THE BREEDING BIOLOGY OF THE HERRING GULL IN NEWFOUNDLAND

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Herring Gull (*Larus argentatus*) populations in Europe have undergone spectacular increases since 1930 (Voous 1960, Harris 1970), the species having extended its range (Géroudet 1968) and type of nesting habitat (Goethe 1960, Cramp 1971). In North America similar increases have been taking place. At the turn of the century egging and taking of chicks had reduced the Herring Gull population of the New England States and Maritime Provinces to a low level, but legal protection and progressive urbanization have allowed it to recover, and populations have been doubling every 12 to 15 years since the early 1900's (Kadlec and Drury 1968). Because of the increasing threat of gull strikes to aircraft (Drury 1963), their encroachment on waterfowl (Amadon 1958, Grenquist 1965), pollution of reservoirs, and possible role in the dissemination of disease (Silverman and Griffiths 1955, Brough 1969), their biology has been studied intensively in recent years. As this species has been little studied in the northwestern North Atlantic, we studied its breeding biology in a colony on Gull Island, Witless Bay, Newfoundland during the summers of 1969–71.

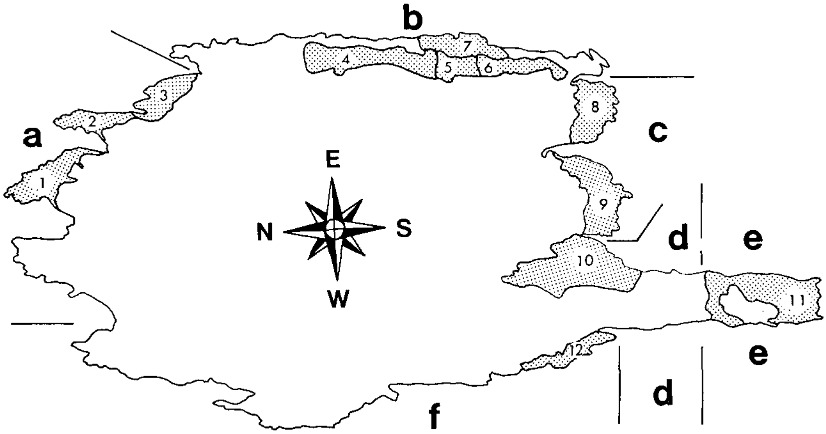

Fig. 1. Showing parts of Gull Island where density of Herring Gull nests was determined. Predation study nests in area 12. The Point is area 11. The east side square was located in regions 5 and 7. a, Northeast Sector; b, east side; c, south side; d, Peat Valley and base of Point; e, the Point; f, west side.

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MATERIALS AND METHODS

Gull Island (47° 15′ N, 52° 46′ W) is briefly described in Maunder and Threlfall (1972). Various aspects of the breeding biology of the gulls investigated during the May–August period of 1969–71 included the density of nests in various parts of the colony, nesting materials, time course of egg-laying, incubation period, size and weight of eggs, growth of embryos and chicks, loss of eggs and young, and food.

We determined the density of gull nests in various parts of the island during the first half of June. The nests were counted in 5 to 15 10 × 10 m squares in each of the areas shown in Fig. 1 (natural divisions separate the areas), the average number of nests per square being taken as the nest density for that area. Random placement of the squares was attempted, using the grid system described in Haycock (1973).

Progress of egg-laying was followed in two places, the Point (Fig. 1) and a sector on the east side that was measured off to contain a comparable number of nests. In each of these sectors, the number of nests containing 0, 1, 2, and 3 eggs were counted approximately once a week, from mid-May, when the first visits were made to the island, until the eggs began to hatch. Earlier visits to the islands were prevented by arctic pack ice and the unavailability of boats for transportation. The peak laying time for each sector was then calculated, as was clutch size. The normal clutch for the Herring Gull is three eggs, but some lay two, a few lay one, and exceptionally a few lay four (Paludan 1951). Clutch size for 1970 was taken as the maximum average clutch size reached in periodic surveys of the Point and east side square; for 1971 it was the average of 109 marked nests on the Point.

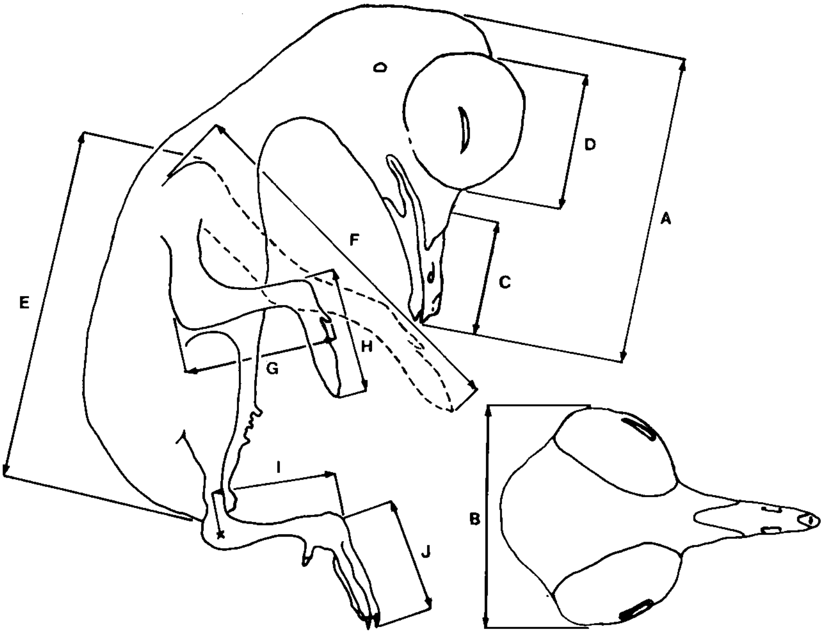

Fig. 2. Measurements taken on Herring Gull embryos. A, head length; B, head width; C, culmen; D, eye diameter; E, shoulder to tail length; F, arm length; G, forearm; H, hand; I, tarsus; J, middle toe.

We investigated egg-laying, incubation, and fate of eggs and young by making regular observations at a number of nests that initially had no eggs in them (in mid-May) or were only just being built. We checked nests in 1969 and 1970 until the young were a few days old. In 1971, we followed the progress of 113 nests until the chicks were about 5 weeks old, daily counts being replaced by checks at 2- to 7-day intervals when the chicks were about 3 weeks old. Information on incubation period, size of eggs, and weight changes of eggs during incubation were also determined at the marked nests. Eggs were measured with Vernier calipers and weighed in a plastic bag suspended below a spring balance (Ohaus Model 8011, 250 g capacity, accurate to ± 5 g).

We studied embryonic growth using the embryos from 25 known-age Herring Gull eggs taken at various stages of incubation. The embryos were dissected from their extraembryonic membranes, preserved in 5% formalin, and later drained on a paper towel and weighed and measured (Fig. 2).

We designated 22 3-egg clutches for a study of chick growth and surrounded nine nests with pens of ½-inch mesh hardware cloth 1.2 m in diameter and 0.6 m high.

Chicks were weighed in a plastic bag suspended below a spring balance. Culmen and tarsus were measured in the same way as the embryos. Wing measurements were taken along the natural curve of the wing after primaries erupted from their sheaths. Measurements were made daily (less often in older chicks) at about the same time, until the chicks fledged or disappeared. Notes were taken on ptilosis.

Records were kept of regurgitations of chicks, food found at the nests, and pellets found on visits to the study tracts.

RESULTS AND DISCUSSION

Templeman (1945) noted that the Herring Gull was the most common Newfoundland "sea-bird," while both Peters and Burleigh (1951) and Tuck (1967) reported that its numbers were increasing. On Gull Island the number of breeding pairs rose from 2033 in 1969 to 2663 in 1972. The average annual rate of increase is comparable with some of the most rapidly increasing colonies reported (Brown 1967, Parsons 1969). To determine if any changes in nest density had taken place during the period of increase, nests were counted in randomly placed 10-m squares and various areas were compared (Table 1, Fig. 1). A great deal of variation was found, which generally did not reflect the population changes in the same regions of the island. Thus either the placement of squares or the placement of nests was nonrandom within the area. Random placement of squares was difficult over large tracts, and errors from nonrandom placement were accentuated by the small sample size (5 to 15 squares per tract). The more important factor was nonrandom placement of nests. Nests were built on rock or on grass and bare peat. Nest density was higher on the rock surfaces than on the grass (3.98 vs. 3.07/100 m^2, $P < 0.01$) and still higher at the interface between them (8/100 m^2). In area 4 (Fig. 1), the density of the southern half was approximately twice that of the northern half, although the habitat appeared identical; possibly this indicates a spread from the

TABLE 1
DENSITY OF GULLS' NESTS IN VARIOUS NATURAL REGIONS OF GULL ISLAND

	Numbered areas in Fig. 1	Number of nests/100 m^2		
		1969	1970	1971
Northeast sector	1	3.0	2.2	–
	2	–	2.6	–
	3	4.5	3.0	4.4
East side	4	2.5	3.5	4.2
	5	2.6	2.7	3.0
	6	2.7	2.4	2.8
	7	6.6	3.5	7.0
South side	8	6.2	3.2	4.1
	9	4.2	2.9	3.3
Peat Valley and base of Point	10	3.4	3.4	2.8
The Point	11	5.0	2.9	3.9
West side	12	2.1	3.2	2.8

more densely occupied area 7. Even minor variations in topography result in changes in spacing of nests. Intervisibility of nests is important (Bongiorno 1970); on bare peat visibility was totally unobstructed, and very few gulls nested here. On grass, with a few additional obstructions such as dead trees, nests were more numerous, but still more widely spaced than on the rough, craggy terrain of rocks. On the rocks, nests were occasionally placed as little as 30 cm apart, though on different levels, or where the view was obstructed between them.

On grassy slopes we noted a strong tendency to place nests at the base of some prominence, such as a boulder, tree, or tree stump. No gulls nested among dense shrubs such as raspberries (*Rubus idaeus*), but a few Herring Gulls (30 pairs) nested up to 4 m into open woods, usually building the nest under a fir tree, always with a well-worn access tunnel leading through the vegetation. We found about 20 nests in small clearings high in the woods, on terrain sloping toward the sea.

Nests were situated in a small depression, crack or crevice, 6 to 15 cm deep (the nest scrape, Tinbergen 1953), such depressions being plentiful on the rock surfaces of the Point and the east side (Fig. 1). Particular sites were used year after year, e.g. the locations of many nests on the Point were identical in 1970 and 1971. Salomonsen (1939) attributed the high tenacity of rock nesting Herring Gulls to their nest sites (compared to those nesting in grass) to the comparative difficulty of finding suitable depressions.

Nest building was well underway by mid-May, and continued until the chicks hatched. As various plant species developed they were added to the nests. During inclement weather all nest building ceased for as much as a week; with improvement in the weather, much new material appeared on the nests. Nest building was at a peak on the day immediately following a period of rain. Maunder (1971) found a similar correlation between periods of rain and nest building in kittiwakes, but associated this with softness of the turf, which kittiwakes may need to take the roots and earth they use in their nests. Roots and earth formed only a minor component of most Herring Gulls' nests; apparently the rain had an inhibiting effect on the normally frequent collection of nesting material in this species. Nests were normally composed of the most readily available organic material 50 to 100 m from the nest site, e.g. grasses (*Festuca* and *Deschampsia* spp.), *Rubus idaeus, Rumex acetosella, Lathyrus japonicus, Stellaria media, Dryopteris spinulosa,* and *Osmunda cinnamomea.* Nests often contained gull feathers and the indigestible remains of food, such as bones, mussel (*Mytilus edulis*) shells, sea urchin (*Strongylocentrotus drobachiensis*) tests, petrel (*Oceanodroma leucorhoa*) feathers, and occasionally such man-made objects as plastic gill net floats and prayer beads. The size and weight of the nests reflected the materials they were made of. The usual inside diameter across the top of the nest cup was 20 cm while the external width at the base of the nest varied from 40 to 60 cm, and the height of the rim from 8 to 15 cm above the substrate. Weights varied from 192 g (one nest made of dry twigs) to 3177 g (one nest composed of compacted grass, mosses, roots, and earth).

By the time the first observations were made in May egg-laying had already begun. We followed the continuing progress of laying on the Point and in the east side square (Fig. 1). Average clutch size reached a maximum earlier (25 May 1971) in the east side square than on the Point (30 May 1971) and the rate of egg-laying (measured by the increase in average clutch size) was also greater in the east side square. Hatching began in the east side square earlier than anywhere else on the island (31 May 1970 and 22 May 1971). Taking the incubation period for Herring Gulls as 28 days, the first successfully hatched eggs must have been laid on 3 May 1970, and on 24 April 1971. Goethe (1937) and Paynter (1949) found that hatching (and therefore laying) first occurred in places of highest nest density, from which it radiated outward as the season advanced. The same situation obtained on Gull Island, chicks first being noted in the densely populated east side square.

Fig. 3 shows the pattern of clutch initiation in 1971 in a set of marked nests on the Point. It is similar to the latter half of the clutch-initiation pattern found by Paludan (1951) and Harris (1964). Thus by comparison with the above studies, the probable mean date of clutch initiation on Gull Island (the Point) would be about 10 to 14 May 1971. This date is comparable to the mean laying date at more northerly colonies

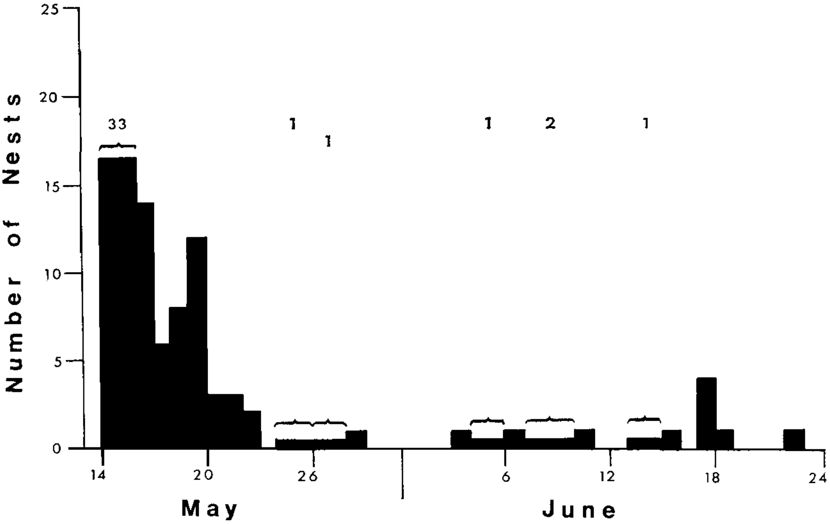

Fig. 3. Pattern of laying in Herring Gulls from Gull Island, Newfoundland, 1971. (Number of nests in which the first egg was laid on a given date.)

in the eastern North Atlantic, such as Troms, Norway (16 May, Barth 1968); Priest Island, Scotland (15 May, Darling 1938); and the Isle of May, Scotland (18 May, Parsons 1971a). In North American coastal colonies the mean laying dates (calculated from hatching dates) were 1 June on Kent Island, Bay of Fundy (Paynter 1949) and 14 to 27 May in several New England colonies (Kadlec and Drury 1968). Thus while egg-laying tends to be delayed with increasing latitude, exceptions and reversals occur, of which several European colonies (Paludan 1951, Barth 1968, Drent 1970) and Gull Island are examples. Light regime, a constant and dependable factor of the environment, directly related to latitude, is an important factor in the timing of avian breeding cycles; however, modifying or supplementary factors in local conditions seem also to be critical (Marshall 1959, Farner 1964).

Seven of the last eight clutches shown in Fig. 3 were replacements of clutches that had been destroyed. Of these, one in a place subject to heavy predation was begun 30 to 32 days and another 22 days after the loss of the original clutch. In the other five laying began 12 to 14 days (mean, 12.6 days) after the disappearance of the first clutch, this being the time reported by Paludan (1951) and Parsons (1971a). Heavy predation may have obscured the actual pattern of repeat laying in the two nests built after 30–32 and 22 days as predators such as Great Black-backed Gulls (*Larus marinus*) and Herring Gulls sometimes fly off with a whole egg before devouring its contents.

TABLE 2

SEASONAL VARIATION IN CLUTCH SIZE OF HERRING GULLS

Gull Island 1971			Walney Island (Brown 1967)		
Date of commencement of clutch	Number of clutches	Average clutch size	Date of commencement of clutch	Number of clutches	Average clutch size
14–17 May	61	2.75	Until 2 May	40	2.77
18–21 May	31	2.77	3–7 May	40	2.50
22–25 May	5	2.20	8–12 May	29	2.51
26–29 May	4	2.00	After 12 May	30	2.40
After 29 May[1]	12	2.67			

[1] Higher figure may be due to inclusion of replacement clutches.

On Gull Island, the average clutch size was 2.70 in 1970 and 2.73 in 1971, only two nests with four eggs being seen among the 5000 nests examined in the 2 years. Clutch size on Gull Island is comparable to the Harris (1964) mean of 2.76, Parsons (1971a) 2.73, Paynter (1949) 2.46, Paludan (1951) 2.91, and Brown (1967) 2.56. Parsons (1971a) suggested that differences in clutch size may reflect the techniques used in the various studies and the amount of disturbance of the nests, more than real geographical differences.

Clutch size (Table 2) decreased as the season advanced, as Brown (1967) also noted. Parsons (1971a) also noted a decrease in clutch size from 2.92 to 2.36 during May, but he excluded replacement clutches from his calculations, as they are usually smaller. The exclusion of replacements and his large sample size (677 nests) leave little doubt that a seasonal decrease in clutch size is also a characteristic of Herring Gull populations on the Isle of May (replacement clutches in the Gull Island data appeared only after 29 May). Parsons found no evidence of a declining food supply, and postulated that intrinsic factors are responsible for decreasing clutch size. With replacement clutches this could be the short period (12 days) before laying, compared to the longer pre-egg stage of the original clutch (Parsons 1971a). Paynter (1949) and Harris (1964) found no such decrease.

Egg size varied with order of laying within the clutch, the mean widths and lengths of 58 first, second, and third eggs being 49.3 ± 1.4 × 70.9 ± 3.1 mm, 48.9 ± 1.2 mm × 70.2 ± 2.9 mm, and 47.6 ± 1.3 mm × 67.7 ± 3.1 mm respectively. The sizes of first and second eggs showed no significant differences, but the third egg was smaller than the first two ($P < 0.005$). This phenomenon has been noted before (Keith 1966, Brown 1967, Barth 1968, Parsons 1971a) and seems not to be related to lack of materials but to a waning of physiological processes associated with egg production (Harris 1964). Parsons (1971a,

1972) views it as a means of synchronizing the hatching of the eggs, and of giving rise to a reduced survival rate in the third chick during adverse conditions, thus improving the chance of survival of the first two. In two cases where both original and replacement clutches were measured, the replacements had a slightly lower total volume than the original clutch. Two abnormally small eggs were found, one of which measured 30.8 mm by 40.7 mm, the other being of similar size. Neither contained an embryo. Goethe (1937) reported finding such eggs, which he speculated had formed when albumen and membranes were laid down upon traces of yolk.

The incubation periods of 44 first, 48 second, and 28 third eggs were determined to within ± 1 or 1.5 days (Moreau 1946), and averaged 29.4, 28.2, and 27.1 days respectively. Incubation period is influenced by the size of the egg (Parsons 1972) and by laying date (MacRoberts and MacRoberts 1972). Parsons found the incubation period of first-laid eggs over 76 cc in volume (volume = $\text{width}^2 \times \text{length} \times 0.476$) was 29.98 ± 0.08 days. For those under 76 cc, the mean incubation period was 29.31 ± 0.11 days. The Gull Island eggs had an average volume of 79 cc, and incubation periods of 29.4 ± 1 days.

In the present study the original weight of 24 eggs averaged 95 g, and ranged from 65 to 105 g. The rate of weight loss varied substantially among individual eggs, losses during the incubation period ranging from 10.3 to 24.7% of the original weight. The average weight loss was 15.8%. These figures agree closely with Harris' (1964) mean of 15% and range of 9 to 24%. Harris stated egg weight decrease was due to loss of gaseous wastes and water vapor through the porous shell.

Development of the embryo during incubation was examined. Weight of the embryos reached 50% of the embryonic maximum at 22 days. An initial period of very rapid gain in weight was followed by a period of steady logarithmic growth when embryos were 8 to 18 days of age (Fig. 4). After 18 days the rate of weight gain decreased, as energy became concentrated on organogenesis rather than growth (Harris 1964). Drent (1970) found a steadily declining rate of weight gain, while Harris' (1964) curve showed an exponential increase in weight until the 15th day, followed by a sharp falling off in the rate of increase. The average rate of weight increase Harris (1964) noted over the whole incubation period was 2.0 g per day, compared to 1.9 g per day on Gull Island. Data on embryonic growth are presented below and in Fig. 5.

Day 6, embryonic heart, brain, eye lenses well formed; small forelimbs, hind limb buds. Day 7, mouth, bill and rudimentary digits on forelimbs visible; eyelids beginning to cover heavily pigmented eyes; fore- and mid-brain growing rapidly. Day 10 (head width: 50% embryonic maximum).

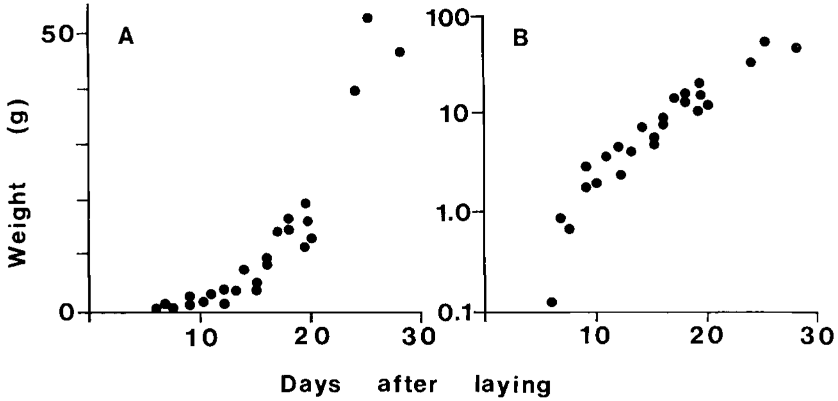

Fig. 4. Weights of Herring Gull embryos. A, linear scale; B, logarithmic scale.

Day 11, pterylae visible; eyes, eyelids, bill further developed; forelimbs winglike; three anterior toes of feet webbed; feather papillae became pigmented after this day; hallux and alula start to become prominent. Day 12 (eye diameter: 50% embryonic maximum). Day 13 (body length, head length, bill length: 50% embryonic maximum); growth after this day included eyelids, feathers, body size, hardening of bill. Day 15 (arm length: steady growth from day 10–28). Day 16 (tarsal length: 50% embryonic maximum); egg tooth and toenails visible. Day 18–20 (middle toe: 50% embryonic maximum).

Maunder's (1971) growth curves for kittiwake embryos show a time course of development almost identical to that of the Herring Gull (Fig. 5). The middle toe reached the midpoint of its embryonic growth on the 19th day, as it did in the Herring Gull. However the tarsus of kittiwake embryos reached this point later (18 days) than those of Herring Gull embryos (16 days). Thus at hatching the legs are relatively underdeveloped compared to those of the Herring Gull. The slow development of the legs (but not the feet) in the kittiwake may be correlated with the chicks' precipitous habitat and tendency to crouch when alarmed (Cullen 1957), in contrast to Herring Gull chicks, which tend to run. Eggs hatched approximately 28 days after laying; chicks emerged from first- and second-laid eggs 1 to 4 days before those from the third egg.

Preliminary plotting of the weights of chicks used in the growth study showed a great deal of individual variation in maximum weight attained and time required to attain it, as well as large daily fluctuations in the weight of individuals, which apparently resulted from their feeding schedules and whether they regurgitated before being weighed. An

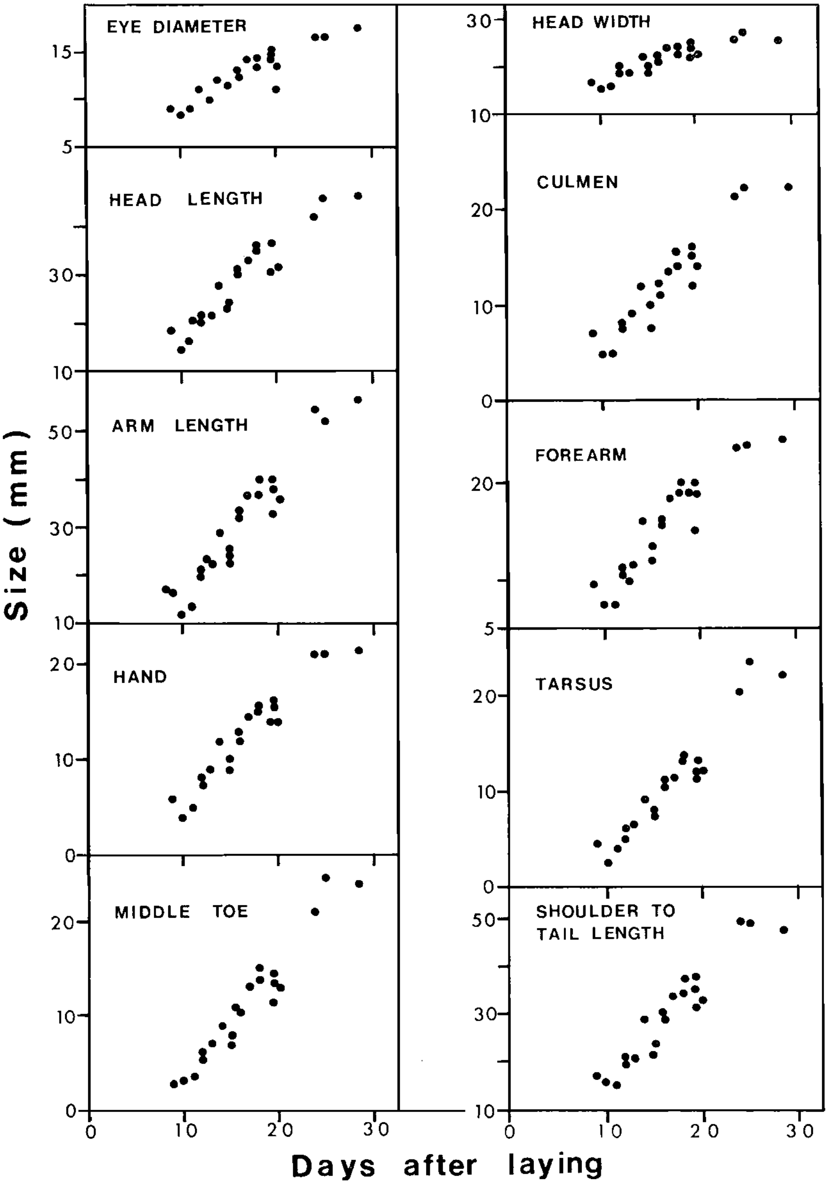

Fig. 5. Measurements of various parts of Herring Gull embryos taken at various stages of incubation.

analysis of variance among measurements on chicks that eventually fledged showed a significant difference in growth among the chicks, even among those treated in the same way (kept in pens or free). Therefore averaging the growth curves to compare the effect of the treatment (penning the chicks) would have no meaning: individual curves had to be compared rather than the average growth curves. Large individual differences in the weights attained by gull chicks were also found by Harris (1964), Kadlec et al. (1969), and Smith and Diem (1972).

The general shapes of the growth curves were quite uniform, and similar to a third order (cubic) function. Thus a third order regression line $y = b(0) + b(1)\ x + b(2)\ x^2 + b(3)\ x^3$ was fitted to each curve by the method of the least square fit (Fisher 1967). This reduces the data to four parameters without any significant loss of information (b(0), b(1), b(2), b(3)). The parameters of the curves of individual birds could then be compared. When the growth parameters were derived from the equation above for all the chicks and these were compared using a multivariate analysis, this variation did not seem to be related to order of hatching in the brood, and the experimental pens had little if any effect. Differences may be partly due to sexual dimorphism. Adult male Herring Gulls taken at Witless Bay were somewhat heavier than adult females, 32 males ranging from 1093 to 1336 g, and 9 females ranging from 937 to 1118 g. Goethe (1956) found similar ranges (1025 to 1315 g for males, 865 to 1090 g for females) in weights of birds taken in November of their first year, that is at about 5 months of age. Thus it is not unreasonable to suspect that the sexes may fledge at different weights. Food has also been noted as a factor in some studies (Harris 1964, Fordham 1970, Hunt 1972); while inherent genetic variability, rivalry among siblings, and parental care are probably also important factors causing individual differences in growth (Brown 1967, Smith and Diem 1972). In general, maximum weight growth of the chicks occurred at about 18 days of age, reaching 40 g/day at this time.

Culmen growth rate changed very little through the whole prefledging period: its growth gradually slowed and it was almost complete at fledging (approximately 50 mm or 93% of the adult size). Tarsi developed rapidly between hatching and 25 days, attaining 64 mm (95% of the adult size) by this time. The average growth rate of wings was practically constant between 12 and 40 days. Parsons (1971a) used winglength for aging chicks between 16 and 28 days of age.

The young at first remain in the nest, but begin to walk short distances 2 or 3 days after hatching. In a sample of 21 chicks, the egg tooth disappeared between 3 and 12 days of age (mean 6.0 days). By 11 to 12 days the sheaths of the scapulars and ventral contour feathers were well developed, and the primary sheaths were prominent, but extended only slightly past the edge of the wing.

By 20 days, the primaries were 1 to 3 cm long, the secondary coverts began to emerge, the scapulars and contour feathers of the ventral pterylae were well formed, and the dorsal contour feathers, upper tail coverts, and rectrices appeared. At 24 to 25 days the rectrices protruded past the surrounding down. The auriculars were visible, but emerging feathers at the center of the crown were still obscured by down.

Development of contour feathers then spread from the above-mentioned areas until the ventral and dorsal surfaces were covered (30 to 35 days). At 35 days the head was completely feathered except for a fringe of down on the postorbital crease and occipital region. The top of the bill, chin, and neck were still downy, but feather sheaths were developing in these regions. Down also remained on the flanks at this time. By the time of fledging only a few strands of down could be seen.

On Gull Island the rate of plumage development differed among individuals as did the weight, e.g. the wing coverts of a 31-day-old chick were far more advanced than those of another chick at 30 days, though both chicks appeared healthy. Development of plumage may compete with other growth processes for the energy resources of nestling birds (Kahl 1962). Kadlec et al. (1969) found that some Herring Gull chicks, which appeared sick and soon died, showed markedly delayed feather development.

For the purposes of this study, fledging period is defined as the age at the first strong flight. Gull chicks do not usually leave the colony until several days after they are able to fly (Moreau 1946, Drent et al. 1964). The mean fledging age of 12 chicks in 1970 was 45.2 days, ranging from 42 to 48 days. Various other authors report a variety of times (Paynter 1949, mean, 43 days; Kadlec et al. 1969, mean, 51 days; Goethe 1956, 43 to 62 days).

On the Point in 1971 a total of 199 chicks (72.9%) hatched from 273 eggs. Of 88 eggs in 35 nests in the predation nest area (Fig. 1) in 1969, 62.5% hatched. These figures are similar to the findings of Paynter (1949), Harris (1964), Brown (1967), Kadlec et al. (1969), and Parsons (1971a), who reported 71%, 64.1%, 66.6%, 79.1%, and 64.3 to 69.9% hatching success, respectively. All these authors also indicated a reduced hatching success in one- and two-egg clutches. A similar trend was evident on Gull Island, even though the sample size was small (76.4% for 57 clutches of 3, and 34.5% for 18 clutches of one or two). This was probably the result of carelessness or inexperience in the individual laying less than the normal clutch, and may indicate a low reproductive drive (Parsons 1971a).

TABLE 3
HATCHING SUCCESS OF EGGS AND SOURCES OF EMBRYONIC MORTALITY OF HERRING GULLS

	Order of laying, in clutch			
	First	Second	Third	Total
Hatching success				
Number laid	102	95	76	273
Number hatched	74	74	51	199
% hatched	72	78	67	73
Causes of hatching failure				
Predated	2 (2%)	2 (2%)	2 (3%)	6 (2%)
Disappeared without trace	11 (11%)	5 (5%)	6 (8%)	22 (8%)
Dead, no embryo	4 (4%)	3 (3%)	5 (6%)	12 (4%)
Dead, with embryo	3 (3%)	2 (2%)	0 (0%)	5 (2%)
Rejected[1]	2 (2%)	2 (2%)	2 (3%)	6 (3%)
Died while pipping	6 (6%)	5 (5%)	8 (11%)	19 (7%)
Accidental breakage by investigator	0 (0%)	2 (2%)	2 (3%)	4 (1%)

[1] An egg was designated rejected if abandoned in a nest, or if found intact within a short distance (0.5 m) of the nest.

The causes of egg loss are presented in Table 3. The third egg in a clutch appears subject to higher mortality than the first two. The most frequent cause of failure in these eggs was parental neglect during pipping. Often by the time the third chick was about to hatch, the first and second chicks had already hatched, and the parents had made the behavioral transition from incubation to feeding of the young. Frequently the third egg was crushed, with the dead chick partially emerged, presumably trampled on by the parents.

The incidence of infertility (dead, no embryo column, Table 3) was low, but a trend toward higher infertility in the third egg may exist.

Eggs that disappeared without trace were considered to have been taken by predators, as eggs are frequently stolen rather than devoured at the owner's nest.

Thus predation amounted to a 10% loss of all eggs laid, and failures in the behavioral transition of parents at the end of incubation accounted for a further 7% loss. The losses from death of the embryo or rejection of the egg during incubation were slight. Drent (1970) found that egg loss from predation by other gulls was highest at the beginning and end of the incubation period, when attentiveness was relatively low. Whether the daily disturbance of the gulls when the nests were checked increased the incidence of predation is not known.

The chick mortality described in Table 4 represents the maximum mortality that could have occurred, as all chicks that disappeared before 38 days of age were assumed to have died. Probably some of the older ones did survive to fledge.

TABLE 4

EARLY MORTALITY OF HERRING GULL CHICKS 1969 TO 1971

			Number/percent dead or missing in age class			
Area/treatment	Year	Number hatched	0–5 days	6–10 days	11–25 days	More than 25 days
Area 12, Fig. 1	1969	28	13/46.4	2/13.3	–[1]	–
Area 11, Fig. 1	1969	32	5/15.6	–	–	–
Area 12	1970	70	21/29.6	–	–	–
Area 11; penned nests	1970	22	3/13.6	1/5.3	1/5.6	4/23.5
Area 11; unpenned nests	1970	35	4/14.2	0/0	2/6.9	4/14.3
Area 12	1971	33	4/12.1	0/0	2/6.9	–
Area 11	1971	147	24/16.3	4/3.3	13/10.9	–
Combined	1969–1971	367	75/20.4	7/3.2	18/9.2	8/17.8

[1] – = no information.

Most of the chicks that died before fledging did so before they were 6 days old (Table 4). Paynter (1949), Paludan (1951), Harris (1964), Brown (1967), and Kadlec and Drury (1968) all reported that highest mortality occurred during the first 7 to 10 days of life. In some studies a major source of mortality was predation by Great Black-backed Gulls (Paynter 1949, Paludan 1951) or adult Herring Gulls (Brown 1967, Parsons 1971b), but this phenomenon was rare at Gull Island. No partly eaten chicks were seen in 1970 and 1971, despite the fact that several carcasses were lying about in various states of decay. In 1967 a large number of chicks of all ages were found dead from unknown causes, but none of these carcasses showed signs of being eaten. Although thousands of Herring Gull chicks were banded on the island each year, no regurgitated bands were found near nests of Great Black-backed Gulls or Herring Gulls, in contrast to the findings of Harris (1964) and Parsons (1971b). The remains of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) were found by many nests of both species, and the headless corpses of Common Murre (*Uria aalge*) and Common Puffin (*Fratercula arctica*) chicks were frequently found near certain Great Black-backed Gull nests. Brown (1967) suggested that Herring Gulls might turn to cannibalizing the young of their own species in dense colonies where other food is less readily available. If so, the dense murre colony on Green Island and the abundance of petrels and puffins on Gull Island may provide an adequate alternative to Herring Gull chicks.

To some extent, either the low density of gulls' nests, compared to Brown's colony (Walney Island), or individual food preferences (Parsons 1971b) may have helped account for the infrequency of cannibalism on Gull Island.

Kadlec et al. (1969) felt that mortality from all causes until the young are partially independent is fundamentally a result of problems in behavioral transition of the adults from incubation to brooding and feeding the young. This is clearly seen in the present study, as mortality from other causes (such as predation) was low: chicks were sometimes built into the nest, or found dead beside it. Mortality of gull chicks was sometimes seen after sudden temperature changes or heavy rains (small dead chicks were seen after heavy rains 28 June 1970) possibly as a consequence of chilling from inadequate brooding.

Mortality of chicks later in the prefledging period was associated most frequently with injuries to the occipital region. The skin there was usually denuded of feathers and often the skull was broken. Seldom were injuries found elsewhere on the body. Kadlec et al. (1969) and Parsons (1971b) associated this type of injury with territorial defense by the adults when chicks wandered (or were frightened by human disturbance) onto their territory. Fordham (1970) reported on the numbers of young Dominican Gulls (*Larus dominicanus*) killed by adults in Wellington, New Zealand. Some chicks went to sea before they were able to swim strongly, were caught in the swells, and were unable to land. They rapidly became waterlogged and either drowned or died from the cold (mean summer water temperature 6.5–9°C).

The abnormally high mortality after 25 days (Table 4) was caused by the death of four of the penned chicks. Harris (1964) noted this phenomenon in some of his penned chicks. Only one, or possibly two, of the unpenned chicks in the present study showed extreme weight loss and death after 25 days of age. Even including the penned nests, the probable number of chicks fledging from the 23 nests of the growth study was 22. Thus the overall breeding success was slightly less than one fledged chick per nest. This figure is high compared to the breeding successes reported by Paynter (1949) of 0.03 to 1.0 chick per nest, Drost et al. (1961) 0.7, Harris (1964) 0.6, and Parsons (1971a) 0.7 to 0.9. Kadlec and Drury (1968) found that productivity in several New England colonies was usually between 0.8 and 1.4 fledged young per nest. Year after year certain of these colonies had a higher breeding success than others only a few miles away. The islands farthest from the coast had a conspicuously low reproductive success, similar to that reported by Paludan (1951) (about 0.5 chicks per nest). Kadlec and Drury felt that this low breeding success represented the natural reproductive rate of gulls, while the higher ones reflected easy access to human garbage. Fordham (1970) and Hunt (1972) also noted the effect of access to refuse on the breeding success of gulls (*Larus dominicanus*, *L. argentatus* respectively).

TABLE 5

MAJOR COMPONENTS OF GULL REGURGITATIONS AND PELLETS 1970 AND 1971[1]

Food item	Number (%) of occurrences Mid-May to mid-June	 Mid-June to mid-July	 Mid-July to mid-August
Invertebrates:			
Hyas sp. (crab)	2 (0.7)	0 (0)	0 (0)
Oniscus sp. (woodlice)	0 (0)	2 (1.7)	0 (0)
Insects[2]	0 (0)	3 (2.7)	3 (2.3)
Acmaea sp. (limpet)	1 (0.3)	0 (0)	0 (0)
Mytilus edulis	90 (30.9)	1 (0.9)	12 (9.1)
Illex illecebrosus	0 (0)	0 (0)	2 (1.5)
Asterias sp.	0 (0)	1 (0.9)	1 (0.7)
Strongylocentrotus drobachiensis	17 (5.8)	0 (0)	6 (4.5)
Vertebrates:			
Fish[3]	33 (11.4)	81 (71.1)	25 (18.9)
Rana clamitans	0 (0)	2 (1.7)	0 (0)
Oceanodroma leucorhoa	65 (22.4)	8 (7.0)	21 (15.9)
Fratercula arctica adults	17 (5.8)	0 (0)	2 (1.5)
Fratercula and *Uria* chicks	0 (0)	4 (3.5)	12 (9.1)
Fratercula and *Uria* eggs	4 (1.4)	2 (1.7)	1 (0.8)
Gull (*Larus* sp.) chicks	0 (0)	1 (0.9)	3 (2.3)
Gull (*Larus* sp.) eggs	9 (3.1)	6 (5.3)	1 (0.8)
Rissa tridactyla chicks	0 (0)	0 (0)	2 (1.5)
Plants:			
Vaccinium angustifolium blueberries	–	–	13 (9.9)
Miscellaneous:			
Gadus morhua offal	36 (12.4)	2 (1.7)	19 (14.4)
Assorted refuse: bologna ends, vegetables, meat, fat, chicken bones, seal bones, shoelaces, bath sponge, plastic forks, crockery etc.	17 (5.8)	1 (0.9)	9 (6.8)
Total number of samples	291 (100)	114 (100)	132 (100)

[1] *Larus argentatus* and *L. marinus*. Pellets from different gull species cannot be differentiated in the field.

[2] Including Odonata (dragonflies), Hymenoptera F. Formicidae (flying ants), Coleoptera F. Carabidae (beetles), Trichoptera (caddis flies), Chironomidae (larvae).

[3] Including *Clupea harengus*, *Microgadus tomcod* and small *Gadus morhua*, *Mallotus villosus*, *Ammodytes americanus*.

Herring Gulls are opportunists, feeding on fish found near the surface, crustaceans and molluscs, small birds and mammals, fish stolen from other birds, and the young of various seabird species (Hatch 1970, Nettleship 1972), but where human waste and garbage are available, these form a large part of their diet (Mills 1957; Harris 1965; Threlfall 1968a, 1968b; Vauk and Löhmer 1969; Löhmer and Vauk 1969, 1970). Harris (1965) and Parsons (1971a) found that gulls breeding near fishing ports fed heavily on fish dock waste. Local availability of a prey species or food source is the main factor affecting the gulls' diet (Meijering 1954) but individual preference is important where food is plentiful (Harris 1965).

Because of the large murre, puffin, and petrel colonies on Gull and Green Islands and the two fish processing plants in the coastal community of Witless Bay, food for the gulls was plentiful and accessible. Three million pounds of cod (*Gadus morhua*) were processed at one of the fish plants in 1971, where production had been steadily increasing for several years (O'Brien, pers. comm.). Large numbers of Herring Gulls and Black-legged Kittiwakes (*Rissa tridactyla*) frequented the area near the Witless Bay wharf to pick up floating offal.

In June of each year, large schools of capelin (*Mallotus villosus*) move into Witless Bay to spawn on the beaches. Many of these fish, as well as other species, and codfish offal were stored outside the other plant prior to processing into fish meal. Hundreds of gulls often gathered on top of this unsavory pile, fighting to secure morsels. When capelin were spread on gardens as fertilizer, the gulls frequently stole them. Herring Gulls were also seen near the dump that received refuse from several communities near Witless Bay. Thus human activities have provided the gulls with several readily available food sources.

The arrival of capelin during the 3rd or 4th week in June was associated with a major change in food habits of the gulls (Table 5). The proportion of petrels, *Mytilus*, human refuse, and offal, which had been the major food items during the previous month, dropped abruptly as the gulls began to concentrate on capelin. The arrival of capelin and the shift in food corresponded closely to the peak of hatching of the chicks. Goethe (1937) and Meijering (1954) reported changes from hard (*Carcinus* and insects) to soft food (fish and *Asterias*) when the chicks hatched, and it is probable that the great abundance and accessibility of capelin at the appropriate time is a major factor in the high breeding success of the Herring Gull on Gull Island.

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SUMMARY

A study was made of the breeding biology of Herring Gulls on Gull Island, Witless Bay, Newfoundland, during the summers of 1969–71.

The nests of the gulls are described, with respect to size, composition, immediate surroundings, and density in various parts of the island.

Egg-laying began as early as 22 April and reached a peak about 10 to 14 May. New clutches were begun an average of 12.6 days after the loss of the original clutch. The average clutch size was 2.70 in 1970 and 2.73 in 1971. Clutch size decreased as the season progressed.

The third laid egg was smaller than the first two. Eggs lost 16% of the fresh weight during incubation. The mean incubation periods were 29.4, 28.2, and 27.1 days for first, second, and third eggs.

Development of embryos and chicks is described. There was no difference in growth of chicks in pens and at large, and no significant differences in the growth of first-, second-, and third-hatched chicks in a brood. The development of the plumage is described.

Breeding success was measured by hatching success (62.5%–72.9%) and chick mortality up to 25 days of age (24.9%). A small sample (23 nests) fledged an average of just less than one chick per nest.

The food of the gulls is noted, and the possible influence of food availability on breeding success and population growth is discussed.

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