or more eggs and were thought to be laid by female-female pairs (Ryder and Somppi 1979). If these are excluded from the analysis, mean clutch size for "peak"-nesting gulls was 3.05 ± 0.69 ($n = 121$) eggs in 1978 and 2.88 ± 0.48 ($n = 67$) eggs in 1979. These values are still significantly greater than those of "late"-nesting pairs ($t_{175} = 7.22$, $p < 0.01$, 1978, $t_{174} = 11.92$, $p < 0.001$, 1979). The modal clutch size was three eggs for "peak" nests (1978 and 1979) and for "late" nests in 1978 but only one egg for "late" nests in 1979.

3.1.3. Egg size

When all eggs were analyzed together, eggs from "peak" nests were significantly larger than eggs from "late" nests in both years (Table 1). However, when three-egg clutches were analyzed separately, using Duncan's Multiple Range Test, only width of a- and b-eggs remained significantly greater in "peak" eggs (Tables 2 & 3). The c-egg in "peak" clutches was significantly narrower than the b-egg ($F_{2,118} = 3.51$, $p < 0.05$) in 1978, and narrower than both the a-egg and b-egg in 1979 ($F_{2,158} = 5.62$, $p < 0.05$). Additionally, egg volume of the c-egg was significantly smaller than that of the a- and b-egg in 1979 ($F_{2,158} = 5.89$, $p < 0.05$).

3.1.4. Incubation period

The mean incubation period for eggs of all clutch sizes was 27.5 ± 2.1 (1978) and 26.1 ± 1.87 (1979) days for "peak" clutches and 26.4 ± 3.6 (1978) and 25.9 ± 1.9 days (1979) for "late" clutches. These differences were significant in 1978 but not in 1979 ($Z = 1.96$, $p < 0.05$ and $Z = 1.10$, NS, respectively; Mann-Whitney U Test). There were no significant differences within "peak" two- or three-egg clutches either year (Table 4) (F-test and Duncan's Multiple Range Test, respective to clutch size). The mean incubation period was longer in "peak" than in "late" three-egg clutches and was longer in "late" than in "peak" two-egg clutches (significant only in 1978, $p < 0.01$).

Table 1. A comparison of egg length (mm), width (mm), weight (g), volume (mm^3) and shape index of all "peak"- and "late"-nesting Ring-billed Gull eggs, 1978 and 1979[a].

	1978			1979		
	Peak	Late	Student's t	Peak	Late	Student's t
Length	59.3 ± 2.9 (433)[b]	53.3 ± 2.9 (121)	1.08, N S[c]	59.1 ± 2.2 (218)	58.6 ± 2.5 (192)	2.24, $p < 0.05$
Width	42.2 ± 1.2 (433)	41.4 ± 1.3 (121)	6.18, $p < 0.001$	42.2 ± 1.2 (218)	41.3 ± 1.2 (192)	7.80, $p < 0.001$
Weight	57.0 ± 4.5 (426)[d]	53.4 ± 5.1 (121)	7.87, $p < 0.001$	---- ---	---- ---	----
Volume	51.58 ± 4.13 (433)	49.49 ± 4.28 (121)	4.89, $p < 0.001$	51.59 ± 3.72 (218)	48.92 ± 3.56 (192)	7.39, $p < 0.001$
Shape	71.27 ± 3.67 (433)	70.30 ± 3.15 (121)	2.63, $p < 0.01$	71.52 ± 3.18 (218)	70.64 ± 3.53 (192)	2.66, $p < 0.01$

[a] Nine "peak" eggs and five "late" eggs in 1978 were not measured, the total number of eggs actually being 442 and 126, respectively. In 1979, two "peak" eggs were not measured.

[b] Mean ± S D (n)

[c] No significant difference

[d] Eggs were only weighed in 1978; seven "peak" eggs were not included because they were not weighed within two days of laying.

Table 2. A comparison of egg length (mm), width (mm), weight (g) and volume (mm^3) in 3-egg clutches of "peak"- and "late"-nesting Ring-billed Gulls, 1978 and 1979.

	1978[a]			1979		
	Peak	Late	Student's t	Peak	Late	Student's t
Length						
Egg a	59.2 ± 3.1 (40)[b]	59.2 ± 2.7 (23)	NS[c]	59.1 ± 2.3 (54)	58.5 ± 2.2 (28)	NS
b	59.4 ± 2.9 (40)	58.9 ± 2.7 (23)	NS	59.5 ± 2.2 (53)[d]	58.9 ± 2.5 (28)	NS
c	59.2 ± 2.5 (41)	58.9 ± 2.6 (23)	NS	58.9 ± 2.2 (54)	58.5 ± 2.4 (28)	NS
Total	59.2 ± [illegible].7 (259)	58.8 ± 2.5 (69)	NS	59.2 ± 2.3 (161)	58.7 ± 2.4 (84)	NS
Width						
Egg a	42.4 ± 1.2 (40)	41.7 ± 1.3 (23)	2.17, $p < 0.05$	42.0 ± 1.3 (54)	41.2 ± 1.1 (28)	2.68, $p <$ 0.01
b	42.7 ± 1.1 (40)	41.8 ± 1.3 (23)	3.13, $p < 0.01$	42.6 ± 1.1 (53)	41.6 ± 1.2 (28)	3.52, $p <$ [illegible]
c	41.96 ± 1.5 (41)	41.5 ± 1.3 (23)	NS	41.8 ± 1.3 (54)	41.4 ± 1.1 (28)	NS
Total	42.2 ± 1.3 (258)	41.5 ± 1.3 (69)	3.75, $p < 0.001$	42.1 ± 1.3 (161)	41.4 ± 1.1 (84)	4.25, $p < 0.001$
Volume						
Egg a	52.09 ± 4.50 (40)	50.35 ± 4.62 (23)	NS	51.32 ± 3.89 (54)	48.69 ± 2.99 (28)	3.11, $p <$ [illegible]
b	59.92 ± 4.01 (40)	50.33 ± 4.28 (23)	2.42, $p < 0.05$	52.88 ± 3.70 (53)	49.96 ± 3.59 (28)	3.41, $p < 0.001$
c	51.01 ± 5.06 (41)	49.69 ± 4.04 (23)	NS	50.34 ± 3.94 (54)	49.20 ± [illegible].81 (28)	NS
Total	51.7[illegible] ± 4.50 (258)	49.80 ± 4.08 (69)	3.31, $p < 0.01$	51.51 ± 3.90 (161)	49.29 ± 3.48 (84)	4.34, [illegible] <
Weight						
Egg a	57.6 ± 5.8 (40)	53.8 ± 4.8 (22)	2.29, $p < 0.05$			
b	58.5 ± 4.7 (40)	54.0 ± 4.3 (22)	3.22, $p < 0.01$			
c	56.[illegible] ± [illegible].9 (41)	54.7 ± [illegible] (22)	NS			
Total	57.[illegible] ± 4.9 (256)	54.[illegible] ± 4.5 (66)	4.59, $p < 0.001$			

[a] Includes only clutches of known a-, b- and c-eggs, totals include all 3-egg clutches; one known a- and b- "peak" egg in [illegible] not measured or weighed, and two additional "peak" eggs were not weighed; one a-, b- and c- egg of "late" [illegible] were not [illegible].

[b] Mean ± SD (n)

[c] No significant difference

[d] [illegible]-egg was not measured.

[illegible] comparison of egg length (mm), width (mm), weight (g) and volume (cm^3) in 2-egg clutches [illegible] and "late"-[illegible] Gulls, 1978 and 1979.

	1978[a]			1979		
	Peak	Late	Significance	Peak	Late	Significance
[illegible]						
	[illegible] (7)[b]	[illegible] (14)		57.7 ± [illegible] (9)	[illegible] ± [illegible] (27)	
	[illegible] (7)	59.6 ± 3.9 (15)	N[illegible]	57.9 ± [illegible] (9)	[illegible] ± [illegible] (27)	
	[illegible] (32)	59.[illegible] ± [illegible] (31)	N[illegible]	57.8 ± [illegible] (18)	[illegible] ± [illegible] (54)	
	[illegible] (7)	[illegible] ± 1.3 (14)	[illegible]	[illegible] ± [illegible] (9)	[illegible] ± [illegible] (27)	p < [illegible]
	[illegible] ± 1.[illegible] (7)	41.[illegible] ± 1.3 (15)	NS	42.8 ± 0.5 (9)	41.[illegible] ± 1.1 (27)	p < [illegible]
	[illegible] (32)	[illegible] ± [illegible] (31)	[illegible] = [illegible]	[illegible] ± [illegible] (18)	[illegible] ± [illegible] (54)	p < [illegible]
	[illegible] ± [illegible] (7)	48.17 ± 4.0[illegible] (14)	[illegible]	[illegible].51 ± [illegible].15 (9)	[illegible] ± [illegible] (27)	p < [illegible]
	[illegible] ± [illegible] (7)	[illegible] ± 5.2[illegible] (15)	N[illegible]	51.62 ± 1.55 (9)	46.62 ± [illegible] (27)	p < 0.05
	[illegible] ± [illegible] (32)	[illegible] ± [illegible] (31)	[illegible]	[illegible].55 ± [illegible].57 (18)	48.[illegible] ± [illegible] (54)	p < [illegible]
	(7)	51.[illegible] ± 4.[illegible] (14)				
	[illegible]	[illegible] (15)				
	[illegible] ± [illegible] (32)	[illegible] ± 5.[illegible] (31)	[illegible] = [illegible], p < [illegible]			

[illegible] and [illegible] 3- and 1-eggs; in 1978 the "peak" egg was not weighed, five "late" eggs were not measured: [illegible]-egg clutches in 1978.

[illegible] recorded a Mann-Whitney U Test was used

Table 4. Differences in incubation period (days) of eggs that hatched in 2- and 3-egg clutches of "peak"- and "late"-nesting Ring-billed Gull nests, 1978 and 1979.[a]

	1978			1979		
	Peak	Late	Significance[b]	Peak	Late	Significance
3-egg clutches						
a-egg	28.1 ± 2.4 (23)[c]	27.7 ± 2.1 (3)	NS	27.3 ± 1.1 (46)	25.8 ± 2.1 (8)	$p < 0.05$
b-egg	27.9 ± 1.7 (24)	23.0 ± 1.8 (4)	$p < 0.001$	26.0 ± 1.1 (44)	25.4 ± 1.5 (9)	NS[d]
c-egg	27.8 ± 1.9 (20)	24.8 ± 2.9 (6)	$p < 0.05$	24.7 ± 1.4 (40)	25.0 ± 0.8 (7)	NS
Total	27.6 ± 1.9(159)	24.9 ± 2.9 (13)	$p < 0.001$	26.1 ± 1.6(130)	25.4 ± 1.5 (24)	NS
2-egg clutches						
a-egg	25.5 ± 2.1 (2)	31.2 ± 3.3 (4)	NS	26.3 ± 2.1 (8)	27.5 ± 3.5 (2)	NS
b-egg	26.8 ± 3.3 (5)	26.0 (1)	----	24.3 ± 1.7 (4)	27.0 ± 2.0 (3)	NS
Total	25.5 ± 2.3 (17)	30.2 ± 3.7 (5)	$p < 0.01$	25.6 ± 2.1 (12)	27.2 ± 2.3 (5)	NS

[a] Includes only clutches of known a-, b- and c-eggs, totals include all eggs that hatched from the respective clutch size.

[b] Mann-Whitney U Test

[c] Mean ± SD (n)

[d] No significant difference

3.1.5. Incubation behavior

Attentiveness, or amount of time spent on the nest exceeded 95% throughout the incubation period for both "peak" and "late" nests (Table 5). However, "late"-nesting gulls were twice as restless as "peak"-nesters (Table 6) and deserted their nests more frequently in both 1978 (36.2%, (21/58) vs 5.2%, (7/135), $X^2 = 31.47$, $p < 0.001$) and 1979 (28.4%, (31/109) vs 4.2%, (3/72), $X^2 = 16.74$, $p < 0.001$).

3.1.6. Hatching and reproductive success

"Late"-nesting individuals had significantly poorer success in reproduction than "peak"-nesting individuals in both years, as measured by four parameters (Table 7).

Clutches greater or smaller than the modal three eggs (with the exception of the two four-egg clutches in late 1978 nests) experienced lower hatching success in both years, regardless of initiation date (Table 8 and Figure 7). "Peak" three-egg clutches had a significantly higher hatching success than "late" three-egg clutches in both 1978 ($X^2 = 38.72$, $p < 0.001$) and 1979 ($X^2 = 63.09$, $p < 0.001$). Hatching success of two-egg clutches was also significantly greater in "peak" than in "late" nests in 1978 and 1979 ($X^2 = 11.91$, $p < 0.001$; $X^2 = 24.67$, $p < 0.001$). In "peak" clutches more a- and b- than c-eggs hatched ($P < 0.05$, Duncan's Multiple Range Test) but this was not observed in "late" clutches (Table 9). Two-egg clutches showed no consistent pattern in hatching success (Table 9).

Table 5. Percent of time spent incubating by "peak"- and "late"-nesting Ring-billed Gulls in weeks 1-3 of incubation in 1978 and 1979[a].

	1978				1979			
	Peak	n	Late	n	Peak	n	Late	n
Week 1	98.3 ($\frac{4967}{5050}$)[b]	19	99.6 ($\frac{248}{249}$)	1	99.8 ($\frac{1725}{1728}$)	36	96.9 ($\frac{569}{587}$)	2
2	----[c]		97.5 ($\frac{3187}{3268}$)	3	99.6 ($\frac{4291}{4305}$)	36	97.2 ($\frac{681}{700}$)	3
3	95.5 ($\frac{4152}{4346}$)	17	99.3 ($\frac{439}{442}$)	1	99.7 ($\frac{5563}{5580}$)	36	99.5 ($\frac{734}{748}$)	3
Total	97.0 ($\frac{9119}{9396}$)		97.8 ($\frac{3874}{3959}$)		99.7 ($\frac{11579}{11613}$)		97.5 ($\frac{1984}{2035}$)	

a Photograph taken once an hour for "peak"-, every three minutes for "late"- (Section 2.4.3) in 1978, observations recorded every five minutes for "peak" and every two minutes for "late" in 1979.

b No. of times on the nest/ total no. observations.

c No data

Table 6. Incubation behavior of "peak"- and "late"-nesting Ring-billed Gulls, 1979[a]

	Peak			Late			Significance
	Sitting	Restless[b]	n	Sitting	Restless	n	
Week 1	1646	49 (2.9%)	36	350	16 (4.6%)	2	$x^2 = 2.16$, NS[c]
2	4299	79 (1.8%)	36	465	17 (3.6%)	3	$x^2 = 6.65$, $p < 0.010$
3	5493	132 (2.4%)	36	822	43 (5.2%)	3	$x^2 = 19.68$, $p < 0.001$
Total	11438	260 (2.3%)		1637	76 (4.6%)		$x^2 = 29.98$, $p < 0.001$

[a] Behavior of "peak"-nesting gulls was recorded in five minute intervals, totalling 28 hours of observation; that of "late"-nesting gulls was recorded in two minute intervals totalling 30 hours of observation.

[b] Explained in Section 2.4.3.

[c] No significant difference

Table 7. Reproductive parameters of "peak"- and "late"-nesting Ring-billed Gulls, Granite Island, 1978 and 1979.

	1978			1979		
	Peak	Late	Significance	Peak	Late	Significance
Modal date of hatching	12 June (10-21)	28 June (23-6)		19 June (13-26)	5 July (25-17)	
Hatching success	45.0 $(\frac{199}{442})$	16.7 $(\frac{21}{126})$	$X^2 = 33.2$, $p < 0.001$	73.2 $(\frac{161}{220})$	16.1 $(\frac{31}{192})$	$X^2 = 134.03$, $p < 0.001$
Nesting success	67.4 $(\frac{91}{135})$	23.2 $(\frac{13}{56})$	$X^2 = 31.2$, $p < 0.001$	88.9 $(\frac{64}{72})$	14.7 $(\frac{16}{109})$	$X^2 = 118.27$, $p < 0.001$
Fledging Success	43.2 $(\frac{86}{199})$	47.6 $(\frac{10}{21})$	$X^2 = 0.2$, NS[b]	69.6 $(\frac{112}{161})$	38.7 $(\frac{12}{31})$	$X^2 = 10.81$, $p < 0.001$
Breeding success	19.5 $(\frac{86}{442})$	7.9 $(\frac{10}{126})$	$X^2 = 9.3$, $p < 0.005$	50.9 $(\frac{112}{220})$	6.2 $(\frac{12}{192})$	$X^2 = 97.19$, $p < 0.001$
Reproductive success	0.6 $(\frac{86}{135})$	0.2 $(\frac{10}{56})$		1.6 $(\frac{112}{72})$	0.1 $(\frac{12}{109})$	

[a] Range of hatching dates

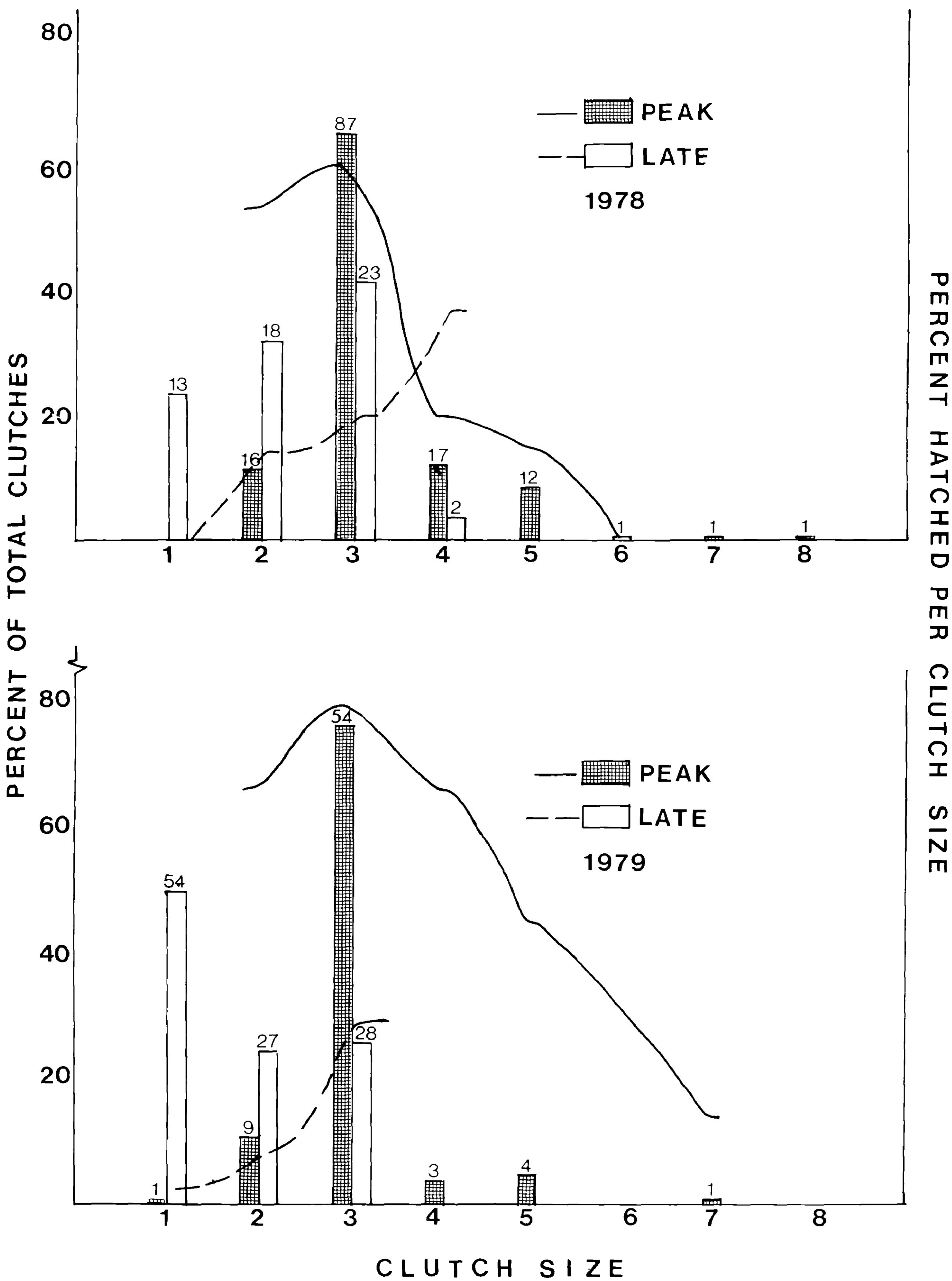
[b] No significant difference

Table 8. Hatching and fledging success by clutch size for "peak"- and "late"-nesting Ring-billed Gulls, 1978 and 1979.

Clutch Size	1978 No. of Clutches	1978 Hatching success	1978 Fledging[a] success	1979 No. of Clutches	1979 Hatching success	1979 Fledging success
Peak 1	--	--	--	1	100.0 (1/1)	100.0 (1/1)
2	16	53.1 (17/32)	64.7 (11/17)	9	66.6 (12/18)	91.6 (11/12)
3	87	60.9 (159/261)	42.7 (68/159)	54	80.2 (130/162)	66.9 (87/130)
4	17	20.6 (14/68)	35.7 (5/14)	3	66.6 (8/12)	87.5 (7/8)
5	12	15.0 (9/60)	22.2 (2/9)	4	45.0 (9/20)	66.6 (6/9)
6	1	0 (0/6)	--	--	--	--
7	1	0 (0/7)	--	1	14.2 (1/7)	0 (0/1)
8	1	0 (0/8)	--	--	--	--
Total	135	45.0 (199/442)	43.2 (86/199)	72	74.1 (161/220)	69.6 (112/161)
Late 1	13	0.0 (0/13)	--	54	3.7 (2/54)	0.0 (0/2)
2	18	13.9 (13/36)	92.0 (4.6/5)	27	9.2 (5/54)	0.0 (0/5)
3	23	18.8 (13/69)	41.5 (5.4/13)	28	28.6 (24/84)	50.0 (12/24)
4	2	37.5 (3/8)	0 (0/3)	--	--	--
Total	56	16.7 (21/126)	47.6 (10/21)	109	16.1 (31/192)	38.7 (12/31)

[a] This value was calculated - refer to Section 3.1.8

Figure 7. Hatching success of "peak"- and "late"-nesting Ring-billed Gulls in relation to clutch size, Granite Island, 1978 and 1979.



PERCENT OF TOTAL CLUTCHES
PERCENT HATCHED PER CLUTCH SIZE
PEAK
LATE
1978
80
60
40
20
87
23
18
13
16
17
2
12
1
1
1
1
2
3
4
5
6
7
8
PEAK
LATE
1979
80
60
40
20
54
54
27
28
9
1
3
4
1
1
2
3
4
5
6
7
8
CLUTCH SIZE

Table 9. Hatching frequency of a-, b- and c-eggs of "peak"- and "late"-nesting Ring-billed Gulls, 1978 and 1979[a].

	1978		1979	
	Peak	Late	Peak	Late
3-egg clutches				
Egg a	56.1 (23/41)	13.0 (3/23)	85.2 (46/54)	28.6 (8/28)
b	58.5 (24/41)	17.4 (4/23)	81.5 (44/54)	32.1 (9/28)
c	48.8 (20/41)	26.0 (6/23)	74.1 (40/54)	25.0 (7/28)
Total	54.5 (67/123)	18.8 (13/69)	80.2 (130/162)	28.6 (24/84)
2-egg clutches				
Egg a	28.6 (2/7)	23.5 (4/17)	88.9 (8/9)	7.4 (2/27)
b	71.4 (5/7)	5.9 (1/17)	44.4 (4/9)	11.1 (3/27)
Total	50.0 (7/14)	14.7 (5/34)	66.7 (12/18)	9.2 (5/54)

[a] Only clutches with known a-, b- and c-eggs were used.

3.1.7 Fate of unhatched eggs

The majority of eggs that failed to hatch, disappeared or rolled out of the nest (Table 10). In 1979 high winds and rain between 21-23 June destroyed many "late" nests which were on the rock face unprotected by vegetation. A significantly higher percentage of "peak" eggs in 1978 (55%) than 1979 (27%) did not hatch ($X^2 = 45.27$, $p < 0.001$). This was thought to be largely a consequence of increased disturbance to peak-breeding gulls in 1978. The proportion of unhatched "late" eggs was 83% in 1978 and 81% in 1979.

3.1.8. Survival and growth of chicks

Fledging success was not significantly different between "peak" and "late"nests in 1978 but was significantly greater for "peak" nests in 1979. Two-egg clutches had the highest fledging success except in "late" 1979 when three-egg clutches had the highest (and except in "peak" 1979 when the only one-egg clutch that was laid hatched) (Table 8).

Fledging success had to be estimated since not all chicks were recaptured or found dead. This estimation was based on a method devised by Ryder and Carroll (1978). I estimated fledging success for "peak" nests in 1979 as follows: 16 of 22 (73%) of the chicks died at 10 days of age or less. Thus 27% were between 11-20 days of age when they died. If a chick was missing between 11-20 days of age, the chance of it being alive was 73%. To calculate fledging success I added the number of chicks known to be 21 days old to the number of missing chicks which I calculated to have fledged, based on

Table 10. Fate of eggs that did not hatch, Granite Island.

Eggfate	1978		1979	
	Peak	Late	Peak	Late
Disappeared	75 (30.8)[a]	38 (36.2)	17 (28.8)	35 (25.9)
Rolled out of Nest	44 (18.1)	12 (11.4)	19 (32.2)	10 (7.4)
Deserted	31 (12.8)	19 (18.1)	5 (8.5)	35 (25.9)
Destroyed in Nest	32 (13.2)	14 (13.3)	--	--
Addled/Rotten/Dead Embryo	31 (12.8)	12 (11.4)	1 (1.7)	1 (0.7)
Pipped and Died	10 (4.1)	3 (2.9)	1 (1.7)	4 (3.0)
Cracked	8 (3.3)	5 (4.8)	10 (16.9)	10 (7.4)
Infertile	1 (0.4)	2 (1.9)	1 (1.7)	4 (3.0
Buried in Nest			1 (1.7)	
Windstorm				20 (14.8)
Unknown	11 (4.5)		4 (6.8)	16 (11.9)
Total	243	105	59	135

[a] sample size (%)

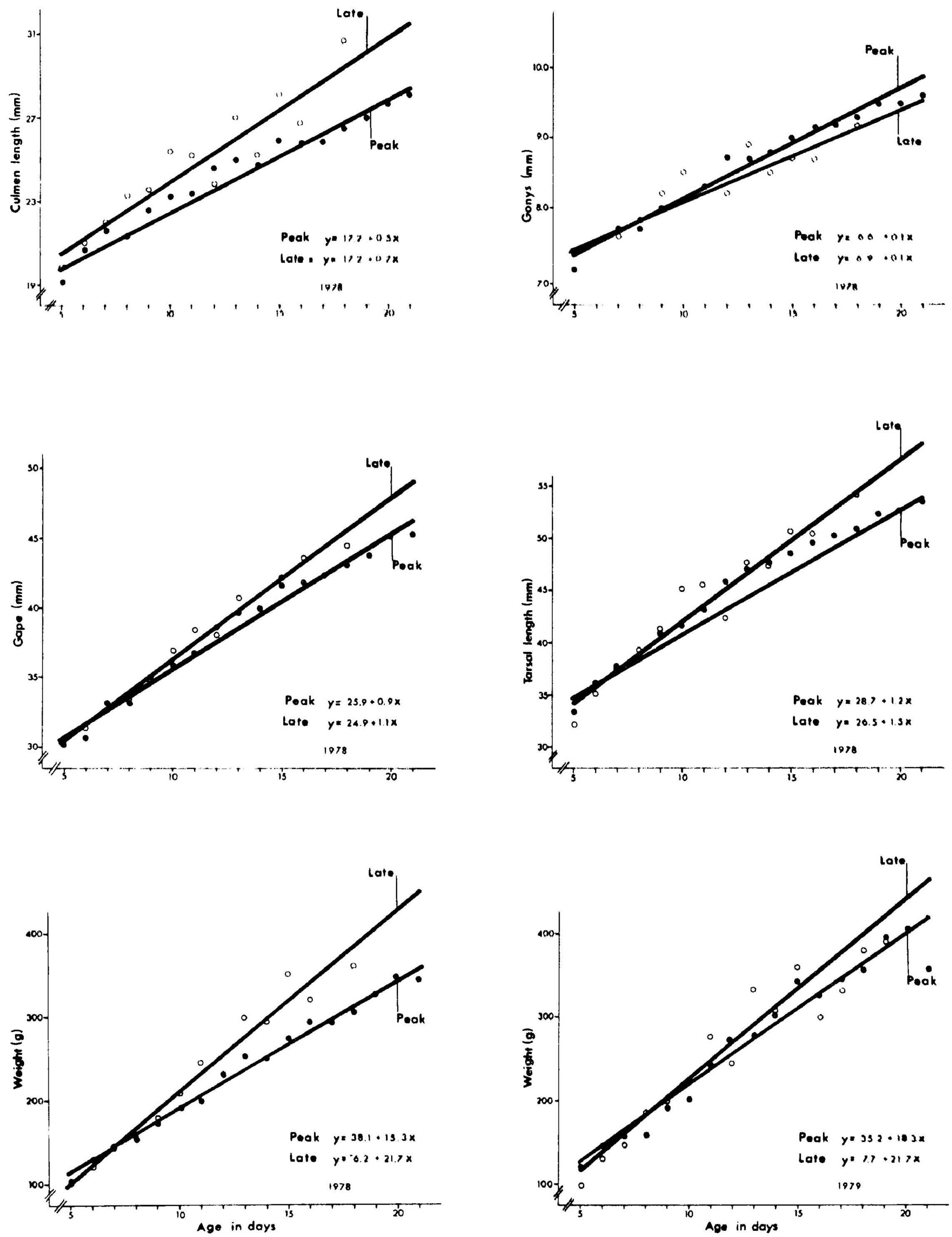
the above proportions. This was recalculated for "peak"- and "late"-nesting gulls each year.

The median age of death for "peak"- and "late"-hatched chicks in 1978 was 6.5 days (range 0-20, $n = 68$) and 2.0 days (range 0-12, $n = 11$), with "late"-hatched chicks dying at a significantly younger age ($Z = 2.45$, $p < 0.05$, Mann-Whitney U Test). In 1979 these values were 5.5 (range 0-20, $n = 22$) and 3.0 (range 2-6, $n = 5$) days ($Z = 1.93$, $0.10 > p < 0.05$, Mann-Whitney U Test).

Data for the growth of "peak"- and "late"-hatched chicks are given in Appendix 1-7. Regression lines were calculated from day 5 to day 22, the linear portion of the growth curve (Kirkham and Morris 1979) (Figure 8). The data in 1978 were corrected for autocorrelation but this was not necessary in 1979 (Koutsoyiannis 1977). The regression lines for "peak" and "late" chicks were compared using the test statistic in Neter and Wasserman (1974), with a significant F Value indicating a difference in the two lines. If a difference existed, confidence intervals were calculated to test for differences in slopes (Neter and Wasserman 1974). A non-significant slope contains zero in the confidence interval.

In 1978 there was no difference in growth of gape between "peak" and "late" chicks. Confidence intervals (Appendix 7) showed a barely significant difference in slope for culmen, gonys and tarsal length indicating that most of the statistical difference (as indicated by the F value) lies in the intercept.

Figure 8. Growth of "peak"- and "late"- Ring-billed Gull chicks, Granite Island, 1978 and 1979 (closed and open dots indicate means for "peak" and "late" chicks, respectively).



Culmen length (mm)
Late
Peak
Peak y= 17.2 + 0.5x
Late y= 17.2 + 0.7x
1978
Gonys (mm)
Peak
Late
1978
Gape (mm)
Late
Peak
Peak y= 25.9 + 0.9x
Late y= 24.9 + 1.1x
1978
Tarsal length (mm)
Late
Peak
Peak y= 28.7 + 1.2x
Late y= 26.5 + 1.5x
1978
Weight (g)
Late
Peak
Peak y= 38.1 + 15.3x
Late y= 6.2 + 21.7x
1978
Age in days
Weight (g)
Late
Peak
Peak y= 35.2 + 18.3x
Late y= 7.7 + 21.7x
1979
Age in days

Regression lines for weights of "peak" and "late" chicks were also significantly different each year, but in 1979, the difference lay solely in the intercept, with "late" chicks hatching at a lighter weight than "peak" chicks. This result emphasizes the point that small differences are exaggerated with statistical analysis especially since I measured a process over time using the same individuals.

3.2. Artificially incubated eggs

In 1978 significantly more artificially incubated "peak" than "late" eggs hatched while in 1979 the difference was not significant ($X^2 = 12.61$, $p < 0.001$, 1978, $X^2 = 3.82$, $p < 0.05$, 1979, respectively) (Table 11). Lack of replication of the first year results in the second year may be accounted for by a difference in the hatching success of "peak" eggs between years ($X^2 = 4.58$, $p < 0.05$) while that of "late" eggs was similar ($X^2 = 0.49$, NS). Each year all 10 "peak" three-egg clutches hatched at least one egg, while three out of three "late" three-egg clutches in 1978 and only two out of four "late" three-egg clutches in 1979 hatched at least one egg.

In 1978, artificially incubated "peak" eggs had a far greater hatching success than eggs in the field (Table 12). In addition, hatching success for "late" eggs was significantly greater when artificially incubated each year (Table 12), indicating that environmental factors such as inadequate incubation affected the hatching success of those eggs. All dead embryos were

Table 11. Fate of artificially incubated eggs for "peak"- and "late"-nesting Ring-billed Gulls, 1978 and 1979.

	Clutches Collected	Eggs that Hatched	Eggs That Did Not Hatch			% of Eggs Hatched
			Dead Embryo	Rotton	Infertile	
1978 Peak						
3-egg clutch	10	28 (93.3)[a]	2 (6.7)			93.3 (28/30)
1978 Late						
3-egg clutch	3	8 (88.8)			1 (11.1)	
2-egg clutch	5	3 (30.0)	5 (50.0)	2 (20.0)		
1-egg clutch	8	3 (37.5)	3 (37.5)	2 (25.0)		
						51.9 (14/27)
1979 Peak[b]						
3-egg clutch	10	21 (72.4)	5 (17.2)		3 (10.4)	72.4 (21/29)
1979 Late						
3-egg clutch	4	4 (33.3)		5 (41.7)	3 (25.0)	
2-egg clutch	4	5 (62.5)	1 (12.5)	2 (25.0)		
1-egg clutch	2	1 (50.0)		1 (50.0)		
						45.5 (10/22)

[a] total (%)

[b] one egg cracked during transport

Table 12. A comparison of the hatching success of natural (field) and artificially incubated Ring-billed Gull eggs, Granite Island.

		Field	Artificial	Significance
1978	Peak	45.0 $(\frac{199}{442})$	93.3 $(\frac{28}{30})$	$x^2 = 26.26$, $p < 0.001$
	Late	16.7 $(\frac{21}{126})$	51.9 $(\frac{14}{27})$	$x^2 = 15.60$, $p < 0.001$
1979	Peak	73.2 $(\frac{161}{220})$	72.4 $(\frac{21}{29})$	$x^2 = 0.007$, NS[a]
	Late	16.1 $(\frac{31}{192})$	45.5 $(\frac{10}{22})$	$x^2 = 10.95$, $p < 0.001$

[a] No significant difference

aged at 19-20 days (Ryder and Somppi 1977). A significantly higher number of "late" eggs were either rotten or infertile each year ($X^2 = 5.76$, $p < 0.05$, 1978, $X^2 = 9.87$, $p < 0.01$, 1979).

3.3. Egg quality

The width and volume of eggs used in egg quality analysis in 1979 were numerically, but not statistically larger in "peak" than in "late" samples (Table 13). This is consistent with previously stated field results (Section 3.1.3). In clutches initiated during the peak of laying, dry shell weight differed significantly between a-, b- and c-eggs ($p < 0.05$, Duncan's Multiple Range Test). Most of these differences are a result of decreases in the c-egg component (Tables 14, 15 and 16). Within "late" clutches the Ratcliffe Index and eggshell thickness differed significantly ($p < 0.005$ and $p < 0.01$ respectively; Duncan's Multiple Range Test). Each of these components decreased with successive eggs in the clutch. When "peak" and "late" eggs were compared, there was a significantly larger amount of dry albumen in "peak" eggs which correspondingly decreased the yolk: albumen ratio in "peak" eggs. The Ratcliffe Index and dry shell weight were also significantly larger in "peak" than "late" eggs although there was no difference in eggshell thickness when measured directly. This indicated that the shell of "late" eggs had a lower density than that of "peak" eggs.

A-, b- and c-eggs laid during the "peak" of clutch

Table 13. Egg size, weight of components and chemical composition of the yolk for "peak" and "late" 3-egg clutches, 1979[a].

	Peak	Late	Significance[b]
Egg length (mm)	58.4 ± 2.2 (32)[c]	58.6 ± 0.2 (20)	NS[d]
Egg width (mm)	41.9 ± 2.1 (33)	40.9 ± 0.1 (20)	$p < 0.10$
Egg volume (mm^3)	50.3 ± 5.6 (32)	48.0 ± 4.2 (20)	$p < 0.10$
Yolk: Wet yolk (g)	17.34 ± 2.45 (8)	16.28 ± 1.51 (18)	NS
Dry yolk (g)	7.20 ± 0.73 (21)	7.07 ± 0.49 (17)	NS
% water	58.78 ± 5.37 (8)	56.71 ± 2.65 (17)	NS
Lipid (g)	5.23 ± 0.61 (20)	4.96 ± 0.57 (19)	NS
Non-lipid dry (g)	2.59 ± 0.24 (15)	2.49 ± 0.26 (18)	NS
Nitrogen (g)	13.05 ± 0.44 (13)	13.45 ± 0.70 (13)	$p < 0.10$
Dry Albumen	4.21 ± 0.42 (23)	3.99 ± 0.40 (18)	$p < 0.05$
Yolk/Albumen (dry)	1.74 ± 0.25 (21)	1.80 ± 0.24	NS
Eggshell thickness (mm)	0.302 ± 0.015 (33)	0.295 ± 0.021 (20)	NS
Dry shell (g)	3.58 ± 0.26 (31)	3.34 ± 0.31 (18)	$p < 0.05$
Ratcliffe Index	1.47 ± 0.11 (32)	1.55 ± 0.74 (19)	$p < 0.005$

a Sample sizes vary as not all tests were performed on every egg; if the embryo was older than four days egg contents were excluded from analyses as yolk is difficult to separate from albumen after this point.

b Mann-Whitney U Test

c Mean ± SD (n)

d No significant difference

Table 14. Size of egg, weight of components and chemical composition of the yolk for the a-egg, 1979[a].

	Peak	Late	Significance[b]
Length (mm)	58.6 (54.7 - 61.0) 11[c]	59.5 (54.7 - 63.0) 12	NS[d]
Width (mm)	41.8 (39.5 - 43.8) 11	40.6 (38.7 - 44.3) 12	NS
Volume (mm^3)	50.4 (44.1 - 54.8) 11	48.3 (40.1 - 58.2) 12	NS
Yolk: weight, wet (g)	----	15.93 (13.48 -20.02) 10	--
weight, dry (g)	7.06 (6.96 - 8.39) 3	7.17 (5.96 -7.83) 10	NS
% of water	----	55.65 (54.6 - 60.9) 10	--
lipid (g)	4.84 (4.28 - 5.53) 4	5.31 (4.18 - 6.05) 11	NS
non-lipid dry (g)	2.64 (2.39 - 2.73) 4	2.38 (1.96 - 3.07) 11	NS
nitrogen (g)	12.67 (12.41 - 13.49) 4	13.46 (12.02 - 14.97) 8	NS
Dry Albumen (g)	4.44 (3.29 - 4.66) 5	3.92 (3.06 - 4.27) 10	$p < 0.10$
Yolk/Albumen (g)	1.95 (1.49 - 2.15) 3	1.86 (1.44 - 2.21) 10	NS
Eggshell thickness (mm)	0.310 (0.294 - 0.330) 11	0.309 (0.278 - 0.333) 13	NS
Dry Shell (g)	3.73 (3.44 - 4.04) 9	3.52 (2.89 - 3.76) 10	$p < 0.10$
Ratcliffe Index	1.52 (1.40 - 1.61) 11	1.42 (1.36 - 4.58) 11	$p < 0.01$

[a] Sample sizes vary as not all tests were performed on every egg; if the embryo was older than four days egg contents were excluded from analyses as yolk is difficult to separate from albumen after this point.

[b] Mann-Whitney U Test

[c] Median (range) n

[d] No significant difference

Table 15. Size of egg, weight of components and chemical composition of the yolk for the b-egg, 1979[a].

	Peak	Late	Significance[b]
Egg length (mm)	51.9 (54.2 - 60.9) 11[c]	57.7 (56.6 - 59.7) 6	NS[d]
Egg width (mm)	41.8 (39.6 - 43.2) 11	40.4 (39.8 - 42.4) 6	NS
Egg volume (mm^3)	50.6 (44.3 - 55.6) 11	46.5 (44.6 - 52.5) 6	NS
Yolk: wet yolk (g)	16.5 1	16.39 (14.52 - 17.42) 6	NS
dry yolk (g)	7.46 (5.25 - 8.45) 7	7.05 (6.63 - 7.48) 5	NS
% of water	54.1 1	55.8 (54.3 - 61.9) 5	NS
lipid (g)	5.23 (4.98 - 6.32) 6	4.71 (4.21 - 5.12) 6	$p < 0.01$
non-lipid dry (g)	2.67 (2.11 - 2.97) 5	2.64 (2.21 - 2.78) 5	NS
nitrogen (g)	13.12 (12.56 - 13.80) 5	13.38 (12.38 - 13.79) 4	NS
Dry Albumen	4.48 (3.45 - 4.80) 7	3.99 (3.58 - 4.69) 6	NS
Yolk/Albumen (dry)	1.67 (1.11 - 2.19) 7	1.74 (1.41 - 2.09) 5	NS
Eggshell thickness (mm)	0.310 (0.270 - 0.310) 11	0.280 (0.250 - 0.290) 6	$p < 0.05$
Dry shell (g)	3.66 (3.09 - 3.97) 11	3.17 (2.86 - 3.53) 6	$p < 0.01$
Ratcliffe Index	1.48 (1.31 - 1.72) 11	1.36 (1.25 - 1.39) 6	$p < 0.005$

[a] Sample sizes vary as not all tests were performed on every egg; if the embryo was older than four days, egg contents were excluded from analyses as yolk is difficult to separate from albumen after this point.

[b] Mann-Whitney U Test

[c] Median (range) n

[d] No significant difference

Table 16. Size of egg, weight of components and chemical composition of the yolk for the c-egg, 1979[a].

	Peak	Late	Significance[b]
Egg length (mm)	58.6 (54.7 - 62.1) 10[c]	57.0 (56.4 - 57.6) 2	NS[d]
Egg width (mm)	41.2 (39.3 - 51.0) 11	40.8 (40.2 - 41.3) 2	NS
Egg volume (mm^3)	49.8 (42.8 - 75.3) 10	46.3 (44.6 - 48.0) 2	NS
Yolk: wet yolk (g)	18.45 (12.76 - 20.44) 7	16.68 (15.05 - 18.31) 2	NS
dry yolk (g)	7.25 (5.89 - 7.92) 11	6.89 (6.83 - 6.96) 2	NS
% of water	61.40 (53.50 - 66.00) 7	58.25 (54.50 - 62.00) 2	NS
lipid (g)	5.16 (4.01 - 5.92) 10	4.72 (4.63 - 4.80) 2	NS
non-lipid dry (g)	2.42 (2.18 - 2.90) 6	2.54 (2.36 - 2.72) 2	NS
nitrogen (g)	13.07 (12.84 - 13.43) 4	13.91 1	NS
Dry Albumen	4.15 (3.23 - 4.51) 11	4.29 (4.04 - 4.54) 2	NS
Yolk/Albumen (dry)	1.71 (1.46 - 2.08) 11	1.61 (1.53 - 1.69) 2	NS
Eggshell thickness	0.290 (0.280 - 0.340) 11	0.280 (0.260 - 0.320) 2	NS
Dry shell (g)	3.37 (3.14 - 4.10) 11	3.11 (2.71 - 3.52) 2	NS
Ratcliffe Index	1.40 (1.11 - 1.68) 10	1.28 (12.0 - 13.6) 2	NS

[a] Sample sizes vary as not all tests were performed on every egg; if the embryo was older than four days, egg content were excluded from analyses as yolk is difficult to separate from albumen after this point.

[b] Mann-Whitney U Test

[c] Median (range) n

[d] No significant difference

initiation were then compared to the respective eggs of "late"-laid clutches (Tables 14, 15 and 16). "Peak" a-eggs contained more dry albumen than "late" a-eggs but the differences in dry albumen in a-, b- or c-eggs were not significant between these two groups. However, the Ratcliffe Index and dry shell weight were significantly larger in "peak" than in "late" a- and b-eggs, although there was no apparent difference in c-eggs. Eggshell thickness and lipid content of the yolk were significantly larger in "peak" than in"late" b-eggs but there were no differences between a- or c-eggs. In summary, differences in egg quality were most pronounced in the dry albumen and shell components.

3.4. Age of gulls in relation to time of breeding

In 1978 I captured 15"peak"-nesting gulls of known age (Appendix 8). The mean and median age was five years, though age ranged from two to seven years. No "late"-nesting gulls of known age were captured.

In 1979 a total of 39 gulls was trapped. Three of these were "peak"-nesting gulls and five were "late"-nesting gulls of known age (Appendix 9). The mean age of the "peak"-nesters was 4.0 (3-6) and that of the "late"-nesters 4.4 years (2-7). One of the three year old "peak"-nesting gulls was in immature plumage, as was the two year old "late"-nesting gull. Combined with all other gulls which were trapped and aged by plumage, 18% of the "peak"-nesters (n = 11) and 36% of the "late"-nesters (n = 28) were in subadult plumage. This difference was not significant ($X^2 = 1.14$). No adult: adult plumaged pairs were observed on known "late" nests.

3.5. Physiological condition

3.5.1. Body weight and condition index

Weights of captured gulls are summarized in Table 17. One-tailed tests of significance are used here, as I assumed "peak"-breeding gulls to be in better condition than "late"-breeding gulls. Of the total number of birds trapped, males were heavier than females both years ($p < 0.10$, NS, 1978, $p < 0.005$, 1979, Mann Whitney U Test). "Peak"-nesting males and females in 1979 were significantly heavier than "late" individuals of the same sex (Table 17).

The condition index, a parameter which takes structural size into account, was significantly larger in "peak" than "late" gulls of each sex.

3.5.2 Metabolite levels in blood plasma

The nutritional status of a gull was assessed using various blood chemistry parameters (Table 18). Sexes were not separated for analysis due to the small sample size and the apparently similar contribution of both sexes to incubation. Levels of urea, calcium and thyroxine were significantly higher in "late"-nesting gulls, while glucose levels were significantly lower. Cholesterol was substantially elevated in "late"-nesting gulls.

3.5.3 Hormone levels in blood plasma

"Late"-nesters tended to have higher progesterone levels

Table 17. Weights and condition indices of "peak"- and "late"-nesting Ring-billed Gulls, 1978 and 1979.

	Peak	Late	Significance[a]
MALE			
Weight 1978	540.0 (445-570) 14[b]	-----[c]	
1979	601.5 (530-650) 8	550.0 (430-590) 10	$p < 0.05$
Condition index			
1979	4.40 (4.16-4.87) 7	4.14 (4.12-4.21) 3	$P < 0.05$
FEMALE			
Weight 1978	470.0 (420-545) 18	-----	
1979	506.0 (470-555) 5	463.0 (405-530) 12	$p < 0.005$
Condition index			
1979	4.29 (4.14-4.73) 3	3.68 (3.31-4.24) 7	$p < 0.05$

a Mann-Whitney U Test

b Median (range) n

c No data

Table 18. Medians of metabolite and thyroxine levels for "peak"- and "late"-nesting Ring-billed Gulls, 1979.

	Peak[a] (9)[b]		Late (10)		Significance[c]
Urea mg/100 ml	3.6	(0.9-6.1)	4.2	(2.1-9.9)	$p < 0.05$
Uric Acid mg/100 ml	16.8	(7.4-32.7)	16.2	(5.3-31.8)	NS[d]
Total Protein g/100 ml	4.1	(3.1-5.8)	4.4	(2.5-5.1)	NS
Amino Nitrogen mg/100 ml	7.5	(5.0-9.8)	7.5	(5.5-14.1)	NS
Cholesterol mg/100 ml	348.0	(318.0-601.0)	364.5	(295.0-456.0)	NS
Triglycerides mg/100 ml	67.0	(21.0-286.0)	73.0	(33.0-390.0)	NS
Calcium mg/100 ml	9.3	(8.5-11.3)	10.2	(9.5-14.2)	$p < 0.025$
Glucose mg/100 ml	425.0	(360.0-505.0)	342.5	(260.0-495.0)	$p < 0.05$
Thyroxine (T_4) ug/ml	13.6	(10.0- 21.6)	19.0	(8.4-23.2)	$p < 0.05$

[a] One gull was excluded from analysis as she had not yet completed her clutch when trapped.

[b] (n)

[c] Mann- Whitney U Test, 1-tailed

[d] No significant difference

than "peak"-nesters, regardless of sex, but the differences were not statistically significant (Table 19). Estrogen levels in "peak" males were significantly higher than in "late" males with a similar but not significant result in the females. There were no significant differences in blood androgen or corticosterone between birds of either sex regardless of the time of clutch initiation.

3.5.4. Appearance of brood patch

All but two "peak"-nesting gulls (n = 11, 82%) had large, well-vascularized brood patches. The two exceptions were banded second year males with black tail-bands, both in their first week of incubation (Appendix 10). Feather papillae generally appeared on the edges of the brood patch in the second week of incubation although there was much individual variation.

Only four of 21 "late"-nesting gulls (19%) had large, well-vascularized brood patches without any refeathering. These included two females and a male in immature plumage and one female in adult plumage. All were in week one of incubation. The remainder of the brood patches examined were all refeathering, some with only a few feather papillae, others with extensive refeathering. The difference in brood patch development between "peak" and "late" nesters was significant ($X^2 = 11.79$, $p < 0.001$).

Table 19. Blood level comparisons of steroid hormones from "peak"- and "late"-nesting Ring-billed Gulls, 1979.

	Progesterone ng/ml	Estrogen pg/ml	Androgen ng/ml	Corticosterone ng/ml
Peak Male (7)[a]	1.4 (0.6-2.6)	180 (120-230)	0.41 (0.11-1.20)	15.0 (2.8-26.9)
Late Male (3)	2.0 (1.8-2.1)	120 (110-150)	0.53 (0.37-0.62)	15.7 (9.1-17.0)
Significance[b]	NS[c]	$p < 0.05$	NS	NS
Peak Female (2)	1.4 (1.0-1.8)	180 (171-180)	0.36 (0.18-0.36)	18.3 (18.3-19.3)
Late Female (6)	3.8 (0.3-6.3)	140 (130-210)	0.52 (0.08-0.72)	18.6 (13.6-27.0)
Significance	NS	NS	NS	NS

a (n)

b Mann-Whitney U Test

c No significant difference

4. Discussion

4.1. Reproductive Success

4.1.1. Human disturbance

Adverse effects of human disturbance on the reproductive success of gulls have previously been demonstrated (Kadlec and Drury 1968, Hunt 1972, Robert and Ralph 1975, Gillett *et al*. 1975, Hand 1980). I believe that disturbance in 1978 had a definite impact on the breeding success of "peak"-nesting gulls for the following reasons: 1) performance of an additional project on the summit study area necessitated entrance to the colony in periods of my absence; 2) construction of fences around groups of nests and 3) measuring various growth parameters of chicks all contributed to time spent in the colony.

The first two reasons mentioned above involved disturbance during the incubation period, a time when productivity could be affected due to loss of eggs or their failure to hatch (Robert and Ralph 1975). Disturbance after hatch generally causes frightened chicks to run into other territories and be attacked by adults (Ashmole 1963, Robert and Ralph 1975). In 1978, five growth parameters were measured and even though I moved quietly and bent over while retrieving the chicks, much pecking of chicks occurred as a result of my presence. The additional project in the area also caused disturbance during this period. Chicks were often unable to escape attacks of neighbouring gulls as they invariably ran into a fence. Nisbet and Drury (1972) found the overall effects of small fences to be negligible in a study of Common Terns and Roseate Terns (*Sterna dougallii*). However, my observations showed otherwise. Using the experience gained in 1978, every effort was made to minimize disturbance in 1979. This included a reduction in the total sample of "peak" clutches, less frequent nest checks, construction of larger enclosures which took little time to construct, and measurement of only one growth parameter - chick weight. The resulting decrease in disturbance may have been a factor contributing to the increase in both hatching and fledging success in 1979.

4.1.2 Clutch size and egg size

Clutches laid late in the season were significantly smaller than those laid earlier in the season. This was also found by Coulson and White (1961), Parsons (1975), Ryder (1975), Chardine (1978) and Somppi (1978) in their studies of larids. Egg size in larids also tends to decrease as the breeding season progresses (Coulson 1963, Coulson *et al*. 1969, Parsons 1970, 1972, this study). In larids c-eggs are usually smaller than a- and b- eggs (Preston and Preston 1953, Coulson 1963, Parsons 1972, Davis 1975, Schreiber *et al*. 1979). However, although these differences were evident in "peak" clutches of Ring-billed Gulls, they were absent in "late" three-egg clutches. Mills (1979) has shown that factors affecting egg size and clutch size of Red-billed Gulls (*Larus novaehollandiae scopulinus*) are linked. One correlation he noted was a decreasing volume of two-egg clutches and an increasing number of one-egg clutches later in the season. Perhaps, as suggested by Parsons (1975), there is a minimum size at which a follicle will rupture. If a female cannot produce a second or third follicle of a sufficient size to rupture, a smaller clutch size will result.

The smaller egg width in "late" clutches of Ring-billed Gulls in this study resulted in a smaller shape index than that found in eggs from "peak" clutches. This may reflect the age or breeding experience of the "late"-nesting gulls as older birds tend to have more spherical eggs (Richdale 1955, Coulson 1963), largely because of the muscular tone of the oviduct (Romanoff and Romanoff 1949).

4.1.3. Incubation behavior

"Peak"-breeding gulls had a significantly longer incubation period than "late"-breeding gulls in 1978 while there was no difference in 1979. Parsons (1972) noted that smaller Herring Gull eggs required less time for incubation while Schreiber et al. (1979) found no such trend in Laughing Gull eggs (Larus atricilla). My results agreed with the former in 1978 and with the latter in 1979. More frequent disturbance in 1978 may be a contributing factor to the longer incubation period in this year. Thus sample size and lack of consistency tend to obscure any biological significance in my data. Percentage of time spent sitting on the nest was the same for "peak"- and "late"-nesting gulls in each year of my study. Morris and Haymes (1977) and Somppi (1978) found no difference in attentiveness of Common Terns and Ring-billed Gulls, respectively, with regard to clutch size or time of clutch initiation. However, I did record a difference in behavior of gulls on the nest. Though limited, my data suggest that "late"-breeders are more restless on the nest. The most important tactile and thermal sensors are the receptors located in the brood patches. "If nest conditions do not send back the necessary stimulation after quivering has been affected, then rising is activated and settling repeated" (Beer 1961). Perhaps "late"-nesting gulls receive insufficient stimuli from the eggs, resulting from: 1) a smaller clutch and egg size, 2) poorly developed and thus less sensitive brood patches, 3) lack of breeding experience of the adult (Drent 1972), or a combination of all these factors. One would expect a higher rate of desertion in birds receiving insufficient stimuli; this effect did indeed occur in the "late"-nesting gulls.

Efforts at trapping may also reflect the attentiveness of these birds. "Peak"-nesting birds were usually incubating within one to two minutes after the trap was placed over their eggs: these birds generally walked around the trap once then walked in. None of these gulls deserted after trapping.

"Late"-nesting gulls were relatively difficult to capture: they walked around the trap repeatedly, began to enter on several occasions, pulled back, and stood nearby. These gulls were usually impossible to trap after 7-10 days of incubation. At this time, "peak"-breeders were feeding young, thus social stimulation may be a contributing factor here (Somppi 1978). Additionally, three of the "late"-nesting gulls which were trapped, and one pair that I attempted, unsuccessfully, to trap, deserted two days later. This could suggest, as well, that any disturbance to the "late"-nesting gulls in this study is detrimental to their nesting success.

4.1.4. Hatching success

As reported by Ryder (1976) and Somppi (1978), "peak" clutches had a significantly higher hatching success than "late" clutches each year. Some of this difference may have been due to clutch size, as three-egg clutches had the highest hatching success. If clutch size was the major factor contributing to hatching success, then success for "peak" and "late"-nesting gulls with the same clutch sizes should be equal. However, this was not the case. Age may be one explanation for this as hatching success is lower in young kittiwakes (Coulson and White 1958), Herring Gulls (Drent 1972, Parsons 1975) and Ring-billed Gulls (Ryder 1975) relative to older birds. However, not all the "late"-nesting birds appeared to be younger. It is possible that "late"-nesting Ring-billed Gulls are on average younger than earlier nesters but do not exhibit immature plumage (Chardine 1978).

Some of the "late"-nesters which were successful in hatching their eggs may have been repeat layers with more breeding experience than that of gulls laying their first clutches at the same time (observed in female kittiwakes by Wooler 1980). I did not have a sufficiently large sample of banded birds to determine the frequency of renesters on

Granite Island. A second clutch was noted in the original or renovated nest only four times - a criterion for renesting in Herring Gulls (Parsons 1976). Vermeer (1970) reported a very low incidence of renesting in Ring-billed Gulls.

Colony synchrony is another factor influencing hatching success. "Late"-nesters were spaced over the entire colony and initiated their clutches in a period of two to four weeks long, at a time when "peak"-nesters had already been incubating for a few weeks. While these birds were in the first half of the incubation period the stimulus to stay on the nest would be low since the majority of other adults would have finished incubating (Somppi 1978). Parsons (1975) suggested that Herring Gull eggs that are laid when most laying occurs are the most likely to hatch. He noted a selection against any deviation from the main peak of laying, be it early or late, which would maintain breeding synchrony. Thus, lack of synchronization could be a major reason for the poor success experienced by the "late"-nesting Ring-billed Gulls on Granite Island.

Lower hatching success in "peak" 1978 nests (compared to "peak" 1979) was likely a result of greater disturbance. This seems to have two main effects: firstly, eggs are knocked out of a nest when an incubating bird suddenly takes flight, secondly, exposed eggs are exposed to predation from other gulls. These observations were also reported by Robert and Ralph (1975) and Schreiber (1979), respectively. Disappearance of "late"-laid eggs each year may ultimately have occurred as a result of restlessness and desertion. These gulls may have been subject to intrusions from earlier nesting adults and their chicks (Somppi 1978) or they may have found it difficult to obtain sufficient food, thus requiring longer foraging times than more efficient feeders. Newton (1979) noted that a bird subject to food shortage may desert its eggs, leaving them more susceptible to predation.

Incubating eggs artificially is one way in which parental care and natural environmental variables can be excluded from factors contributing to hatching success. In 1978 artificially incubated "peak" eggs had a far greater success than eggs in the field, indicating that hatching was probably affected by disturbance, as previously discussed (Section 4.1.1.). In 1979 a similar percentage of eggs hatched in the field and in the incubator possibly indicating that the disturbance had been reduced and/or removed. The lower hatching success of "peak" eggs in the incubator in 1979 as compared to 1978 may have resulted from jarring of the eggs while in transport or from unknown factors within the incubator itself. "Late" eggs had a significantly greater hatching success when artificially incubated each year. This implies inadequate parental incubation in "late" nests. In addition, the low percentage of "late" eggs hatching in the incubator relative to "peak" eggs suggests that the quality of the egg itself is poor.

4.1.5. Survival of chicks

In both 1978 and 1979 fledging success was higher for nests initiated earlier in the season. This is in accordance with previous findings (see Vermeer 1970) and has been attributed by several authors (as described in Section 1.) to interrelated factors including synchronization of nesting, nest location, previous breeding experience and variations in available food supply as well as foraging efficiency of the adults. I found that "late"-hatching Ring-billed Gull chicks tended to be smaller at hatch than "peak"-nesters in the parameters I measured, but were of equal or slightly larger size by 10 days of age. The difference in weight between "peak" and "late" chicks was larger in 1978 than in 1979. Some of this difference may have resulted from increased disturbance to "peak"-nesting gulls in 1978 (Section 4.1.1.), which in turn could have affected growth of their young.

The statistical differences found in the regression lines between "peak" and "late" chicks must also be assessed biologically as I am actually looking for a trend in a biological growth process. Ricklefs (1968) noted similar growth in early and late broods of the Starling (*Sternus vulgaris*) and Great Tit (*Parus major*) but noted a lower asymptote in late broods. Unfortunately I did not obtain growth rates past the linear portion of the growth curve thus the weight at which chick growth levelled off is unknown. I consider it likely that "late"-hatched chicks made their first flights at a lighter weight, and possibly a younger age than earlier chicks. This is supported by the observation that "late" chicks began feathering at a younger age than earlier chicks. This would undoubtably affect their post-fledging success (suggested also for other species c.f., Perrins 1965, Great Tit; Perrins *et al.* 1973, Manx Shearwater, *Puffinus puffinus*; O'Connor 1976, Blue Tit, *Parus caeruleus*; Hedgren and Linnman 1979, Guillemot, *Uria aalge*). The results in this study do illustrate an important point, that "late"-nesting adults feed their chicks as well as "peak"-nesting adults. Chick mortality in "late" nests peaked in the first few days after hatch. This may have resulted from an inadequate parental behavioral transition from incubation to care of the young and/or insufficient nutrient reserves in the eggs. Additional study of Ring-billed Gulls may show that the difference in fledging success between "peak"- and "late"-hatched chicks is minimal, with differences in reproductive success being related primarily to hatching success. Lower hatching success could also result from a new pair-bond (Coulson 1966, Mills 1973), especially in pairs containing new breeders (Brooke 1978).

4.2. Age of gulls

Small sample sizes of known-age birds nullified any existing differences in age between "peak"- and "late"-nesting Ring-billed Gulls. However, no adult: adult plumaged pairs were seen on known "late" nests. Ryder (1975) found that pairs of Ring-billed Gulls which contained at least one immature-plumaged individual started nesting activities later in the season and laid smaller eggs which were less likely to hatch than pairs composed of two mature-plumaged gulls. Haymes and Blokpoel (1980) found that as age increased, Ring-billed Gulls laid consistently earlier in the season and that hatching success of young birds, but not of old birds, declined substantially in the late period. Thus younger age and lack of breeding experience appear to be among the factors retarding clutch initiation and reducing breeding success of "late"-nesting Ring-billed Gulls.

4.3. Egg quality and condition of adults

The higher Ratcliffe Index in "late" eggs may indicate a lower shell density than that of "peak" eggs. However, there was no statistical difference in eggshell thickness, thus rendering interpretation difficult at this point.

The significant difference in dry albumen weight between "peak"- and "late"-eggs paralleled the difference in egg size between these two groups, with smaller ("late") eggs containing less albumen. Variation in egg size in the Great White Pelican (Pelecanus onocrotalus) also depends mainly on the amount of albumen laid down (Jones 1979) as it does in the Starling (Ricklefs 1977a) and the Herring Gull (Parsons 1976). The lower albumen content in "late" eggs may imply that the female Ring-billed Gulls are not obtaining enough nutrients at the time of egg-laying. This could result from nutrient deprivation because of the inept foraging of their partners (mentioned previously) or themselves. Nisbet (1977, 1978) found that egg size differences between two colonies of Common Terns were associated with a greater food intake by females at the time of egg-laying. In Common Terns, quantity as well as quality of food received by the female is reflected in their eggs (Nisbet 1978). However, the critical lower limit of albumen, a level known to have deleterious biological implications has not been documented. Thus it cannot be ascertained as to how the reduced amounts of albumen found in "late" Ring-billed Gull eggs in this study affected embryonic development and egg hatchability.

Changes in body weights provide an approximate index of the metabolic resources of an organism (Korschgen 1977) but there is often considerable variation of weight between individuals at the same point in the reproductive cycle. For this reason, condition indices have been used to adjust body weights of birds with regard to structural size differences which theoretically should reflect the relative fitness of individuals with respect to energy reserves (Bailey 1979).

On average, throughout the nesting season, "late"-nesting Ring-billed Gulls had significantly lower condition indicies than "peak"-nesting gulls, indicating that "late"-nesters had poorer energy reserves. This could result from a smaller relative food intake or greater energy expenditure during the pre-breeding period. Unfortunately the blood data cannot be interpreted at this time as a result of the inherent field sampling problem. Ideally the samples should have been taken on the same day of the nesting cycle.

Development of brood patches in gulls begins before egg-laying and is complete about the time that the last egg is laid (Paludan 1951, Beer 1961, 1963). Full development of brood patches may depend on a sequential action of estrogen, progesterone and prolactin (Selander and Kuich 1963) although it is possible that other hormones (e.g., coricoids, growth hormone, insulin) also play a role in brood patch development as they do in mammary gland development (Bern and Nicoll 1968 cited in Jones 1971). Prolactin and estrogen work together to influence feathering in the Ruffed Grouse (*Bonasa umbellus*) (Etches *et al.* 1979), icterids (Selander and Kuich 1963) and passerines (Bailey 1952). High prolactin levels maintain brood patch development in the Ruffed Grouse (Etches *et al.* 1979). Silver and Buntin (1973) noted that it is the ratio of progesterone:estrogen that is important in brood patch formation and crop growth in Ring Doves (*Streptopelia risoria*), a species in which prolactin does not play a role in brood patch formation. Perhaps the poor development of brood patches in "late"-nesters results from a non-optimal ratio of progesterone:estrogen. The altered progesterone and estrogen levels in "late"-breeding gulls, as compared with "peak"-breeding gulls may be a cause of the poor quality of their brood patches.

External factors become a dominant force in the regulation of hormone levels as incubation proceeds (Emlen and Miller 1969). Environmental change can cause a decrease in prolactin from the very high levels of a brooding hen to levels in the range of laying birds in 24 hours or less (Burke and Dennison 1980). "Late"-breeding gulls may get environmental cues from near-by nests with chicks, thus a conflict in stimuli arises between incubating and brooding.

4.4. Concluding discussion

Analysis of the data collected indicates to the author that the difference in sampling area and time period between years did not influence the conclusions drawn. The results obtained in this study confirmed previous reports that "late"-nesting colonial nesting pairs of birds have smaller clutches, egg size and lower hatching success than earlier nesting pairs. Chick mortality in the first few days post-hatch was higher in "late"-nests than in "peak"-nests. This may result from an inadequate behavioral transition of the parents from incubating to feeding of the chicks, or to factors intrinsic to the egg itself. After the first three to four days the survival potential of chicks was comparable regardless of the time of hatch. The results of this study indicate that contributing factors to the differential reproductive success are: 1) "late"-nesting gulls have suboptimal incubation behavior, they are more restless on the nest than earlier breeding pairs and have higher desertion rates, and 2) "late"-nesting gulls are affected by social cues given by the activities of earlier nesting gulls.

The above mentioned factors contributing to the differential reproductive success indicate that environmental cues from the activities of "peak"-breeding gulls affect the incubation behavior of "late"- breeding birds. It has previously been reported that performance of courtship or nesting behavior by one or more pairs can stimulate other pairs to do likewise (Brown 1967b, Emlen and Miller 1969, Southern 1974). Lehrman (1959) noted that environmental stimuli such as that provided by the mate and/or young, the activities of the other birds and the nest and/or eggs, can actually stimulate changes in hormone secretion and thus form part of the cause for the succession of changes in physiological state. Thus it appears that the desertion and restlessness shown by the "late"-breeding gulls in this study results in part from the cues they receive from near-by adults with chicks (Somppi 1978). It must also be noted that amongst "late"-breeding birds, disturbance, whether by humans or other predators, may contribute to desertion, as other adverse environmental cues are also affecting them at this time of the season.

I have not found any differences in age of "peak"- and "late"-nesting Ring-billed Gulls on Granite Island but this results from the small sample of known-age birds which I was able to obtain. However, there were plumage differences, and although this is not a reliable aging criterion it does give a relative indication of age. No adult: adult plumaged pairs were observed on known "late" nests (using the criteria of plumage mentioned herein). This could affect the timing of breeding of these pairs in that the gonadal maturation may enable a slightly earlier start each year with increased age or breeding experience of the bird (Coulson and White 1958, Coulson 1966, Mills 1973). Rohwer and Rohwer (1978), through the manipulation of plumage patterns, have supported the conclusion that plumage "improvement" must be backed up by behavioral alterations for a real social promotion to be achieved (Ulfstrand 1979). This suggests that young, aged or other non-"prime" birds (physiologically inferior) may have a reduced social status resulting from their less aggressive behavior. This may also force the individuals to nest later in the season.

The last factor I wish to discuss involves the condition of the adults. "Late"-nesters had a significantly lower condition index than "peak"-nesting pairs, indicating fewer body reserves. The gulls' physiological condition at the time of laying is also reflected in their eggs. The smaller egg size of "late"-nesting Ring-billed Gulls in this study resulted from smaller amounts of albumen deposited in the egg rather than to variations in the size of the yolk. In the Starling this has been related to the weight of the oviduct (Ricklefs 1976). In the domestic fowl the oviduct is more sensitive than the ovary to factors adversely affecting egg formation (Romanoff and Romanoff 1949). Thus under non-optimal conditions the amount of albumen secreted would be affected before the size of the yolk.

In summary, more work could be done on the actual physiological condition of "late"-nesting birds. If standardized, blood tests may indicate altered hormone levels. This could affect egg production, mostly albumen secretion (Taylor 1970, Turner and Bagnara 1976, Kissel *et al*. 1970). Analysis of various body tissues would indicate whether or not the individuals were undergoing nutritional stress. Further work on age structure and social cues and how they affect hormonal levels would also contribute to an understanding of the timing of breeding and the resulting reproductive success.

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Appendix 1. Growth in culmen length (mm) of "peak"- and "late"-hatched chicks, 1978.

	Culmen	
Age	Peak	Late
0[a]	15.3 ± 1.7 (68)[b]	15.9 ± 0.9 (18)
1	16.1 ± 1.6 (43)	16.4 ± 0.9 (14)
2	17.9 ± 0.8 (28)	18.3 ± 1.5 (8)
3	16.8 ± 0.1 (31)	16.9 ± 1.2 (13)
4	17.0 ± 0.2 (17)	18.2 ± 1.1 (8)
5	19.1 ± 1.4 (12)	19.8 ± 2.1 (5)
6	20.6 ± 0.9 (16)	20.9 ± 1.8 (7)
7	21.5 ± 1.3 (21)	21.9 ± 1.6 (10)
8	21.3 ± 1.1 (25)	23.2 ± 2.9 (10)
9	22.6 ± 1.6 (26)	23.4 ± 1.8 (9)
10	23.2 ± 2.2 (21)	25.3 ± 0.4 (3)
11	23.4 ± 1.7 (15)	25.1 ± 0.7 (3)
12	24.6 ± 1.9 (22)	23.7 ± 2.9 (4)
13	25.0 ± 1.2 (19)	27.0 (1)
14	24.8 ± 1.5 (19)	25.2 ± 2.9 (6)
15	25.9 ± 1.4 (22)	28.1 (1)
16	25.8 ± 1.6 (22)	26.7 ± 3.1 (5)
17	25.8 ± 1.3 (14)	----
18	26.5 ± 1.7 (14)	30.7 ± 1.2 (2)
19	27.0 ± 1.4 (14)	----
20	27.7 ± 1.6 (12)	----
21	28.1 ± 1.4 (10)	----

[a] Day 0 is the day of hatch

[b] Mean ± SD (n)

Appendix 2. Growth in gonys (mm) of "peak"- and "late"-hatched chicks, 1978.

Age	Gonys Peak	Gonys Late
0[a]	6.0 ± 0.3 (67)	6.2 ± 0.4 (18)
1	6.4 ± 0.3 (43)	6.5 ± 0.3 (14)
2	6.9 ± 0.3 (28)	6.9 ± 0.5 (8)
3	6.5 ± 0.3 (31)	6.7 ± 0.4 (13)
4	6.7 ± 0.3 (17)	6.9 ± 0.5 (8)
5	7.2 ± 0.3 (12)	7.4 ± 0.6 (5)
6	7.6 ± 0.5 (16)	7.6 ± 0.6 (7)
7	7.8 ± 0.4 (21)	7.7 ± 0.5 (10)
8	7.8 ± 0.3 (25)	7.9 ± 0.6 (10)
9	8.0 ± 0.3 (26)	8.2 ± 0.5 (9)
10	8.1 ± 0.4 (21)	8.5 ± 0.1 (3)
11	8.3 ± 0.4 (15)	8.3 ± 0.4 (3)
12	8.7 ± 0.4 (22)	8.2 ± 0.8 (4)
13	8.7 ± 0.4 (19)	8.9 (1)
14	8.8 ± 0.5 (19)	8.5 ± 0.6 (6)
15	9.0 ± 0.3 (22)	8.7 (1)
16	9.2 ± 0.4 (22)	8.7 ± 0.6 (5)
17	9.2 ± 0.5 (14)	---
18	9.3 ± 0.5 (14)	9.2 ± 0.6 (2)
19	9.5 ± 0.6 (14)	---
20	9.5 ± 0.5 (12)	---
21	9.6 ± 0.6 (10)	---

[a] Day 0 is the day of hatch

[b] Mean ± SD (n)

Appendix 3. Growth of gape (mm) in "peak"- and "late"-hatched chicks, 1978.

Age	Gape	
	Peak	Late
0[a]	23.3 ± 1.6 (61)[b]	24.1 ± 1.4 (18)
1	23.8 ± 2.0 (43)	25.1 ± 1.5 (14)
2	28.4 ± 1.4 (28)	27.9 ± 1.8 (8)
3	25.5 ± 1.5 (31)	25.9 ± 1.6 (13)
4	27.6 ± 2.9 (17)	27.0 ± 1.5 (8)
5	30.1 ± 1.8 (12)	30.5 ± 2.6 (5)
6	30.6 ± 1.3 (16)	31.4 ± 1.6 (7)
7	33.2 ± 1.4 (21)	33.2 ± 1.3 (10)
8	33.4 ± 2.7 (25)	33.6 ± 1.6 (10)
9	35.2 ± 1.6 (26)	35.0 ± 1.9 (9)
10	36.0 ± 1.7 (21)	37.0 ± 0.4 (3)
11	36.8 ± 1.3 (15)	38.6 ± 1.1 (3)
12	38.6 ± 2.1 (22)	37.9 ± 2.9 (4)
13	39.5 ± 1.8 (19)	40.6 (1)
14	40.0 ± 2.1 (19)	40.0 ± 2.4 (6)
15	41.7 ± 1.8 (22)	42.3 (1)
16	41.9 ± 2.1 (22)	43.6 ± 2.2 (5)
17	42.5 ± 1.8 (14)	----
18	43.2 ± 2.4 (14)	44.5 ± 2.3 (2)
19	43.8 ± 1.8 (14)	----
20	45.2 ± 1.4 (12)	----
21	45.3 ± 2.6 (10)	----

[a] Day 0 is the day of hatch

[b] Mean ±SD (n)

Appendix 4. Growth of tarsus (mm) in "peak"- and "late"-hatched chicks, 1978.

Age	Tarsus: Peak	Tarsus: Late
0[a]	26.8 ± 2.0 (68)[b]	25.8 ± 1.6 (18)
1	28.3 ± 1.9 (43)	26.6 ± 1.7 (14)
2	30.4 ± 1.8 (28)	30.4 ± 2.9 (8)
3	29.1 ± 2.6 (31)	27.8 ± 2.1 (13)
4	29.3 ± 1.6 (17)	29.6 ± 2.5 (8)
5	33.2 ± 2.0 (12)	32.5 ± 2.5 (5)
6	36.2 ± 1.9 (16)	35.2 ± 2.5 (7)
7	37.7 ± 2.6 (21)	37.5 ± 2.8 (10)
8	38.4 ± 2.5 (25)	39.4 ± 2.5 (10)
9	41.0 ± 2.3 (26)	41.4 ± 3.5 (9)
10	41.7 ± 2.5 (21)	45.3 ± 1.5 (3)
11	43.1 ± 2.2 (15)	45.7 ± 1.3 (3)
12	45.9 ± 2.8 (22)	42.4 ± 3.7 (4)
13	47.2 ± 2.7 (19)	47.8 (1)
14	47.6 ± 3.9 (19)	47.5 ± 2.9 (6)
15	48.7 ± 2.4 (22)	50.8 (1)
16	49.7 ± 2.8 (22)	50.5 ± 3.1 (5)
17	50.4 ± 3.6 (14)	----
18	50.9 ± 3.1 (14)	54.3 ± 1.7 (2)
19	52.4 ± 1.7 (14)	----
20	52.8 ± 3.7 (12)	----
21	53.5 ± 3.8 (10)	----

[a] Day 0 is the day of hatch

[b] Mean ± SD (n)

Appendix 5. Weight (g) of "peak"- and "late"-hatched chicks, 1978.

Age	Weight	
	Peak	Late
0[a]	39.6 ± 3.8 (68)[b]	42.5 ± 6.3 (18)
1	44.2 ± 5.5 (43)	47.6 ± 8.4 (14)
2	77.9 ± 11.9 (28)	74.0 ± 21.8 (8)
3	53.9 ± 8.2 (31)	52.8 ± 13.3 (12)
4	65.8 ± 12.2 (17)	68.4 ± 20.7 (8)
5	103.2 ± 18.9 (12)	107.6 ± 14.5 (5)
6	133.1 ± 22.4 (16)	120.1 ± 19.5 (7)
7	144.7 ± 19.5 (21)	145.2 ± 22.2 (10)
8	155.9 ± 19.1 (25)	159.1 ± 26.1 (10)
9	173.2 ± 26.7 (26)	181.7 ± 31.9 (9)
10	188.6 ± 28.1 (21)	214.3 ± 16.0 (3)
11	200.7 ± 29.2 (15)	245.3 ± 21.2 (3)
12	233.6 ± 35.3 (22)	233.0 ± 46.4 (4)
13	257.5 ± 30.7 (19)	300.0 (1)
14	252.3 ± 55.1 (19)	293.5 ± 41.6 (6)
15	274.5 ± 43.0 (22)	352.0 (1)
16	291.1 ± 41.7 (22)	320.0 ± 43.8 (5)
17	290.1 ± 55.1 (14)	-----
18	311.3 ± 48.1 (14)	368.5 ± 13.4 (2)
19	326.8 ± 43.0 (14)	-----
20	349.6 ± 50.5 (12)	-----
21	340.2 ± 50.2 (10)	-----

[a] Day 0 is the day of hatch

[b] Mean ± SD (n)

Appendix 6. Weight (g) of "peak"- and "late"-hatched chicks, 1979.

Age	Weight Peak	Weight Late
0[a]	41.3 ± 3.5(107)[b]	39.6 ± 3.9 (19)
1	47.8 ± 4.9 (89)	43.4 ± 6.8 (11)
2	58.3 ± 7.9 (51)	60.1 ± 7.9 (14)
3	72.8 ± 10.3 (33)	67.8 ± 15.9 (11)
4	99.6 ± 0.5 (14)	104.5 ± 37.5 (6)
5	119.6 ± 20.4 (18)	99.1 ± 11.0 (10)
6	143.2 ± 4.9 (5)	133.3 ± 10.8 (6)
7	162.4 ± 35.5 (7)	147.7 ± 24.3 (6)
8	165.2 ± 38.5 (11)	188.0 ± 10.5 (3)
9	189.5 ± 36.5 (28)	200.2 ± 29.4 (4)
10	202.7 ± 54.4 (21)	226.6 ± 54.1 (5)
11	241.3 ± 51.4 (19)	278.0 ± 39.0 (4)
12	274.8 ± 28.5 (2)	243.8 ± 53.7 (4)
13	282.8 ± 20.9 (13)	339.6 ± 31.0 (3)
14	305.6 ± 33.7 (19)	314.7 ± 22.3 (3)
15	341.3 ± 36.8 (17)	367.3 ± 24.5 (3)
16	329.5 ± 38.1 (19)	300.0 (1)
17	348.8 ± 33.6 (16)	335.0 (1)
18	362.4 ± 30.8 (13)	385.2 ± 52.1 (4)
19	395.1 ± 33.6 (16)	389.7 ± 78.2 (3)
20	410.2 ± 45.1 (9)	-----
21	364.6 ± 58.3 (10)	485.0 (1)

[a] Day 0 is the day of hatch

[b] Mean ± SD (n)

Appendix 7. Comparison of regression lines for growth of "peak" and "late" Ring-billed Gull chicks, Granite Island, 1978 and 1979.

		Peak	Late	F Value	Confidence interval for difference between slopes (α = 0.05)
1978	Culmen length[a]	$y = 17.2 + 0.5X$	$y = 17.2 + 0.7X$	23.44[b]	(-0.0251, -0.0017)[d]
	Gonys	$y = 6.6 + 0.1X$	$y = 6.9 + 0.1X$	2.42, NS[c]	
	Gape	$y = 25.9 + 0.9X$	$y = 24.9 + 1.1X$	8.09[b]	(-0.0275, -0.0055)[d]
	Tarsal length	$y = 28.7 + 1.2X$	$y = 26.5 + 1.5X$	5.65[b]	(-0.0579, -0.0143)[d]
	Weight	$y = 38.1 + 15.3X$	$y = -6.2 + 21.7X$	20.08[b]	(-8.5190, -4.3100)[d]
1979	Weight	$y = 35.2 + 18.3X$	$y = 7.7 + 21.7X$	3.32[b]	(-6.8699, 0.0039)

[a] Measurement are in mm; weight is in g.

[b] Indicates a significant difference between the two regression lines.

[c] No significant difference

[d] Indicates a significant difference in slope.

Appendix 8. Leg band number, nest, sex, year banded and age of "peak"-nesting Ring-billed Gulls, 1978.

Band number[a]	Nest	Sex	Year banded	Age in 1978
725-42919			1973	--[b]
725-66507			1973	5
725-66666		M	1973	5
725-66724	SC[c]	F	1973	5
725-66775	SC	F	1973	5
725-74018			1972	6
725-74093	37	M	1971	7
725-74459		F	1972	6
725-77033		F	1973	5
725-77205		M	1972	6
755-42601			1973	5
755-42632	38	M	1973	5
755-42736		M	1973	5
755-42737		M	1973	5
755-42884	SC		1973	5
755-42919	37	F	1973	--
755-42921			1973	--
755-42945		F	1973	--
765-72404	118	F	1976	2

[a] All gulls were banded as chicks with a United States Fish and Wildlife Service Standard band on Granite Island.

[b] These gulls were banded as adults.

[c] Superclutches

Appendix 9. Leg band number, nest, sex, year banded and age of "peak"- and "late"-nesting Ring-billed Gulls, 1979.

Band number	Nest	Sex	Year banded	Age in 1978
Peak				
725-66579		F	1973	6
765-72471		M	1976	3
805-11769[a]		M	1976	3
Late				
725-77111	37	F	1972	7
755-44947	117	F	1976	3
765-70333	8	M	1977	2
765-72425	11	M	1976	3
795-44589[a]	64	F	1972	7
795-77027[b]	24	M	1978	---

[a] These gulls were banded on Granite Island; 805-11769 was banded as a chick near Rogers City, 795-44589 was banded near Toronto, Ontario.

[b] This gull was banded as an adult

Appendix 10. Appearance of brood patches of "peak"- and "late"-nesting Ring-billed Gulls, 1979.

	Peak			Late		
	Week 1[a]	Week 2	Week 3	Week 1	Week 2	Week 3
large, well vascularized	4		1	4		
OK, 1/3 refeathered[b]	1	2	1	4	4	
almost completely refeathered[c]				1	2	
small, not well vascularized, 1/3 refeathered				5		
small, 1/3 refeathered		1				
small, flakey[d]	1				1	

[a] Week of incubation, taken from the date of clutch completion.

[b] Pin feathers with sheaths only partly opened.

[c] Down feathers

[d] Not well vascularized, small bits of skin flaking off.