Frontispiece

A mated pair of Ring-billed Gulls (*Larus delawarensis*) in breeding plumage, Granite Island, June 1976. Note the male, behind the female, has a longer gape and deeper gonys than the female. These are useful field characteristics.

Reproductive Performance of Ring-billed Gulls in Relation to Nest Location

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.

March, 1978

Abstract

Reproductive performance of Ring-billed Gulls (*Larus delawarensis*) in relation to nest location was investigated on Granite Island, northern Lake Superior, in 1976 and 1977. To determine whether any differences existed in the hatching and fledging success of central and peripheral areas of the colony in 1976 and 1977, only 3-egg clutches initiated early in the season were used. This eliminated two variables that may also affect success; they are clutch size and time of clutch initiation. In both years, 25 3-egg clutches in the center of the colony were exchanged with 25 3-egg clutches on the periphery. Twenty-five 3-egg clutches were marked concurrently in each area as controls. In both years, there was no significant difference in hatching success (86%), or fledging success (58%) between exchange and control nests. These results indicated the ability of the gulls to hatch eggs and raise young was not related to nest location. Ten clutches from each area which were artificially incubated, had essentially equivalent hatching success.

To determine if there was a difference in attentiveness in the two areas, 25 nests in each area were monitored photographically for 6 days during the incubation period. In both years, over 90% of the gulls incubated a minimum of 90% of the time regardless of nest location.

In 1977, histories were known for all nests in the study area. Hatching success and clutch size were not correlated with incubation attentiveness. In both the center and periphery of the colony, eggs laid before or at the peak of clutch initiation had a hatching success of 80%, 30% higher than eggs laid after the peak. Hatching success was significantly related to clutch size, 3-egg clutches being the most common (54%) and the most successful (76%) in both areas.

On Granite Island, reproductive success was related to time of clutch initiation and clutch size rather than nest location. The possible reasons for this are discussed.

Acknowledgements

I extend sincere appreciation to my supervisor, Dr. J. P. Ryder, who introduced me to the fascinating world of gulls and then provided encouragement and guidance throughout this investigation.

I thank Dr. S. G. Magwood who made it possible for me to enter graduate school and then take a leave of absence to finish the research. Dr. M. W. Lankester deserves a special thank you for his understanding and cooperation during the past two years. I appreciate the helpful criticism of Dr. R. Freitag and Dr. W. Momot, and Dr. J. Burger (Rutgers University), my external examiner.

Mr. D. Barnes and Mr. T. Carroll helped build the fences; Mr. R. Trowbridge allowed me to base operations at Bonavista; Professor B. Spenceley (Physics Department), designed the timers for the cameras and helped me to operate them, and Ms. L. Crawford assisted in the camera operation in 1977. I am grateful for their help.

I thank Ms. C. Otte for her advice on the computer programs; and Dr. Bruce Batt for allowing me to use the facilities of the Delta Waterfowl Research Station, Delta, Manitoba, in 1976.

Financial support for the electronic equipment and film was obtained from a President's N.R.C. grant to Dr. Ryder and Professor Spenceley.

Finally, I would like to thank my parents for their constant support and encouragement.

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1. INTRODUCTION

Many birds nest in discrete groups known as colonies within which there are often differences in the successful hatching of eggs and rearing of young depending on nest location (Patterson 1965). It has been reported that those birds nesting on the border or periphery of a colony are less successful at hatching eggs and raising young than those that nest in the more central parts (Coulson 1966, Dexheimer and Southern 1974). The following four hypotheses have been advanced to explain this phenomenon:

(a) Coulson et al. (1969) reported that Black-legged Kittiwakes (*Rissa tridactyla*) and Shags (*Phalacrocorax aristotelis*) nesting on the periphery of a colony laid significantly smaller eggs than birds in the center. They postulated such small eggs would have a smaller yolk which would possibly reduce the viability of the eggs.

(b) Peripheral nests may be located in sub-optimal habitat where they are exposed to flooding (Dexheimer and Southern 1974). Nests in peripheral areas may be subject to more intrusions from conspecifics that expose the eggs to predation (Spurr 1975) and temperature fluctuations harmful to the developing embryo (Baerends and Drent 1970). Inter-specific predation was primarily responsible for the reduced hatching success of peripheral-nesting Gannets (Sula bassana) (Nelson 1966b), Black-headed Gulls (Larus ridibundus) (Patterson 1965) and Royal Terns (Sterna maxima maxima) (Buckley and Buckley 1972).

(c) Coulson (1968) and Wooller and Coulson (1977) found that male Black-legged Kittiwakes nesting on the border of the colony were smaller and lighter than those in the center. They postulated there was intense competition for sites in the center, so only the most vigorous males (heavier) were successful in nesting in the center. Gulls that did not win a site in the center, were relegated to the periphery where their low success at hatching eggs reflected their poor quality (i.e. light weight).

(d) Studies of known-age birds have shown that it is primarily the younger, late-nesting birds that occupy the periphery (Sooty Terns (Sterna fuscata) (Harrington 1974), Gannets (Nelson 1966a,b), Adelie Penguins (Pygoscelis adeliae) (Spurr 1974) and Ring-billed Gulls (Larus delawarensis) (Ryder 1975). Ludwig (1974) and Ryder (1975) noted that most immature-plumaged Ring-billed Gulls nest on the fringes of the colony. Ryder (1975) said that these young gulls seemed to be less attentive to their nests with the result that the eggs were destroyed by predators, mostly Common Crows (Corvus brachyrhynchos). Therefore the reduced success at hatching eggs and raising young, often characteristic of peripheral areas, may be the result of a preponderance of young, inexperienced birds.

In view of the reported differences between the center and periphery of a colony, I hypothesized there would be a reduced ability to hatch eggs and raise young in gulls nesting on the border of a Ring-billed Gull colony on Granite Island, northern Lake Superior. My objective was to determine the reason(s) for this difference.

Previous investigations had revealed there was no difference in the amount of lipids, proteins and carbohydrates in egg yolks collected from the center and periphery of the Granite Island colony (Ryder et al. 1977). Additionally, no differences occurred in the growth and development of embryos from these two areas (Ryder and Somppi 1977). The study area was free from flooding and no mammalian predators were seen. Therefore, I decided to collect demographic data from the center and periphery of the Ring-billed Gull colony to determine if a general lack of attentiveness to the eggs on the border of the colony could explain, in part, the poor success of gulls nesting there.

2. MATERIALS AND METHODS

2.1 Definitions

Peripheral nest: A nest on the fringe of the colony, forming the border of the colony (Dexheimer and Southern 1974). The periphery therefore, is one nest deep (W. Southern, pers. comm.).

Central nest: A nest located within the border of the colony and therefore surrounded by other nests (Tenaza 1971).

Hatching success: The percent of eggs laid that hatched (Gilman et al. 1977). I assumed that eggs which pipped, subsequently hatched (Dinsmore and Schreiber 1974). Vermeer (1970) found that less than 1% of pipping Ring-billed Gull eggs failed to hatch.

Fledging success: The percent of chicks that fledge from eggs that hatched (Gilman et al. 1977). I have defined a fledgling as a chick that has reached the age of 21 days (Dexheimer and Southern 1974). Vermeer (1970) reported that 82% of dead pre-fledging Ring-billed Gulls, died before the age of 21 days.

Breeding success: The percent of chicks that fledge from all eggs laid (Gilman et al. 1977).

Reproductive success: The number of chicks that fledge per breeding pair (Gilman et al. 1977).

Nest success: The percent of nests in which at least one egg hatched (Gilman et al. 1977).

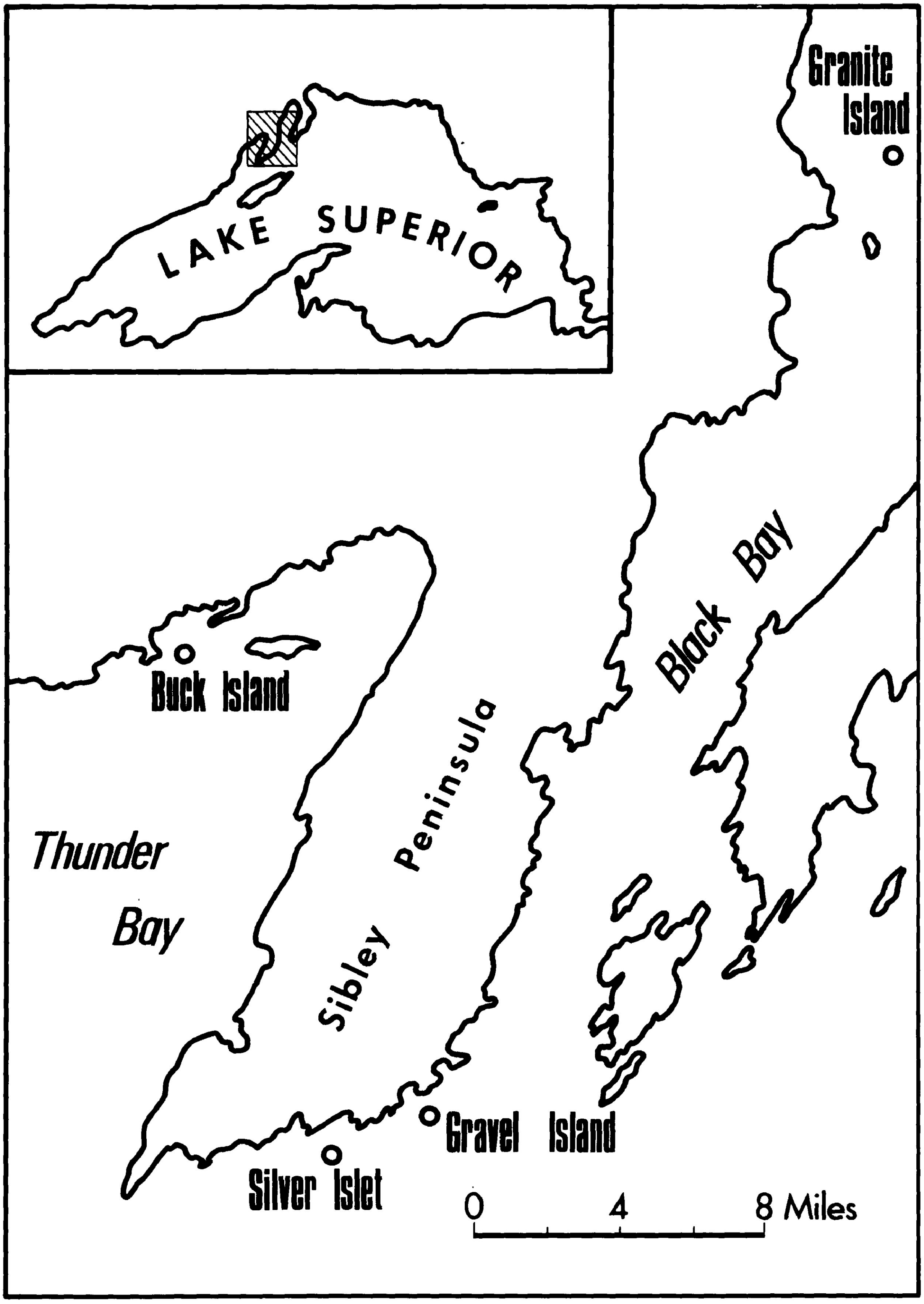
2.2 Statistical methods

Statistical tests were taken from Steel and Torrie (1960). Data were transposed to keypunch cards and stored in SPSS (Statistical Analysis for the Social Sciences, Nie et al. 1970) for analysis. I have assumed significance at $p < 0.05$.

2.3 Study area

The Ring-billed Gull colony of 1600 pairs on Granite Island (48°43' N, 88°29' W) is one of two known in northern Lake Superior, the other being on Gravel Island (Fig 1). Ring-billed Gulls have recently expanded into this area from southern Ontario. Ludwig (1974) did not know of their existence when he surveyed Ring-billed Gull colonies in the Great Lakes in 1967. These gulls traditionally have had a disjunct distribution in North America, being separated into eastern and western segments by the 96 meridian (Southern 1974). The population increase of the eastern segment has been attributed to the low water levels in the Great Lakes between 1962 and 1965 that exposed nesting areas (Ludwig 1974), and to the abundaoce of alewives

Figure 1. Map showing the location of Granite Island and Gravel Island (from Ryder 1974).



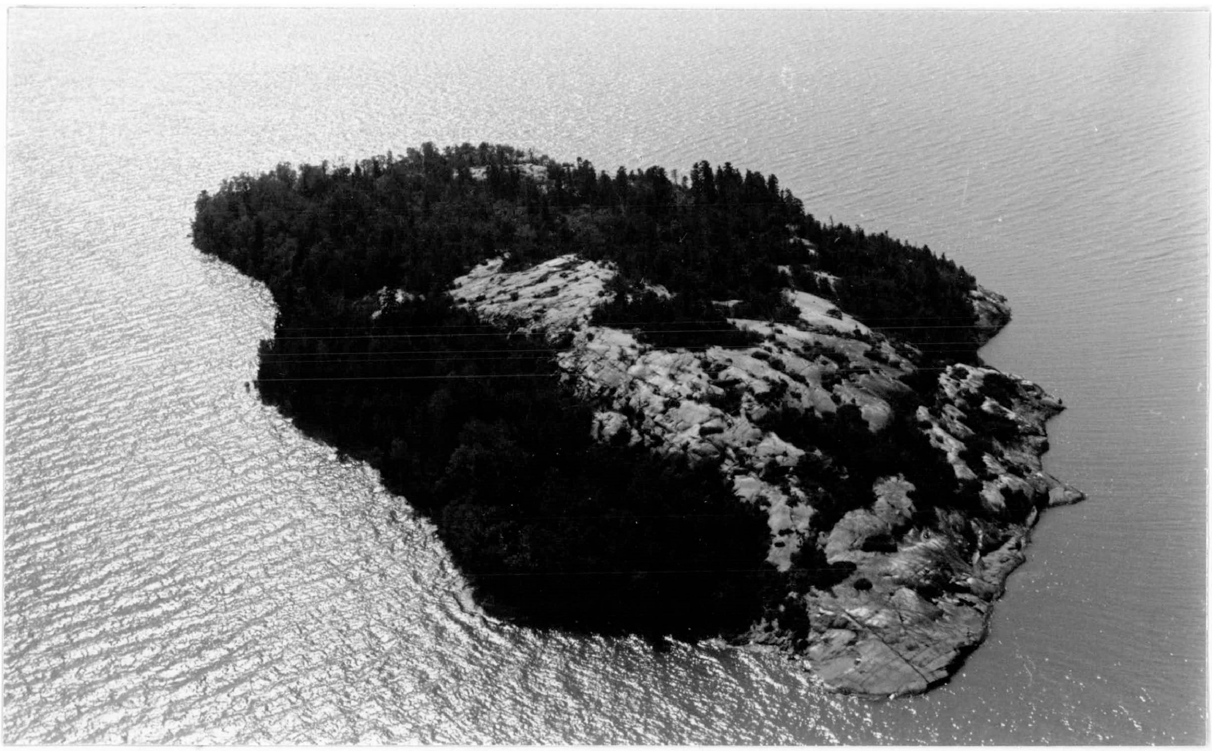
LAKE SUPERIOR
Granite Island
Black Bay
Buck Island
Sibley Peninsula
Thunder Bay
Gravel Island
Silver Islet
0
4
8 Miles

(Graham and Ayres 1975). This may subsequently result in the Great Lakes population of Ring-billed Gulls meeting the western segment.

Granite Island is a rock outcrop 402 m by 201 m with a summit 30 m above the surrounding water (Ryder and Somppi 1977). The closest mainland point is on Sibley Peninsula, 3 miles to the west (Fig. 1). Over 50% of the island is heavily forested, primarily with White Cedar (Thuja occidentalis), White Birch (Betula papyrifera) and Balsam Fir (Abies balsamea). This thick growth makes the south-west side of the island unsuitable nesting habitat for gulls. The forested areas are occupied by approximately 30 nesting species of small birds (Chamberlain 1973) (Fig. 2).

The north side of the island consists of a series of cliffs and ledges occupied by 200 pairs of Herring Gulls (Larus argentatus). There is virtually no overlap between the nesting area of the Herring Gulls and that of the Ring-billed Gulls. The latter nest on the exposed granite slope of the east side of the island, and on the exposed area at the summit. The Ring-billed Gulls nest primarily in soil-filled depressions in the rock. The predominant vegetation in these areas is Kentucky Bluegrass (Poa praetensis),

Figure 2. Aerial photograph of Granite Island. Note the bare rock areas that are occupied by Ring-billed and Herring Gulls.



Rough Cinquefoil (*Potentilla norvegica*) and Red Raspberry (*Rubus strigosus*) (Ryder and Somppi 1977).

My study area was a flat surface at the summit (78 m by 38 m) (Chamberlain 1973) occupied by approximately 500 pairs of Ring-billed Gulls. An observation tower, constructed in 1972, was located at the western edge of my study area. (Fig. 3).

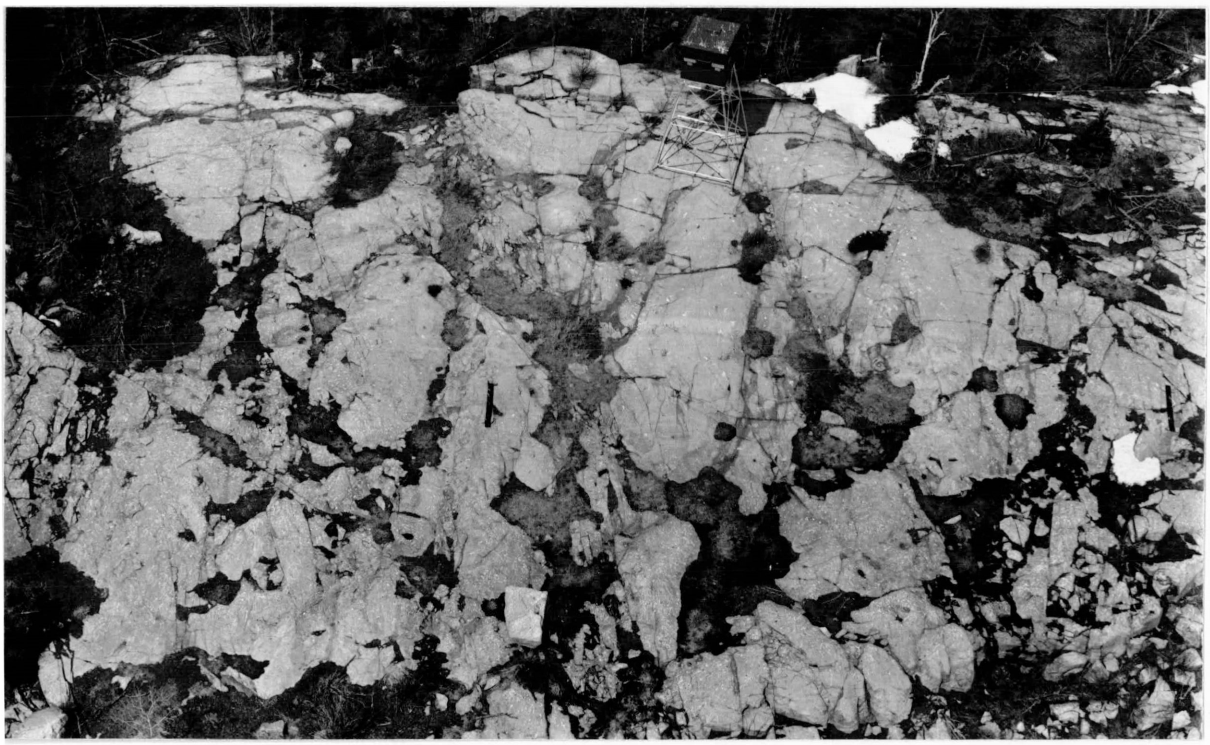
2.4 Nest data

2.4.1. Nest histories

In 1976, I arrived on Granite Island on 10 May and marked nests containing 1 or 2 eggs with a numbered green plastic strip placed under the nest. Only those nests which subsequently contained 3 eggs in the next 2 days were used in the transfer experiment (see Section 2.4.3.1). Upon my arrival on 12 May 1977, I marked all nests in the study area, either with a numbered plastic strip placed under the nest, or a numbered wooden block placed beside the nest. I kept histories of all the nests in 1977 since restricting my sample to 3-egg clutches in 1976 had shown gulls nesting on the periphery were equally as successful as those in the center of the colony (see Section 3.3.1).

In both years I numbered eggs on the blunt end with a non-toxic black felt marker pen. Nest histories were

Figure 3. Study area on Granite Island. Dark areas are grass-filled depressions in which the Ring-billed Gulls nest. Note the observation tower.



kept by visiting the colony every 2 to 3 days. I did not check nests during the hottest part of the day or during rain because I assumed such disturbances would be detrimental to the survival of the embryo. Approximate laying dates for eggs laid before my arrival were determined by back-dating from the day of hatching. Vermeer (1970) reported incubation periods of 27, 26, and 25 days for the first, second and third eggs respectively. In 1977, the breeding season was divided into 5-day 'weeks' starting on 1 May; laying and hatching dates were then recorded to the nearest week.

I measured the distance to nearest neighbor for 98 randomly chosen nests to determine any effect of nest spacing on hatching success and survival of the young. Measurements were taken from the center of the nest cup to the center of the nearest nest.

Chicks were marked upon hatching with a numbered fingerling fish tag fastened through the foot web. When I recaptured them at 1 to 2 weeks of age, their legs were large enough to retain a United States Fish and Wildlife Service aluminum leg band.

To facilitate recovery of the chicks, I fenced the study area in 1976. The fence was 30.5 cm high and was made of 2.54 cm mesh chicken wire. Nisbet and Drury (1972) found that the effect of this type of fencing on breeding success was negligible in their study of Common Terns (Sterna hirundo) and Roseate Terns (*Sterna dougallii*). Additionally, they stated that Pearson (1968) and Langham (1968) had fenced Arctic Terns (*Sterna paradisaea*) and Lesser Black-backed Gulls (*Larus ridibundus*) respectively without detrimental effects.

Whenever possible, I recorded the leg band numbers of gulls on the colony. I did this in 1976 by watching the gulls through a spotting scope mounted in the tower. In 1977, I live-trapped nesting Ring-billed Gulls. Figure 4 shows the trap that was set up over the nest. When the bird sat on its eggs, it pulled a monofilament fishing line that caused the split stick to fall, capturing the gull unhurt (Mills and Ryder, unpub. ms.). It was very important to get some information on known-age birds, to determine if young gulls did nest primarily on the periphery and how successful they were. In 1977, I was also able to sex the trapped gulls using bill length and depth at gonys (Ryder, in press) to determine if one sex returned more than the other.

2.4.2 Artificially incubated eggs

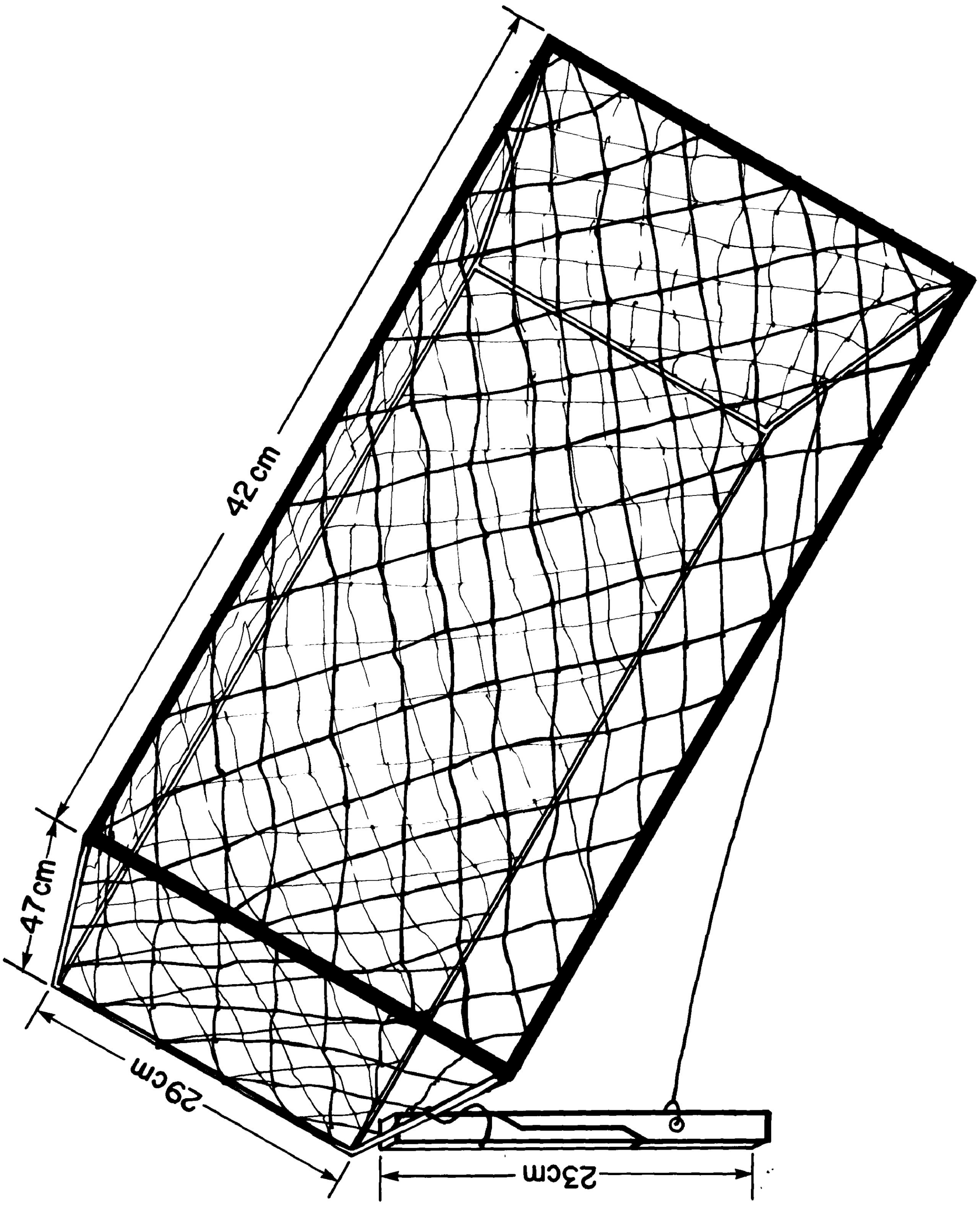
Although Ryder et al. (1977) had shown that there was no quantitative difference in lipids, proteins and carbohydrates present in egg yolks from the periphery and center of the colony, they suggested that the quality of these substances might differ. Consequently, I decided to determine the inherent hatchability of eggs from both areas of the colony by incubating them artificially. This would eliminate the effect of parental behaviour on hatching success. In 1976 and 1977, I collected 10 3-egg clutches (30 eggs) from the center and periphery of the colony, outside of my study area. In 1976, the eggs were collected on 14 May and transported within 12 hours to the Delta Waterfowl Research Station, north of Winnipeg, Manitoba. They were placed in a Robbins incubator at 38 C, 55% relative humidity with a varying turn schedule. In 1977, the eggs were collected on 18 May and within 3 hours were in an incubator at Lakehead University under the same conditions as 1976.

2.4.3. Incubation attentiveness

2.4.3.1 Egg exchange

It has been postulated that the birds on the periphery are poorer parents in that they are less attentive to their nests than birds in the center and this causes their lower success (Patterson 1965, Ryder 1975, Ryder et al. 1977). I therefore set up an experiment in which eggs were exchanged between central and peripheral nests. If the gulls nesting in the center were better parents than those nesting on the

Figure 4. Drawing of box trap used to capture live Ring-billed Gulls.


42 cm
47cm
29cm
23cm

border, then eggs moved from the periphery to the center should have a higher hatching success and subsequent fledging success than those left on the periphery. Similarily, eggs transferred from the center to the periphery should have a low success relative to those left in central nests.

I attempted to eliminate other variables that may affect success by using only 3-egg clutches initiated early in the season. Upon my arrival in both 1976 and 1977, I noted nests that contained 1 or 2 eggs. I then marked 100 of these nests that had an increase in clutch size to 3 within the following 2 days. This ensured that all eggs used in the experiment were the same age. I then exchanged 25 3-egg clutches in the center with 25 3-egg clutches on the periphery. An additional 25 3-egg clutches were marked in each area as controls. Nest histories were kept in both years as described in Section 2.4.1. Only nests which still contained only 3 eggs at hatching were considered in the analysis since a loss or gain of eggs can affect parental behaviour (Beer 1965, Baerends and Drent 1970).

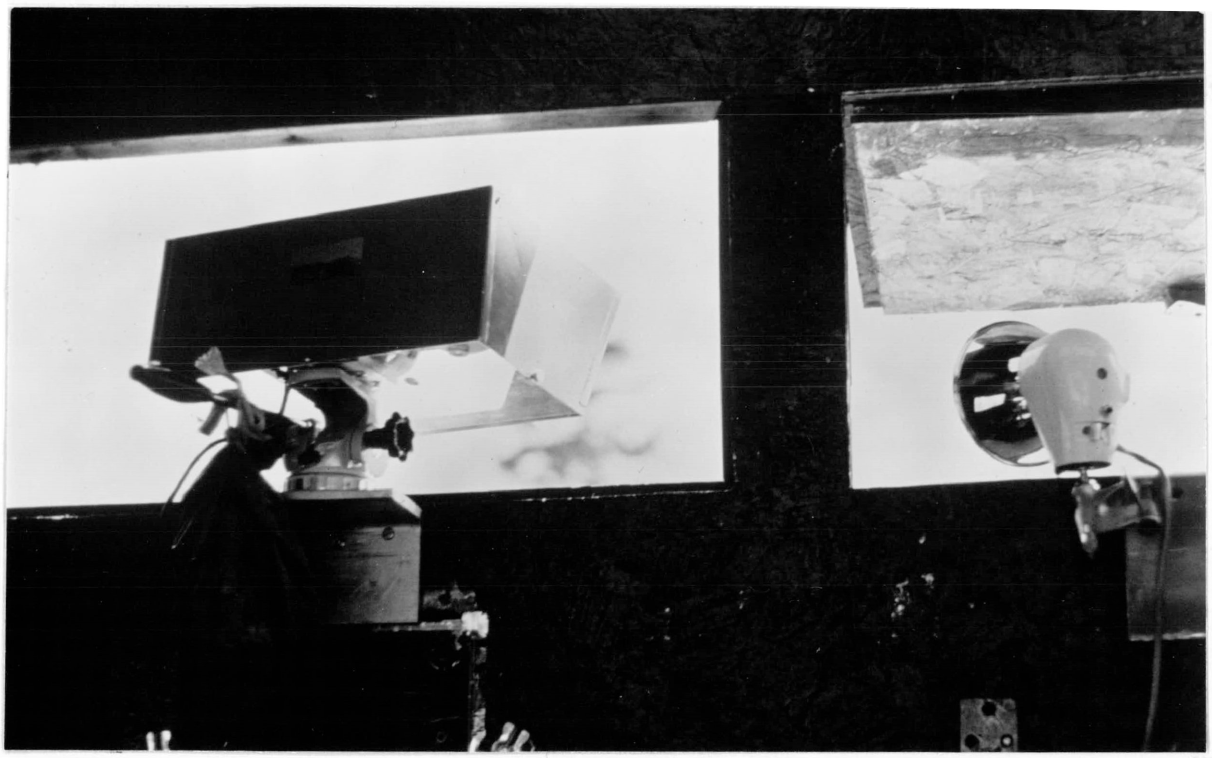
2.4.3.2 Photographic monitoring of attentiveness

Recently, researchers have used several methods to monitor the attentiveness of birds. Burger (1976) watched 20 pairs of Laughing Gulls (Larus atricilla) and noted every half hour whether the nest was attended. Morris and Hunter (1976) designed a ring that fit around the nest cup of a Common Tern. Whenever the bird left its nest, a microswitch was depressed and the action recorded on an Estraline-Angus recorder. Fox et al. (in press) placed telemetered eggs in Herring Gull nests which recorded changes in temperature due to the presence or absence of the incubating gull. Temple (1972) and Derksen (1977) used 16 mm movie cameras to record behaviour at pre-set intervals at a Peregrine Falcon (Falco peregrinus) and Adelie Penguin nest respectively. I decided to use a 35 mm camera with a wide-angle lens. This enabled me to record the behaviour of a large sample of gulls over a wide area. My analysis was then conducted on the basis of point sampling. This involved recording the presence or absence of a behaviour (in my case, incubation) at regular intervals. The smaller the interval, the more accurate is the prediction of the actual amount of time spent in an activity. I recorded the presence or absence of an incubating bird every 3 minutes. Dunbar (1976) stated the point sampling method gave a more statistically valid report of actual behaviour than did alternate methods of observation.

In 1976, I mounted an Olympus OM-1 camera and flash inside the observation tower (Figs. 5 and 6). The center and

Figure 5. Observation tower on study area showing the position of the camera and flash in the window openings.

Figure 6. A photograph showing the position of the camera and flash inside the observation tower.

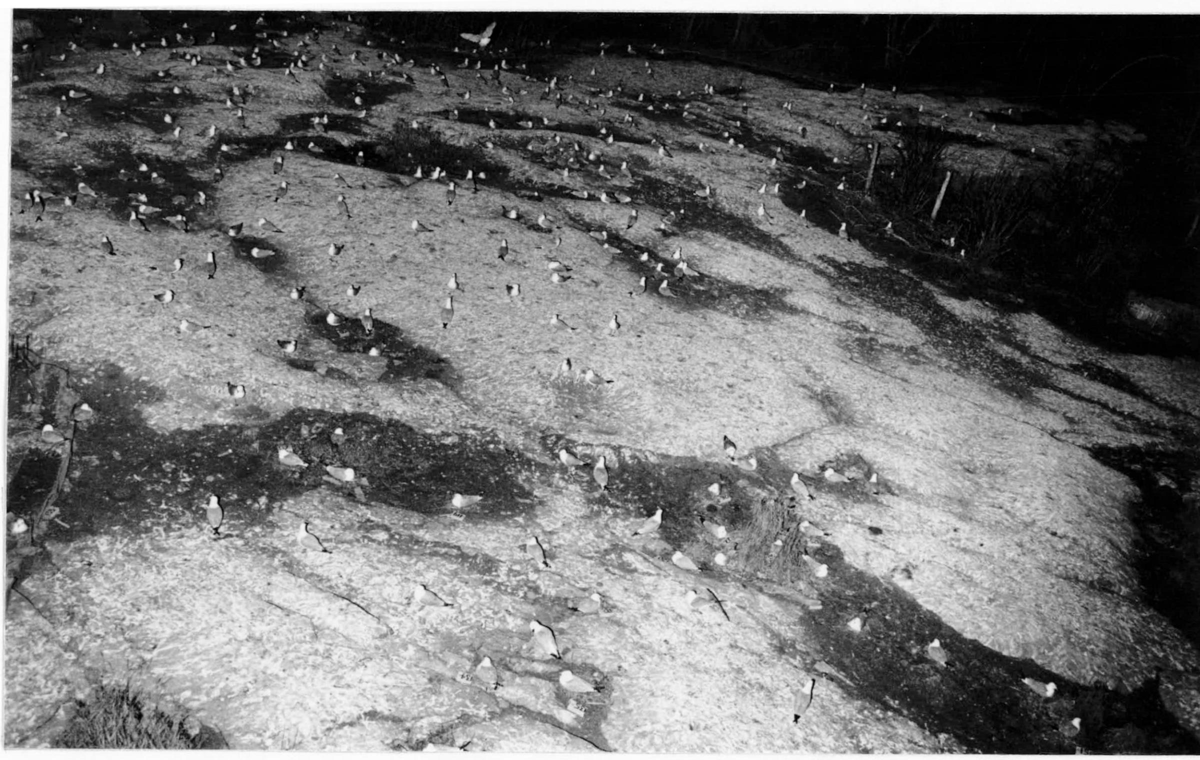


periphery of the colony were photographed alternately for 1 hour periods during each 12 hour period. I stayed in the tower during the observation period to redirect the camera each hour and adjust for light changes. In 1977, I used an Olympus OM-2 camera with automatic shutter control. This enabled me to leave the camera, and to eliminate any effect of my presence on the gulls, I decided to photograph the center for 12 hours one day, and the periphery the next day. The gulls were thus undisturbed during the observation period. The cameras were equipped with 100 foot backs capable of taking 240 pictures; therefore in 12 hours,the timer set the camera off every 3 minutes. In both years I used Kodak Plus-X film during the day and Kodak Tri-X at night. Three diurnal monitoring periods were done in each year during early, mid and late incubation (see table 9 for dates). Nocturnal photography was tried in 1976 in mid incubation when I thought the gulls would be too tied to their nests to desert. The flash seemed to have little effect on their behaviour and I used it again in 1977. However, the coverage was not complete as a result of equipment failure and environmental factors (fog and rain).

The developed film was left in roll form for ease of handling. In 1976, I examined each frame by running the film through a Kodak Ectagraphic Filmstrip Adapter mounted on a 35mm slide projector. In 1977, I traced the outline of the colony from the projected picture and circled 25 randomly chosen nests in both the center and periphery of the colony. I then checked each frame of every roll and noted whether the nest was attended. In 1977, I used the same colony outline as in 1976 and recorded attentiveness at nests as close as possible to those used in 1976. Figures 7 and 8 are pictures developed from these rolls of film. The circled nests were those used in the monitoring study. In 1977, I knew the nest histories for all nests and their location. Consequently, I was able to locate nests started late in the season and record the attentiveness of the gulls on them. The position of these nests is indicated by an X on Figures 7 and 8.

Figure 7. Central (top) and peripheral (bottom) areas of the colony photographed from the observation tower during the day. Circled nests were monitored for attentiveness on 31 May 1977. Nests marked with an X were started late in the breeding season.

Figure 8. Central (top) and peripheral (bottom) areas of the colony photographed at night using the flash.



3. RESULTS

3.1 Demographic data

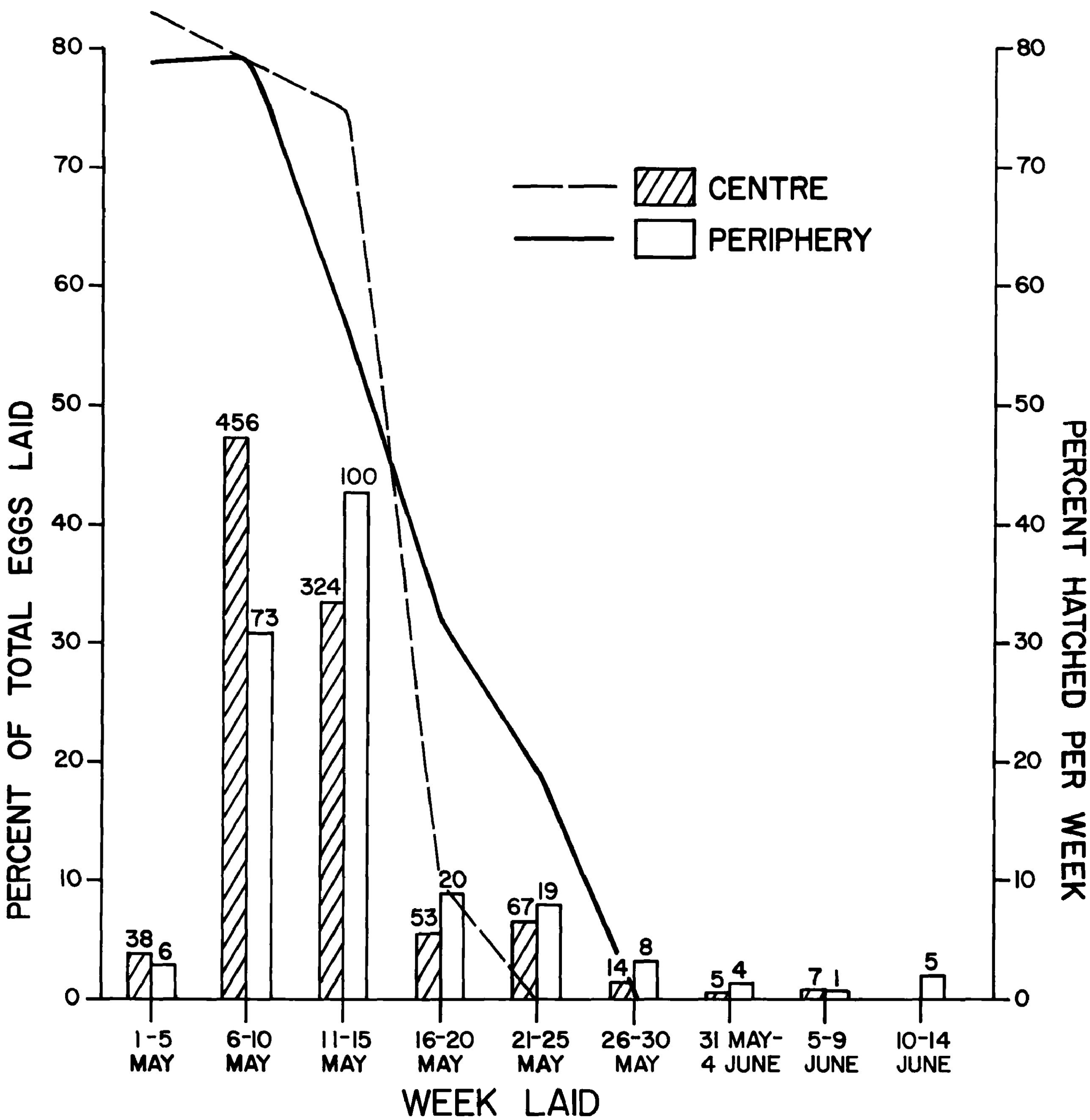
3.1.1. Egg laying

In 1977, gulls nesting in the center of the study area reached a peak of egg laying in week 2 (6-10 May), one week earlier than those nesting on the fringe (Fig.9). Although the peak of egg laying was later on the periphery, both areas initiated most of their clutches in week 2 (Table 1). Egg laying extended from 1 May to 9 June (week 1 to 8) in the center, and until the ninth week on the periphery (Fig.9).

3.1.2 Clutch size

Table 2 shows the average clutch size in the center was slightly, but not significantly larger than that on the periphery of the colony. As found by Vermeer (1970), the modal clutch size was 3 eggs in the center (53.5%) and on the periphery (56.2%), but it ranged from 1 to 7 eggs (Fig. 10). Ryder (1975) suggested that clutches over 4 eggs may have been the result of more than one female laying in the same nest. These superclutches were more prevalent in the center (13.8% - 45/325) than on the periphery of the colony (5.0% - 4/80). If these superclutches are excluded from the analysis, then the remaining 280 nests in the center had a mean clutch

Figure 9. The relation between egg laying and hatching success of Ring-billed Gulls nesting on Granite Island, 1977. There were 74 eggs in the center and 10 eggs on the periphery not included in the figure since their laying date was not known. (See Appendix C)



CENTRE
PERIPHERY
PERCENT OF TOTAL EGGS LAID
PERCENT HATCHED PER WEEK
0
10
20
30
40
50
60
70
80
38
6
456
73
324
100
53
20
67
19
14
8
5
4
7
1
5
1-5 MAY
6-10 MAY
11-15 MAY
16-20 MAY
21-25 MAY
26-30 MAY
31 MAY-4 JUNE
5-9 JUNE
10-14 JUNE
WEEK LAID

Table 1

Clutch initiation in the center

and periphery of the Ring-billed Gull colony

on Granite Island, 1977.

Week of clutch initiation	Center	Periphery
	Number of clutches initiated	
1	25 (8.2%)*	6 (8.0%)
2	208 (68.6%)	41 (54.7%)
3	36 (11.9%)	15 (20.0%)
4	7 (2.3%)	6 (8.0%)
5	19 (6.3%)	5 (6.7%)
6	4 (1.3%)	1 (1.3%)
7	2 (0.7%)	0
8	2 (0.7%)	0
9	0	1 (1.3%)

* percent of clutches initiated.

Note: The total number of clutches differs from that of Table 2 because 22 clutches in the center and 6 on the periphery had an unknown initiation.

Table 2

Success of Ring-billed Gulls

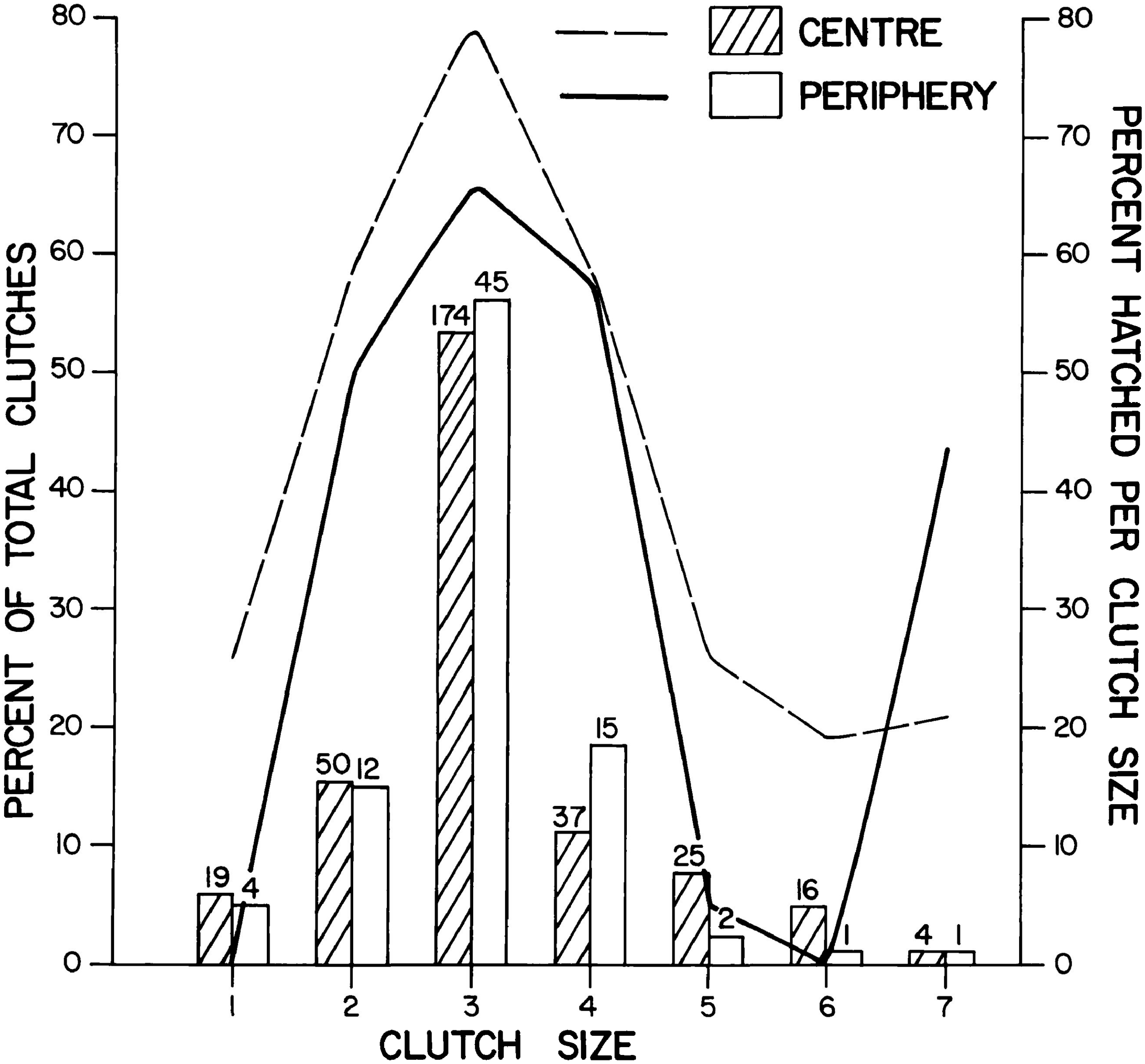
Granite Island, 1977

	Center	Periphery
Number of Nests	325	80
Clutch Size	3.19 ± 1.19[1]	3.08 ± 0.98
Eggs Hatched Per Eggs Laid	0.63 ± 0.41	0.57 ± 0.45
Eggs Hatched Per Nest	1.90 ± 1.24	1.80 ± 1.45
Chicks Fledged Per Egg Hatched	0.65 ± 0.25	0.73 ± 0.26
Chicks Fledged Per Egg Laid	0.33 ± 0.25	0.34 ± 0.30
Chicks Fledged Per Nest	1.03 ± 0.75	1.06 ± 0.95
Nest Success[2]	77.8%	65.0%

[1] Mean ± 1 S. D.

[2] Significant difference between center and periphery ($p < 0.05$)

Figure 10. Frequency of clutch sizes in central and peripheral areas of Granite Island and the relationship between clutch size and hatching success.



CENTRE
PERIPHERY
PERCENT OF TOTAL CLUTCHES
PERCENT HATCHED PER CLUTCH SIZE
CLUTCH SIZE
0
10
20
30
40
50
60
70
80
1
2
3
4
5
6
7
19
4
50
12
174
45
37
15
25
2
16
1
4
1

size of 2.82 ± 0.74. This was insignificantly smaller than the average clutch size of the 76 remaining nests on the periphery (2.93 ± 0.75). The seasonal regression in clutch size was the same in both parts of the study area (Table 3).

3.1.3 Hatching of eggs

Figure 11 shows the hatching frequency in the center and periphery. Most eggs on the periphery hatched 1 week later than those in the center. Hatching was compressed into 5 weeks in the center from the 8 weeks of egg laying, and 4 weeks on the border from a 9 week egg laying period.

The hatching success and the number of eggs hatched per clutch was the same in both areas of the colony (Table 2). However, the percent of nests that hatched at least one egg was significantly higher in the center of the colony. Nest success data should be viewed with caution since it does not take into account the actual number of eggs hatched. A nest that contained 3 hatched eggs out of 3 eggs laid, would be rated the same as a nest with 1 hatched egg out of 3 laid. Therefore, it is not as sensitive a measure of success as hatching success.

Eggs laid at the peak of clutch initiation (6-10 May)

Table 3

Seasonal change in clutch size of marked Ring-billed Gull nests on Granite Island, 1977

Week Initiated	Mean Clutch Size: Center[1]	Periphery[2]
1 (1-5 May)	3.76 ± 1.54 (25)[3]	3.33 ± 0.52 (6)
2 (6-10 May)	3.33 ± 1.15 (208)	3.22 ± 1.11 (41)
3 (11-15 May)	3.06 ± 0.83 (36)	3.27 ± 0.80 (15)
4 (16-20 May)	2.71 ± 1.25 (7)	2.83 ± 0.41 (6)
5 (21-25 May)	2.84 ± 0.76 (19)	2.60 ± 0.55 (5)
6 (26-30 May)	1.50 ± 0.58 (4)	(1 2-egg clutch)
7 (31 May to 4 June)	1.50 ± 0.71 (2)	
8 (5-9 June)	(1 2-egg clutch and 1 1-egg clutch)	

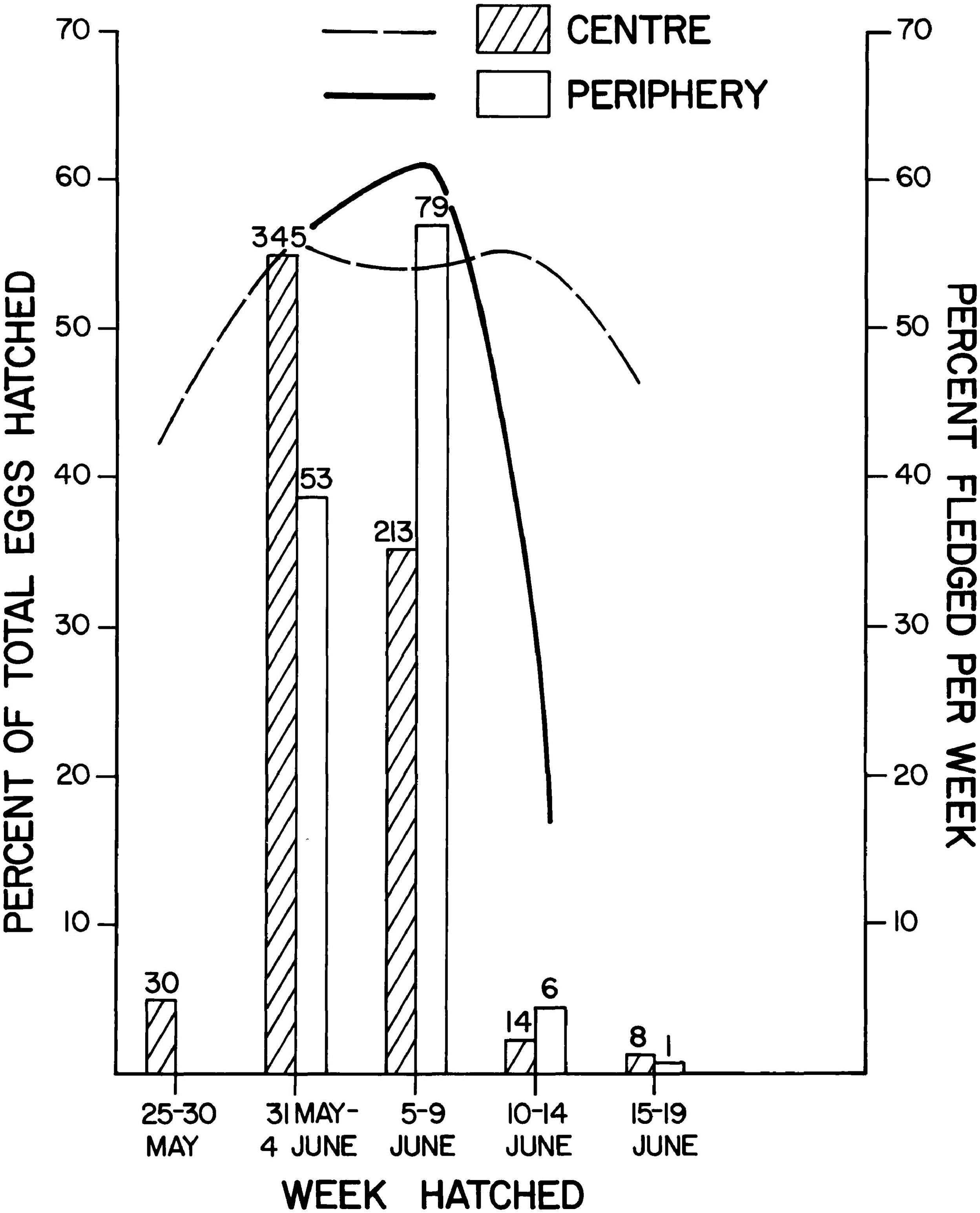
1 $r = -0.945$, $p < 0.05$

2 $r = -0.917$, $p < 0.05$

3 Mean ± 1 S. D. (number of nests)

Note: The total number of clutches differs from that of Table 2 because 22 clutches in the center and 6 on the periphery had an unknown initiation.

Figure 11. The pattern of hatching for central and peripheral eggs on Granite Island and its relationship to fledging success



CENTRE
PERIPHERY
PERCENT OF TOTAL EGGS HATCHED
PERCENT FLEDGED PER WEEK
70
60
50
40
30
20
10
30
345
53
213
79
14
6
8
1
25-30 MAY
31 MAY- 4 JUNE
5-9 JUNE
10-14 JUNE
15-19 JUNE
WEEK HATCHED

had a hatching success of approximately 80% regardless of location (Fig. 9). However, the success of those eggs laid after the peak was 30% lower in both areas. Hatching success varied significantly with week laid in the center ($F_{7,967} = 32$, $p < 0.001$) and on the border ($F_{8,227} = 20.2$, $p < 0.001$).

Three egg clutches had the highest hatching success in both areas (Fig. 10). Hatching success varied significantly with clutch size in the center ($F_{6,1042} = 49.2$, $p < 0.001$) and on the periphery ($F_{6,239} = 3.31$, $p < 0.001$).

When the superclutches were excluded from the analysis, the hatching success increased to 71.1% in the center and 61.0% on the periphery ($p > 0.05$). However, the hatching success of eggs laid early (i.e. at or before the peak of clutch initiation) in the center, was significantly higher (90%) than early eggs laid on the periphery (80%) ($X_2 = 10.3$, $p < 0.01$). Eggs laid late in the season (i.e. after the peak of clutch initiation) had approximately the same hatching success in both areas of the colony (52.2% in the center and 57.4% on the periphery).

3.1.4 Unhatched eggs

Table 4 shows the fate of unhatched eggs. In both areas

Table 4

Fate of unhatched Ring-billed Gull eggs,

Granite Island, 1977

	Center	Periphery
Infertile/Dead Embryo	107 (25.5%)	23 (22.5%)
Disappeared	145 (34.5%)	21 (20.6%)
Rolled out of Nest	62 (14.8%)	7 (6.9%)
Buried in Nest	29 (6.9%)	2 (2.0%)
Nest Destroyed	17 (4.0%)	18 (17.6%)
Eaten	15 (3.6%)	12 (11.8%)
Pipped and Died	14 (3.3%)	4 (3.9%)
Broken	14 (3.3%)	9 (8.8%)
Unknown	17 (4.0%)	6 (5.9%)
Total	420	102

of the colony, disappearance and infertility/dead embryo accounted for most of the unhatched eggs. Infertility had to be classed with dead embryo since the embryo could have died at an early age and thus be indistinguishable from an infertile egg.

3.1.5 Survival of chicks

Table 2 shows the same proportion of chicks fledged in both areas of the colony relative to eggs hatched and eggs laid per nest. There was no relationship between week of hatching and fledging success (Fig. 11).

The number of chicks that fledged had to be calculated since, despite the fences, some chicks were never recaptured or found dead. From my sample of known-age dead chicks (Section 3.1.6), I calculated that 47% had died at less than 1 week old and 53% were between 1 and 3 weeks of age when they died. Therefore, if a chick was last seen at less than 1 week old, the chance of it being alive was 53%; if the chick disappeared at 1-2 weeks, the chance of its being alive was 47%. To calculate fledging success, I added the number of chicks which I knew were at least 21 days old, to the number of unrecovered chicks which I calculated to have fledged, based on the above proportions (Ryder and Carroll 1978).

3.1.6 Mortality of chicks

I collected a total of 86 known-age Ring-billed Gull chicks. Of these, 40 (47%) had died within a week of hatching. The majority (58) died within 10 days of hatching.

The cause of death in most cases could not be determined. The chicks did not seem to have died from injury or starvation. Those chicks that did die of an injury had invariably been pecked on the head by adult gulls. A few chicks that were found dead in their nests after a rainstorm were assumed to have died of exposure.

In the course of the study, two abnormal chicks were found. One hatched successfully from an egg collected on the periphery and indubated artificially. It would not have survived since it had crossed mandibles and the right eye was completely covered with skin. The eye was not visible until the skin was cut open. The other abnormal chick was found dead in pip in its nest. Upon dissecting it, I found that its upper mandible was less than half the length of the lower mandible. This probably prevented it from successfully breaking through the shell.

3.1.7 Nearest-neighbour analysis

Table 5 shows the results of measuring minimum inter-nest distance for 98 randomly chosen nests. Peripheral nests had significantly greater nearest-neighbour distances than central nests, which indicated a lower nest density in the former area.

A statistic of spacing that indicates the degree of randomness is calculated by the following formula:

$$\frac{(\text{geometric mean of nearest-neighbour distance})^2}{(\text{arithmetic mean of nearest-neighbour distance})^2}$$

This statistic (GMASD) was developed by Brown (1975) and used by Newton et al. (1977). In this method, a value of 1 indicates complete regularity. A value below 0.65 shows a tendency to random spacing. According to Rothery (pers. comm.), the value of 0.805 calculated for the center showed the nest spacing varied significantly from random ($p < 0.05$). Peripheral nests tended to be randomly spaced (GMASD = 0.627).

Distance to nearest neighbour was not related to week of clutch initiation ($F_{4,82} = 2.446$, $p > 0.05$), clutch size ($F_{6,91} = 0.435$, $p > 0.05$) or hatching success ($t_{96} = 0.164$, $p > 0.05$). I restricted the analysis to 3-egg clutches to determine if the effect of clutch size on hatching success (Section 3.1.2) was masking the effect of

Table 5

Nearest neighbour distances

between central and peripheral nests,

Granite Island, 1977

	Center	Periphery
Minimum Inter-Nest Distance[2]	74.9 ± 25.9 (70)[1]	95.8 ± 54.9 (28)
GMASD[3]	0.805	0.627

1 Mean ± 1 S.D. (Sample Size)

2 $t_{96} = 2.565$, $p < 0.05$.

3 A statistic of spacing (see Section 3.1.7)

nearest neighbour distance. There was still no relation with hatching success ($t_{46} = 0.394$, $p > 0.05$).

Horn (1968) found that nesting above or below the mean inter-nest distance had different effects on the hatching success of colonially nesting Brewer's Blackbirds (Euphagus cyanocephalus). Consequently, I sorted the data for nests in the center into groups described in Table 6. As Horn (1968) found, birds nesting closer together than the mean (Group C), had the highest hatching success. Birds nesting farther apart than the mean (Group B), had the highest fledging success. Gulls nesting at distances close to the mean inter-nest distance (Group A), were the most successful overall. There were no significant differences between the groups, but it is interesting to note that gulls that compromised between the most favourable distance for hatching success and fledging success produced the most chicks per egg laid. I could not do a similar analysis for peripheral nests since only 2 had distances greater than the mean plus 1 S.D. and none were below the mean minus 1 S.D.

3.1.8 Known-age birds

In 1976, I determined the leg band numbers of 10 Ring-billed Gulls (Appendix A). Six of these gulls were 3 years

Table 6

Reproductive data in relation to distance to nearest neighbour in the center of the Granite Island Ring-billed Gull colony, 1977

Group	Sample Size	Hatching Success	Fledging Success	Breeding Success
A: Inter-nest distance within 1 S.D. of mean	52	56.2%	58.4%	33.3%
B: Inter-nest distance greater than mean + 1 S.D.	9	43.6%	62.9%	30.5%
C: Inter-nest distance less than mean - 1 S.D.	9	62.1%	45.4%	28.2%

Note: No significant difference between any groups for any parameter.

old and were either not nesting (2) or nesting on the periphery. The other 4 gulls were 4 years old. Three of the 4-year olds were nesting in the center and 1 was a late nester on the periphery.

In 1977, I recorded the leg band numbers of 11 gulls (Appendix B). Of the 7 that had nests in the center of the colony, 6 were males (4 4-year olds and 2 5-year olds). Each of the males had a 3-egg clutch. The seventh gull was a 5-year old female with a 2-egg clutch. All 7 clutches were initiated early in the season. The hatching and fledging success was 95% and 51.4% respectively.

Of the 4 banded gulls trapped on the periphery in 1977, 2 were males (3 and 6 years old) and 2 were females (both 5 years old). All had 3-egg clutches initiated early in the breeding season. Hatching and fledging success was 92% and 64.7% respectively.

Five of the nests attended by banded birds in 1977 were included in the study of attentiveness. One of these nests was on the periphery and was attended over 90% of the time. Of the 4 nests in the center, 3 were attended over 90% of the time. The fourth nest was only attended 81% of the time, but successfully hatched all 3 eggs in its nest.

Ring-billed Gulls generally start to breed at 3 years of age (Ludwig 1974). Although my data are sparse, it appears that young gulls are not restricted to the border of the colony, and not all gulls nesting on the periphery are necessarily young. Since these gulls were banded on Granite Island as chicks, it appears males preferentially return to their natal colony (8 vs 3).

3.2 Artificially incubated eggs

In both 1976 and 1977, all 10 clutches collected from the center of the colony, and 9 of the 10 clutches collected from the periphery hatched at least one egg. Table 7 shows the mean number of eggs hatched per clutch was the same for eggs collected from both areas of the colony in both years. In 1976, the hatching success was the same for central and peripheral eggs. In 1977, eggs from the center had a significantly higher hatching success than those from the periphery. This may have been because the eggs from the periphery were at a more sensitive age when transported than those from the center (see discussion). The overall higher hatching success of eggs in 1977 relative to 1976 was probably a result of the shorter transportation time in 1977. The results indicated that there was no difference in the inherent hatchability of eggs from the center and periphery of the colony.

Table 7

Hatching of artificially incubated

Ring-billed Gull eggs, Granite Island, 1976-77

	Center	Periphery
Eggs Hatched Per Egg Laid		
1976	0.63 ± 0.25 (30)[1]	0.57 ± 0.32 (30)
1977	0.93 ± 0.14 (30)[2]	0.73 ± 0.34 (30)
Eggs Hatched Per Clutch		
1976	1.90 ± 0.74	1.70 ± 0.95
1977	2.80 ± 0.42	2.20 ± 1.00

1 Mean ± 1 S.D. (number of eggs)

2 Significant difference between center and periphery ($p < 0.05$)

3.3 Incubation attentiveness

3.3.1 Egg exchange

Table 8 summarizes the results of transferring eggs from one area of the colony to another. Whether an egg was attended by gulls on the border or in the center of the colony, its subsequent success was the same. The only exception occurred in 1977 when fledging success was significantly lower in central control nests than in peripheral control or experimental nests. This was probably an artifact of the small number of chicks recovered in the center. If I had recovered more chicks, then the result most likely would have reflected the situation in the colony as a whole (no difference in fledging success between center and periphery).

3.3.2 Photographic monitoring of attentiveness

Table 9 shows the percent attentiveness of gulls during the monitored periods in 1976 and 1977. In most cases, the gulls spent a minimum of 90% of their time on their nests regardless of location or time of day. The relatively low attentiveness of peripheral gulls in early incubation in 1976, was the result of 3 gulls being off their nests more than half of the time. The other 22 gulls were as attentive as gulls in the center. In 1976, the peripheral gulls were less attentive the night of 31 May (late incubation). All

Table 8

Reproductive success of experimental and control eggs

of Ring-billed Gulls, Granite Island, 1976-77

		Central eggs		Peripheral eggs	
		Experimental (in peripheral nests)	Control (in central nests)	Experimental (in central nests)	Control (in peripheral nests
Eggs Hatched	1976	0.88 ± 0.16 (66)[1]	0.89 ± 0.23 (72)	0.82 ± 0.27 (63)	0.89 ± 0.23 (72)
Per Egg Laid	1977	0.78 ± 0.37 (51)	0.92 ± 0.17 (75)	0.87 ± 0.28 (57)	0.81 ± 0.29 (72)
Chicks Fledged	1976	0.62 ± 0.18	0.56 ± 0.24	0.69 ± 0.20	0.60 ± 0.14
Per Egg Hatched	1977[2]	0.54 ± 0.22	0.48 ± 0.12	0.58 ± 0.18	0.67 ± 0.20
Chicks Fledged	1976	0.54 ± 0.18	0.48 ± 0.23	0.56 ± 0.27	0.54 ± 0.18
Per Egg Laid	1977	0.37 ± 0.22	0.44 ± 0.13	0.48 ± 0.17	0.52 ± 0.26

Table 8 (Cont'd)

Reproductive success of experimental and control eggs of Ring-billed Gulls, Granite Island, 1976-77

		Central eggs		Peripheral eggs	
		Experimental (in peripheral nests)	Control (in central nests)	Experimental (in central nests)	Control (in peripheral nests)
Chicks Fledged	1976	1.64 ± 0.54	1.44 ± 0.70	1.69 ± 0.80	1.62 ± 0.54
Per Nest	1977	1.10 ± 0.66	1.30 ± 0.39	1.40 ± 0.52	1.60 ± 0.77
Eggs Hatched	1976	2.64 ± 0.49	2.67 ± 0.70	2.48 ± 0.81	2.67 ± 0.70
Per Nest	1977	2.35 ± 1.11	2.76 ± 0.52	2.63 ± 0.83	2.42 ± 0.88
Nest Success	1976	100%	96%	95%	96%
	1977	88%	100%	95%	92%

1 Mean ± 1 S.D. (number of eggs laid)

2 Central control nests fledged significantly fewer chicks than either experimental or control peripheral nests, $p < 0.05$.

Table 9

Percent attentivenss of Ring-billed Gulls nesting in the center and periphery of the Granite Island colony, 1976 and 1977

Incubation Period	Date	Center Day	Center Night	Periphery Day	Periphery Night
Early	13 May 1976	99.4		86.2	
	16-17 May 1977	93.3	100	95.2	87.8
Middle	19-20 May 1976	99.8	99.5	93.6	94.5
	24-25 May 1977	93.8	93.4	96.2	
Late	31 May - 1 June 1976	100	96.1	92.6	77.4
	31 May 1977	97.0		89.1	

peripheral gulls left the colony for approximately 1 hour that night. I do not know whether gulls from the center also left, since the camera was trained only on the periphery. The reason for this desertion is unknown, but it is possible the gulls left to feed en masse. Leck (1971) reported that Ring-billed Gulls fed nocturnally if food was available.

There was no relationship between clutch size and attentiveness in early or late nests (Table 10). Attentiveness was correlated with hatching success only in early peripheral nests ($r = 0.51$, $p < 0.05$). Proportionately fewer gulls that started nesting after the peak of clutch initiation were attentive over 90% of the time compared to those nesting earlier. The results indicated that gulls nesting early in the season were attentive to their nests regardless of location. Gulls in both areas which nested late in the season were less attentive than early nesters whether they were nesting on the periphery or in the center. Additionally, in the majority of cases (69%), hatching success could not be predicted by measuring attentiveness.

Table 10

Incubation attentiveness of central and peripheral

Ring-billed Gulls nesting on Granite Island, 1977

Percent time spent on nest		Prepeak / Peak Clutches 1 egg	2 egg	3 egg	4 egg	5 egg	6 egg	Hatching Success %	Percent of Gulls on	Postpeak Clutches 1 egg	2 egg	3 egg	4 egg	Hatching Success %	Percent of Gulls on
90-100	C *		8	14	1	1	3	71.8	90.0		6	4	2	13.0	75.0
	P			17	1	1	1	72.7	83.3			5		0.0	62.5
80-89	C													?	6.2
	P							75.0	4.2						
70-79	C			1				100.0	3.3						
	P														
60-69	C													100.0	6.2
	P							100.0	4.2					0.0	12.5
50-59	C														
	P							0.0	4.2						

Table 10 (Cont'd)

Incubation attentiveness of central and peripheral

Ring-billed Gulls nesting on Granite Island, 1977

Percent time spent on nest		Prepeak / Peak Clutches 1 egg	2 egg	3 egg	4 egg	5 egg	6 egg	Hatching Success %	Percent of Gulls on	Postpeak Clutches 1 egg	2 egg	3 egg	4 egg	Hatching Success %	Percent of Gulls on
40-49	C											1		0.0	6.2
	P														
30-39	C														
	P														
20-29	C							100.0	3.3						
	P							0.0	4.2						
10-19	C							0.0	3.3					0.0	6.2
	P													0.0	25.0

* C - Gulls nesting in the center. Observations per nest ($X \pm 1SD$) : prepeak/peak=612.5 ± 30.5; postpeak=339.8 ± 85.0.

P - Gulls nesting on the periphery. Observations per nest ($X \pm 1SD$) : prepeak/peak=648.2 ± 0.78; postpeak=362.9 ± 78.6.

4. DISCUSSION

4.1 Demographic data

4.1.1. Egg laying

Vermeer (1970) and Ryder (1975) reported that, as in this study, egg laying rose rapidly to a peak within 14 days after the first clutch was initiated, and then tapered off over the next month. This synchronization likely was responsible for the high hatching success through effective social stimulation to incubate. Synchronization of egg laying resulted in the majority of eggs hatching at the same time. The group effort of the parents to find food would be more efficient than an individual attempting to locate a constantly moving food source.

Egg laying peaked a week later than clutch initiation on the periphery. In the center, both peaked in the same week. Possibly there was less social stimulation on the periphery as a result of the lower density. This could cause the gulls to take longer to become attached to their nests and thus protract the egg laying period.

4.1.2 Clutch Size

Clutch size information was basically similar to that reported by Vermeer (1970) and Ryder (1975) in that 3-egg clutches were the most common and the average, weekly clutch size decreased. The center and periphery did not differ significantly in either respect. The prevalence of superclutches in the center (14%) is slightly higher than that derived from Ryder (1975: Table 2) (11%) for mature-plumaged pairs. The only other extensive number of superclutches in a Ring-billed Gull colony has been reported by Merilees (1974). His colony was close to the British Columbia coast and suffered many disturbances from people. The Granite Island colony was not visited by anyone other than the researchers. Hunt and Hunt (1977) found that superclutches in Western Gull (Larus occidentalis) colonies were the result of homosexual pairs of female gulls. They postulated there was a shortage of males in their colony, and even if the success of superclutches was low, it was still preferable to no success at all. Now that we can sex Ring-billed Gulls, the next project would be to trap the birds attending these nests and determine if they are of the same sex. It is possible that older females returning to the colony to breed and unable to find their partner of the previous year cannot find available males. All the superclutches on Granite Island were initiated early in the season and thus presumably by older gulls. Perhaps the females, rather than wait for the young, inexperienced males to arrive, find it more advantageous to mate promiscuously and then nest with a female to help incubate the eggs. Mating with a young male late in the season has virtually no chance of success whereas caring for a large clutch with another female has some chance. Shugart and Southern (1978) recently reported a case of polygyny in Ring-billed Gulls. This could also result in superclutches if both females (mates of the same male) laid in the same nest. Again, it would suggest a shortage of males early in the season. Sharing a male that arrived early could produce more young than waiting for a male that arrived later when nest sites were scarce.

4.1.3 Hatching of eggs

I found that hatching success was related to the time of nest initiation and clutch size rather than nest location. This was contrary to the findings of Dexheimer and Southern (1974) who reported a significantly higher hatching success in the center of the colony relative to the fringe, both in a colony similar topographically to Granite Island, and on an island where the periphery was subject to annual flooding. This is possibly because the authors compared only those nests near the geometric center of the colony to the row of nests forming the border. All nests in between were ignored as being not truely central or peripheral (Southern, pers. comm.). I compared all nests forming the border to all nests within that border because it is too subjective to try and subdivide the nests into true central, true peripheral and not really either. Perhaps this difference in methodology could explain, in part, the different results of our studies.

Ryder (1975) suggested that there would be a lower hatching success on the border of the Granite Island colony relative to the center. He found that immature-plumaged gulls had no success and the majority (62%) nested on the periphery. In 1973 when his study was done, the colony was still expanding and the border constantly changed as more young birds nested later in the season. In 1977, the border was defined and occupied at the same time as the center. Thus there was no space left for young gulls to expand and form a 'poor' peripheral area.

The mean hatching success in 1977 was close to that found by Dexheimer and Southern (1974) at both colonies mentioned previously. It is much lower than that reported by Vermeer (1970) in 1964 (86%), but higher than he found in 1965 (16%). Baird (1977) worked at 2 Ring-billed Gull colonies in Montana and reported hatching successes of 34% and 41%.

Therefore the Granite Island colony is at least as successful, if not more so, than other Ring-billed Gull colonies.

4.1.4 Unhatched eggs

The disappearance of eggs has been reported by Vermeer (1970) as the major cause of unhatched Ring-billed Gull eggs. This was also the fate of most unhatched Herring Gull eggs (Spaans and Spaans 1975, Morris and Haymes 1977). Vermeer (1970) attributed the disappearance of Ring-billed Gull eggs to the habit in the gulls of eating their own cracked or addled eggs. In 1976, I observed a Ring-billed Gull on Granite Island eating an egg in a nest. Unfortunately, I could not tell if the gull was eating its own egg. It would probably be a successful strategy to eat damaged or addled eggs that will not hatch, add thus replace some of the energy lost in producing an egg. Ryder (1975) suggested that Common Crows were responsible for the disappearance of some eggs on Granite Island. Although crows are capable of carrying the eggs (Montevecchi 1976), the gulls ignored the presence of crows rather than reacting to them as predators in the manner described by Tinbergen (1960) for Herring Gulls. It is likely then, that the gulls were responsible for the disappearance of the eggs.

The higher proportion of late nesters on the border of the colony relative to the center, was reflected in the higher proportion of unhatched eggs in the 'eaten' and 'nest destroyed' categories for the periphery. Gulls nesting late in the year were possibly subject to intrusions from adults that had nested earlier and their chicks. The stimulus to stay on the nest would be low since the majority of other adults would have finished incubating. Fewer late nesters were attentive even at the start of their egg laying when the early nesters were still incubating (Section 3.3.2). Thus their tendency to leave the nest more often, coupled with a higher number of mobile gulls, possibly resulted in more of their nests being destroyed and the eggs eaten.

It is common in many larid species that young, late nesters are less attentive to their nests, and have little success (Coulson 1968). Nelson (1966) reported that if first-time breeding Gannets were not included in the analysis, there were no late nesters. These reports and that of Ryder (1975) would suggest that the late nesters whose eggs were destroyed and who nested primarily on the border were young gulls.

4.1.5 Success of chicks

My finding that there was no relationship between fledging success and location in the colony, agrees with the work of Dexheimer and Southern (1974) at a colony topographically similar to Granite Island. They did find a difference between the center and periphery of the colony at Bird Island where the periphery was subject to flooding. Baird (1977) found no difference in fledging success between these areas of the colony, but she based her conclusion on counting dead chicks found in each area of the colony. Although dead chicks were spread evenly throughout the colony, it does not mean that mortality in relation to hatching location was the same since chicks are mobile and more likely to be killed if they stray from their nest.

The breeding success for the study area on Granite Island of 1 chick per nest was approximately the same as that reported by Vermeer (1970) and Dexheimer and Southern (1974) for Ring-billed Gulls.

4.1.6 Mortality of chicks

I found, as did Vermeer (1970), that most chick mortality occurred during the first ten days. This is also typical of the Herring Gull (Gilman et al. 1977, Ryder and Carroll 1978). However, researchers that determine mortality by collecting dead gulls at the end of the season have different results. Baird (1977) found that mortality increased with age, and Emlen (1956) said it was maximum about 2 weeks after hatching. Both authors admitted that they probably missed many chicks that were eaten whole or were blown away in a storm. Of course, they would be the youngest, and therefore the smallest and lightest chicks, which would bias their data towards recovery of older, heavier chicks.

Abnormal chicks have been linked with increasing amounts of PCB's (Gilbertson et al. 1976). However, Pomeroy (1962) suggested that wild populations would show about 1% genetic deformities. In working on the island for 2 years, I have found only two instances of abnormalities, which were probably within the normal range as suggested by Pomeroy (1962). Ryder and Chamberlain (1972) reported an abnormal chick (polydactyly) on Granite Island but pesticide levels were well below that thought to be necessary to cause deformities (Ryder 1974). Thus genetic deformities account for a small percentage of chick mortality on Granite Island, probably well within normal limits.

4.1.7 Nearest neighbour analysis

The mean inter-nest distance on Granite Island was greater than that found by Vermeer (1970) for Ring-billed Gulls (86 cm. vs. 60 cm.), but he had measured from nest rim to rim, rather than from center to center as I did. He found that the nest spacing differed significantly from randomness to aggregated spacing. The gulls on Granite Island did tend to nest in clumps, but the GMASD does not differentiate between uniform and aggregated spacing. The tendency to random distribution on the periphery could have been a result of the low nest density relative to the center. High nest densities, such as those found in Royal Tern colonies, exhibited hexagonal packing of nests (Buckley and Buckley 1977). A tendency to uniformity in spacing has been reported for dense colonial nesters such as Black-headed Gulls (Patterson 1965), Ross's Goose (Anser rossii) (Ryder 1972) and Brewer's Blackbird (Horn 1968).

Hunt and Hunt (1976) found the size and quality of the territory, in terms of cover for the chicks, were more important in determining chick survival than nearest neighbour distance. However, when territory size is at an optimum, inter-nest distances do become important (Hunt and Hunt 1975). Thus in the center of the colony where fledging success was positively correlated with nearest neighbour distance, territory size was likely at an optimum. The negative correlation found on the periphery was difficult to interpret. It was probably an artifact resulting from two nests in the sample whose nearest neighbour distance was far higher than the mean, and whose fledging success was low. All other inter-nest distances were smaller than these and were associated with a higher fledging success.

The optimum nearest neighbour distance in the center of the colony appeared to be the result of a compromise. Gulls that nested closer together than the mean had an increased hatching success, possibly as a result of increased social stimulation to stay on the nest. However, they fledged the fewest chicks since a close neighbour meant an increased chance of being pecked to death. Gulls that nested far apart had the highest fledging success since their chicks were relatively safe from their neighbours. However, they also had the lowest hatching success, possibly because of reduced social stimulation. The result was that gulls that compromised between these two factors produced the most chicks per egg laid.

4.1.8 Known-age birds

My sample of known-age birds is small, but some interesting speculations can be made. In 1976, all the gulls whose leg bands were recorded were 3 or 4 years old. In 1977, most (82%) of the trapped gulls were primarily 4 and 5 years old. All gulls in 1977 had a high hatching success, regardless of age or location. This is in agreement with the colony as a whole in that location is not as important as breeding early and laying 3 eggs. However, it also indicates that age is not as important as time of breeding. A young gull that is aggressive enough to obtain a nest site and nest early will likely be as successful as his elders (Wooler and Coulson 1977). Ryder (1976) suggested that young gulls nesting early were allowed to keep a territory by nesting near a relative that was not as aggressive to him as it would be to an unrelated young gull. The increased stimulation to incubate from the presence of attentive adults would possibly increase its own success.

The banded birds indicated that it is probably the male that returns to its natal colony, bringing a female from another colony with it to promote gene flow between colonies.

Banded birds are going to be of increased importance in future years to learn breeding success in relation to age, site tenacity, mate retention, possible family groups on the colony and longevity.

4.2 Artificially incubated eggs

In 1977, significantly fewer eggs collected from the periphery hatched, relative to those collected from the center. This is possibly a result of jarring during transportation. Romanoff (1972) noted that such jarring increased embryo mortality to over 40% for embryos 4 to 11 days old. Subsequently, such effects decrease rapidly. The eggs I collected from the center were at least 14 days old (based on backdating from the day of hatch), whereas those from the periphery averaged 9 days when collected and transported. Thus, based on the results of artificially incubating eggs for 2 years, there did not appear to be any difference in the inherent hatchability of eggs from the two areas of the colony. This substantiated the results of Ryder et al. (1977) and Ryder and Somppi (1977). These studies and the present one indicated that there was no cause, within the eggs, for a reduced hatching success on the periphery of the colony relative to the center.

4.3 Incubation attentiveness

4.3.1 Egg exchange

Transferring eggs from one nest to another did not reduce the viability of the egg through damage in transport, since they maintained the same hatching success as control eggs. This was probably because the eggs were moved immediately upon clutch completion, before incubation was completely effective (Vermeer 1970). The embryos then, would not have developed to the age when jarring would harm them (Romanoff 1972). Parsons (1975) transferred Herring Gull eggs without ill effect.

The results of this study are at variance with those of Parsons (1976) who reported that Herring Gulls that nested in the less dense areas (on the fringe) had a lower hatching success than those in dense areas even when the former nested early in the season. Possibly, predation was a factor in that study.

4.3.2 Photographic monitoring of attentiveness

Skutch (1976) stated that 60-80% was the normal level of incubation for temperate and tropical birds. Larids typically incubate over 90% of the time as reported for the Herring Gull (Baerends and Drent 1970), the Laughing Gull (Burger 1976) and the Common Tern (Courtney 1977).

I found that Ring-billed Gulls were, on average, over 90% attentive. Emlen and Miller (1968) reported they were virtually 100% attentive late in incubation. This would seem to be more than is required for successful embryo growth since Hunter et al. (1976) exposed Ring-billed Gull eggs to 10 C for 4 hour periods at various stages in incubation without reducing hatching success.

I found no relationship between attentiveness and hatching success. This was probably the result of the gulls spending more than the minimum required time on the eggs so any variations in time spent off the nest above this minimum would not be reflected in hatching success. This was similar to the findings of Courtney (1977) for Common Terns and Morris and Haymes (1977) for Herring Gulls. Morris and Hunter (1976) did find a relationship between attentiveness and hatching success in Common Terns. However, this was based on a sample of 4 nests and the conclusion is therefore tenuous.

Gulls nesting after the peak of clutch initiation were not as attentive as early nesters. Although there was still no relationship between attentiveness and hatching success when all the late nesters were grouped, the very late gulls that started nesting when most other clutches were ready to hatch were interesting. I only have a film record of these gulls for their early incubation (the last day before the early gulls started hatching their eggs). They had no success but five out of the eight gulls were on their nests over 90% of the time. Unfortunately, I could not quantify their attentiveness after this point but nest histories indicated the gulls simply stopped incubating since the eggs became cold and eventually were scattered over the ground. It seemed that these late nesters needed the social stimulation of other incubating gulls to keep them on the nest, especially since late nesters on the less dense periphery were less attentive than those in the dense center. Ryder (1975, 1976) suggested that low egg success of immature-plumaged pairs was the result of reduced attentiveness. I suggest that the late nesters were these young gulls and in this case, where attentiveness dropped below the minimum required amount, it was definitely related to hatching success.

4.4 General discussion

I originally hypothesized, based on literature cited throughout this paper, that gulls nesting on the periphery of the Granite Island Ring-billed Gull colony would hatch fewer eggs and raise fewer young than gulls in the center of the colony. Previous investigations had revealed no difference in component quantities of the eggs or in embryo growth of eggs from the two areas, but had suggested that a lack of attentiveness in gulls nesting on the border was responsible for their poor success.

My study revealed, over the 2-year period, no difference in parental attentiveness with respect to location. However, I also found no difference in the ability of gulls to hatch eggs and raise young relative to location. This was true whether only 3-egg clutches initiated early were considered (as in experimental work during the two years), or whether all nests regardless of clutch size and time of initiation were considered (as in 1977).

The reason for this appeared to be that the study area on Granite Island had stabilized. Gulls are expanding into unused habitat in other areas of the island, but there is no space for them to expand the study area without nesting in the forest. Larids, when possible, do return to the same site to nest each year; gulls that initially nest on the periphery probably do not attempt to enter the center in subsequent years. Thus on Granite Island, where the border is inflexible, the gulls are becoming older and more experienced and their success is equivalent to that of gulls in the center. Proportionately more late-arriving gulls did nest on the periphery since it was still less dense than the center and there was room for more nests. It was these late arrivals that depressed the hatching success of the periphery relative to the center, but there were not enough of them to make the difference significant. Probably in later years, as these young nesters get older, and the border is as dense as the center, with no room for late, less successful breeders, all differences between the center and periphery will disappear.

In summary then, the concept of central versus peripheral areas of a colony is one that cannot be accepted a priori for every colony. Not only is each colony different, but within an individual colony the condition is not static. A new colony will have no difference between its center and periphery since all the gulls will be young and its overall success will be low. A growing colony will exhibit this difference as the periphery is constantly growing out with each influx of young gulls and the center will be occupied by older, more successful pairs. A colony that has reached the limit of its expansion will be composed primarily of older gulls and success will approach, or be, equivalent across the colony. Of course, a colony whose border is subject to flooding or predation will always have a peripheral area in which gulls hatch fewer eggs and raise fewer young than those gulls nesting in the center of the colony free from such distrubances. In a colony such as on Granite Island, success relative to location was unimportant; success depended upon clutch size and timing of breeding.

5. LITERATURE CITED

Baerends, G.P. and R.H. Drent. 1970. The Herring Gull and its Egg. Behaviour Suppl. 17 : 1-312.

Baird, P.A. 1976. Comparative ecology of California and Ring-billed Gulls (Larus californicus and L. delawarensis) Ph. D. thesis, Univ. Montana. 183pp.

Beer, C.G. 1965. Clutch size and incubation behaviour in Black-billed Gulls. Auk 82 : 1-18.

Brown, D. 1975. A test of randomness of nest spacing. Wildfowl 26 : 102-103.

Buckley, F.G. and P.A. Buckley. 1972. The breeding ecology of Royal Terns (Sterna (Thalasseus) maxima maxima). Ibis 114 : 344-359.

Buckley, P.A. and F.G. Buckley. 1977. Hexagonal packing of Royal Tern nests. Auk 94 : 36-43.

Burger, J. 1976. Daily and seasonal activity patterns in breeding Laughing Gulls. Auk 93 : 308-323.

Chamberlain, D. 1973. Nesting Dynamics of Ring-billed Gulls. Hon. B.Sc. thesis Lakehead Univ., Thunder Bay, Ontario. 38pp.

Coulson, J.C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull. J. Anim. Ecol. 35 : 269-279

Coulson, J.C. 1968. Differences in the quality of birds nesting in the center and on the edges of a colony. Nature 217 : 478-479.

Coulson, J.C., G.R. Potts and J. Horobin. 1969. Variation in the eggs of the Shag (Phalacrocorax aristotelis). Auk 86 : 232-245.

Courtney, P.A. 1977. Selected aspects of Common Tern reproductive biology. M.Sc. thesis Brock Univ. 83pp.

Derksen, D. 1977. A quantitative analysis of the incubation behaviour of the Adelie Penquin. Auk 94 : 552-566.

Dexheimer, M. and W. Southern. 1974. Breeding success relative to nest location and density in Ring-billed Gull colonies. Wilson Bull. 86 : 288-290.

Dinsmore, J. and R. Schreiber. 1974. Breeding and annual cycle of Laughing Gulls in Tampa Bay, Florida. Wilson Bull. 86 : 419-427.

Dunbar, R.I.M. 1976. Some aspects of research design and their implications in the observational study of behaviour. Behaviour 58 : 78-98.

Emlen, J.T. Jr. 1956. Juvenile mortality in a Ring-billed Gull colony. Wilson Bull. 68 : 232-238.

Emlen, J. and D. Miller. 1968. Pace-setting mechanisms of the nesting cycle in the Ring-billed Gull. Behaviour 32-33 : 237-261.

Fox, G., A. Gilman, D. Peakall and F. Anderka. 1978. Behavioural abnormalities of nesting Lake Ontario Herring Gulls. J. Wildl. Mange. (in press).

Gilbertson, M., R. Morris and R. Hunter. 1976. Incidence of abnormal chicks and residue levels of PCB in eggs of colonial bird species on the lower Great Lakes (1971-1973). Auk 93 : 434-442.

Gilman, A., G. Fox, D. Peakall, S. Teeple, T. Carroll and G. Haymes. 1977. Reproductive parameters and egg contaminant levels of Great Lakes Herring Gulls. J. Wildl. Mange. 41 : 458-468.

Graham, F. Jr. and C. Ayres. 1975. Gulls : a Social History. Random House, Toronto. 179pp.

Harrington, B.A. Jr. 1974. Colony visitation behaviour and breeding ages of Sooty Terns (Sterna fuscata). Bird-Banding 45 : 115-144.

Horn, H. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (Euphagus cyanocephalus). Ecology 49 : 682-693.

Hunt, G. Jr. and M. Hunt. 1975. Reproductive ecology of the Western Gull: the importance of nest spacing. Auk 92 : 270-279.

Hunt, G. Jr. and M. Hunt. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57 : 62-75.

Hunt, G. Jr. and M. Hunt. 1977. Female - female pairing in Western Gulls (Larus occidentalis) in southern California. Science 196 : 1466-1467.

Hunter, R., H. Ross and A. Ball. 1976. A laboratory simulation of predator-induced incubation interruption using Ring-billed Gull eggs. Can. J. Zool. 54 : 628-633.

Leck, C. 1971. Nocturnal habits of Ring-billed Gulls (Larus delawarensis) at Thimble Shoal, Virginia. Chesapeake Science 12 : 188.

Langham, N.P. 1968. The biology of the terns, Sterna spp. Ph.D. thesis, Univ. Durham. number of pages unknown.

Ludwig, J.P. 1974. Recent changes in the Ring-billed Gull population and biology in the Laurentian Great Lakes. Auk 91 : 575-594.

Merilees, W. 1974. Ring-billed and California Gull nesting colony in south central British Columbia. Can. Field-Nat. 88 : 484-485.

Montevecchi, W. 1976. Egg size and the egg predatory behaviour of crows. Behaviour 57 : 307-320.

Morris, R. and G. Haymes. 1977. The breeding biology of two Lake Erie Herring Gull colonies. Can. J. Zool. 55 : 796-805.

Morris, R. and R. Hunter. 1976. Monitoring incubation attentiveness of ground-nesting colonial seabirds. J. Wildl. Manage. 40 : 354-357.

Nelson, J.B. 1966a. The breeding biology of the Gannet <u>Sula bassana</u> on the Bass Rock, Scotland. Ibis 108 : 584-626.

Nelson, J.B. 1966b. Population dynamics of the Gannet <u>Sula bassana</u> at the Bass Rock, with comparative information from other Sulidae. J. Anim. Ecol. 35 : 443-470.

Newton, I., M. Marquiss, D. Weir and D. Moss. 1977. Spacing of sparrowhawk nesting territories. J. Anim. Ecol. 46 : 425-441.

Nie, N., C. Hull, J. Jenkins, K. Steinbrenner and D. Bent. 1970. Statistical Package for the Social Sciences. McGraw-Hill Inc. N.Y. 675pp.

Nisbet, I.C.T. and W. Drury, 1972. Measuring breeding success in Common and Roseate Terns. Bird-Banding 43 : 97-106.

Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull, <u>Larus argentatus</u>. Ibis 117 : 517-520.

Parsons, J. 1976. Nesting density and breeding success in the Herring Gull <u>Larus argentatus</u>. Ibis 118 : 537-546.

Patterson, I.J. 1965. Timing and spacing of broods in the Black-headed Gull (<u>Larus ridibundus</u>). Ibis 107 : 433-543.

Pearson, T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37 : 521-552.

Pomeroy, D.E. 1962. Birds with abnormal bills. Br. Birds 55 : 49-72.

Romanoff, A.L. 1972. Pathogenesis of the Avian Embryo. Wiley-Interscience, New York. 476pp.

Ryder, J.P. 1972. Biology of nesting Ross's Geese. Ardea 60 : 185-215.

Ryder, J.P. 1974. Organochlorine and mercury residues in gulls' eggs from Western Ontario. Can. Field-Nat. 88 : 349-352.

Ryder, J.P. 1975. Egg-laying, egg size and success in relation to immature-mature plumage of Ring-billed Gulls. Wilson Bull. 87 : 534-542.

Ryder, J.P. 1976. The occurrence of unused Ring-billed Gull nests. Condor 78 : 415-418.

Ryder, J.P. 1978. Sexing live Ring-billed Gulls externally. Bird-Banding (in press).

Ryder, J.P. and T.R. Carroll. 1978. Reproductive success of Herring Gulls on Granite Island, northern Lake Superior, 1975 and 1976. Can. Field-Nat. 92 : (in press).

Ryder, J.P. and D.J. Chamberlain. 1972. Congenital foot abnormality in the Ring-billed Gull. Wilson Bull. 84 : 342-344.

Ryder, J.P., D. Orr and G. Saedi. 1977. Egg quality in relation to nest location in Ring-billed Gulls. Wilson Bull. 89 : 473-475.

Ryder, J.P. and L. Somppi. 1977. Growth and development of known-age Ring-billed Gull embryos. Wilson Bull. 89 : 243-252.

Shugart, G. and W. Southern. 1978. Close nesting, a result of polygyny in Herring Gulls. Bird-Banding 48 : 276-277.

Skutch, A.F. 1976. Parent Birds and their Young. Univ. Texas Press. Austin. 503pp.

Southern, W. 1974. Florida distribution of Ring-billed Gulls from the Great Lakes region. Bird-Banding 45 : 341-352.

Spaans, A. and M. Spaans. 1975. Some data on the breeding biology of the Herring Gull (Larus argentatus) on the Dutch Frisian island of Terschelling. Limosa 48 : 1-39.

Spurr, E.B. 1974. Individual differences in aggressiveness of Adelie Penguins. Anim. Behaviour 22 : 611-616.

Spurr, E.B. 1975. Breeding of the Adelie Penguim Pygoscelis adeliae at Cape Bird. Ibis 117 : 324-338.

Steel, R. and J. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill, Inc. N.Y. 481pp.

Temple, S.A. 1972. A portable time-lapse camera for recording wildlife activity. J. Wildl. Manage. 36 : 944-947.

Tenaza, R. 1971. Behaviour and nesting success relative to nest location in Adelie Penguins (Pygoscelis adeliae). Condor 73 : 81-92.

Tinbergen, N. 1960. A Herring Gull's World. Harper and Row, N.Y. 255pp.

Vermeer, K. 1970. Breeding biology of California and Ring-billed Gulls. Can. Wildl. Serv. Rep. Ser. 12 : 1-52.

Wooller, R. and J. Coulson. 1977. Factors affecting the age of first-breeding of the Kittiwake *Rissa tridactyla*. Ibis 119 : 339-349.

Appendix A

Leg band numbers, age and nest location

of Ring-billed Gulls on Granite Island, 1976 *

Leg Band Number	Year Banded	Age in 1976	Nest Location
72566710	1973	3	not nesting
72577349	1972	4	nest in center
75542884	1973	3	nested late on periphery
27577152	1972	4	nest in center
72577138	1972	4	nest in center
72577164	1972	4	nested late on periphery
72566831	1973	3	nest on periphery
72566775	1973	3	possibly not nesting
72566870	1973	3	nest on periphery
75542907	1973	3	nest on periphery

* All gulls were banded on Granite Island as chicks.

Appendix B

Leg band numbers, age, nest location and sex

of trapped Ring-billed Gulls, Granite Island, 1977

Leg Band Number	Year Banded	Age in 1977	Nest Location	Sex
72577376	1972	5	periphery	female
72577392	1972	5	center	male
72577168	1972	5	periphery	female
72574256	1971	6	periphery	male
75544496	1974	3	periphery	male
72566864	1973	4	center	male
75542640	1973	4	center	male
72574416	1972	5	center	female
72577120	1972	5	center	male
72566912	1973	4	center	male
72566720	1973	4	center	male

Appendix C

Hatching success in relation to
week laid in central and peripheral areas
of the Ring-billed Gull colony, Granite Island, 1977

	Hatching Success	
Week Laid	Center	Periphery
1	79% ($^{30}/38$)*	83% ($^{5}/6$)
2	79.6% ($^{363}/456$)	79% ($^{58}/73$)
3	57.1% ($^{185}/324$)	75.0% ($^{75}/100$)
4	32.1% ($^{17}/53$)	10.0% ($^{2}/20$)
5	19.0% ($^{13}/67$)	0 ($^{0}/19$)
6	0 ($^{0}/14$)	0 ($^{0}/8$)
7	0 ($^{0}/5$)	0 ($^{0}/4$)
8	0 ($^{0}/7$)	0 ($^{0}/1$)
9	-	0 ($^{0}/5$)
	608 hatched	140 hatched

* Number of eggs hatched over number laid.

Note: 74 central eggs and 10 peripheral eggs had unknown laying dates. Of these, 10 hatched in the center and 4 hatched on the periphery (backdating gave a choice of 2 weeks). As a result, totals differ from Appendix D and E.

Appendix D

Hatching success in relation to clutch size in central and peripheral areas of the Ring-billed Gull colony, Granite Island, 1977

	Hatching Success	
Clutch Size	Center	Periphery
1	26.3% (5/19)*	0 (0/4)
2	59.0% (59/100)	50.0% (12/24)
3	78.7% (411/522)	65.9% (89/135)
4	58.1% (86/148)	58.3% (35/60)
5	26.4% (33/125)	50.0% (5/10)
6	18.8% (18/96)	0 (0/6)
7	21.4% (6/28)	42.8% (3/7)

* Number of eggs hatched over number laid. To determine the number of clutches of each size, divide the number of eggs laid by its respective clutch size.

Appendix E

Fledging success in relation to date hatched

in central and peripheral areas

of the Ring-billed Gull colony, Granite Island, 1977

	Fledging Success	
Week Hatched	Center	Periphery
6	42.4 % ($\frac{12.71}{30}$)*	
7	55.8% ($\frac{195.2}{350}$)	56.5% ($\frac{31.07}{55}$)
8	54.1% ($\frac{116.9}{216}$)	60.6% ($\frac{49.71}{82}$)
9	55.5% ($\frac{7.77}{14}$)	17.7% ($\frac{1.06}{6}$)
10	46.4% ($\frac{3.71}{8}$)	Only 1 egg hatched

* Calculated number fledged over number hatched. For calculation of number fledged, see Section 3.1.5.