THE BREEDING BIOLOGY OF THE BLACK-LEGGED KITTIWAKE IN NEWFOUNDLAND[1]

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THE Black-legged Kittiwake (*Rissa tridactyla*) has been the object of many studies through large parts of its range. Some of the more recent works are those of Coulson and White (1956, 1958a, 1958b, 1960, 1961), Coulson (1959, 1963a, 1963b, 1966, 1969), Coulson and Macdonald (1962), and Hodges (1969) in Great Britain; Uspenski (1956) and Belopol'skii (1961) in the U.S.S.R.; and Swartz (1966) in Alaska. Cullen (1957) described the adaptations of Black-legged Kittiwakes to cliff-nesting, and Paludan (1955) investigated their behavior. As data on this species' breeding biology in the northwestern North Atlantic are sparse, we studied a kittiwake colony on Gull Island, Witless Bay, Newfoundland during the summers of 1969 and 1970.

MATERIALS AND METHODS

Gull Island (47° 15′ N, 52° 46′ W) is the northernmost of three islands comprising the Witless Bay Seabird Sanctuary at the mouth of the aforementioned bay, approximately 1.5 miles from the nearest point of land. Gull Island is about 1 mile long and ½ mile wide with the long axis running north–south. The island reaches an elevation of 228 feet (Canadian Wildlife Service, 1969) and is heavily wooded, except for a grassy perimeter (Puffin slopes) and rock surfaces. The underlying rock is medium- to fine-grained red sandstone of the Cabot Group (Signal Hill Formation), and is part of the major Bay Bulls syncline (Rose, 1952). The strata of the island dip in an easterly direction at 50–55°, giving rise through weathering to long, narrow, westward-leaning coves on the north and south ends of the island, and providing large numbers of slanting ledges of the type apparently ideal for kittiwake nesting.

The kittiwake breeding population of Gull Island was censused in both 1969 and 1970. All counts were made from the island, nests being counted individually except for four places where nests were not readily visible or accessible. In these four cases estimates were made by scaring birds from their nests and counting them as they soared into view (there are usually 1.2 birds per nest at any given time; Coulson and White, 1956) and/or by extrapolation from the density of the birds on visible parts of the same cliff.

The locations of 112 nests in 1969 and 184 in 1970, which were used in the detailed studies, were designated by numbers painted on an adjacent rock face. Nests chosen at random before the birds started laying were checked daily in 1970 and less often in 1969 to investigate the method of nest construction and materials used, dates of egg laying, and egg mortality. Three nests were fully dissected to determine details of their construction. The length and breadth of eggs were measured with vernier calipers and the weight was taken by suspending the eggs in a plastic bag below a spring balance.

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Egg volumes and shape indices were calculated according to formulae derived by Coulson (1963b). Volume is calculated as $0.4866 \times b^2 \times 1$, while shape index is equal to $(100 \times b)/1$, where "b" is the breadth of egg at its widest point and "1" is the maximum length of egg.

The onset of incubation was judged by the relative warmth of eggs, which were examined daily. Egg temperatures were also taken periodically with a telethermometer using a flat-surfaced probe placed against the nest material below the egg. All egg temperatures were taken on cool, cloudy days to avoid possible inaccuracies resulting from solar heating.

To facilitate identification, squares of masking tape were placed on the side of the first egg laid in each nest studied, and on the blunt end of the second egg. Chicks were marked either on the top of the head or on the back with a picric acid solution. When chicks grew large enough, a U. S. Fish and Wildlife band (#5) was placed on one tarsus.

We collected 46 eggs of known age for a study of embryos, and then checked the nests from which these eggs were taken daily to note whether more eggs were laid. The shells and extraembryonic membranes (including yolk sacs) were dissected from the embryos, which were then weighed and measured fresh, and preserved in 10 percent formalin for later pterylographic investigations. Weights of embryos were taken on a triple-beam balance sensitive to 0.1 g. Figure 1 shows the regions of the developing embryos that we measured.

Marked nests were further checked daily in 1970 and less often in 1969 to determine hatching dates, chick mortality, and length of fledging period. In 1969 30 chicks of known age and in 1970 64 chicks of known age were weighed and measured every 2 days (conditions permitting). Weights were taken by placing chicks in a plastic bag suspended from a spring balance.

Chick measurements including culmen, tarsus, middle toe, hand, forearm, primary, and tail were taken, as for embryos (Figure 1), with the following additions and modifications: tail, posterior extremity of body (between the two central rectrices) to the tips of the innermost rectrices; hand, anterior hand-forearm joint to solid flesh just anterior to longest primary (#9); primary, tip to beginning of fleshy basal sheath (of primary #9). A record of feather development from hatching to fledging was also kept.

Rectal temperatures of chicks of known age were taken with a telethermometer with an insert probe.

Studies of the food of chicks were made by analyzing regurgitations and by direct observations.

RESULTS AND DISCUSSION

Census.—We divided the island arbitrarily into five natural geographical sections (Figure 2) for the census. The breeding population of kittiwakes was 6,977 pairs in 1969 and 8,306 pairs in 1970, an increase of 1,329 pairs (19.1%). Both the 1969 and 1970 counts are many times greater than the estimate of 500 pairs for Gull Island by Peters and Burleigh (1951:238). The most substantial increase in 1970 was on the northwest side (area 4, 55.3%) while the east side (area 1) showed a decrease of 1.5 percent. Estimates were made of the number of nests in two areas on the east side (estimated total of 100 nests) and two areas

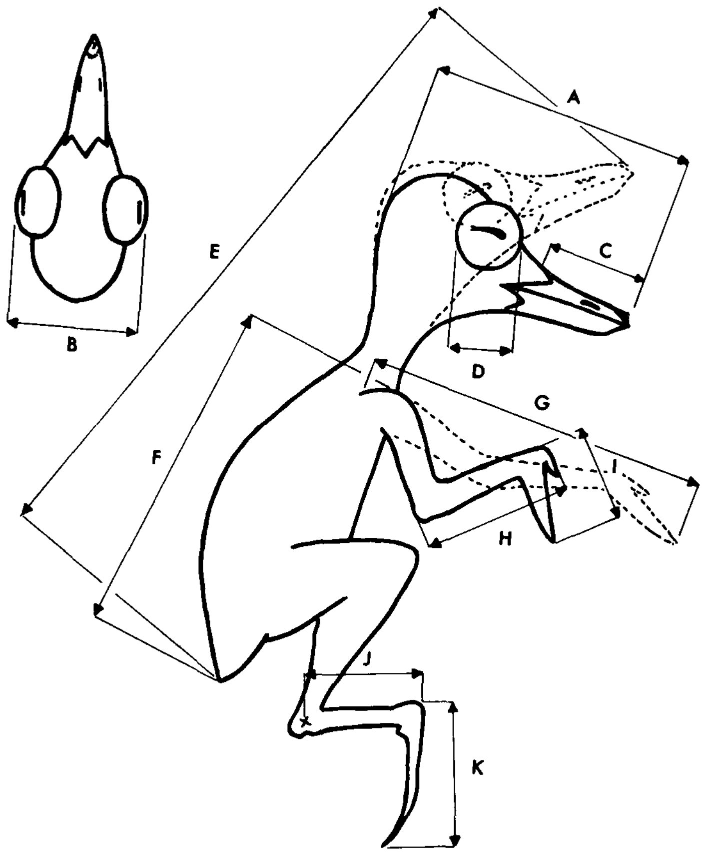

Figure 1. Measurements of kittiwake embryos taken on Gull Island, 1970. A, head length; B, head width; C, culmen; D, eye diameter; E, length; F, length shoulder to tail; G, arm length; H, forearm; I, hand; J, tarsus; K, middle toe.

on the southwest side (estimated total of 50 nests). These numbers amounted to 2.2 percent of total count in 1969 and 1.8 percent of total count in 1970. Specific cliffs occupied by kittiwakes are detailed in Figure 2.

Topography of nest sites.—Because of the inclined strata, cliffs facing east lean inward at approximately 40° from the vertical, while those facing west overhang or are near vertical. East-facing ledges are few, most of them resulting from the downward shifting of rock sheets and the accompanying rubble. The rock contains many fractures and is uneven at the individual stratum level. Ledges facing west are more numerous,

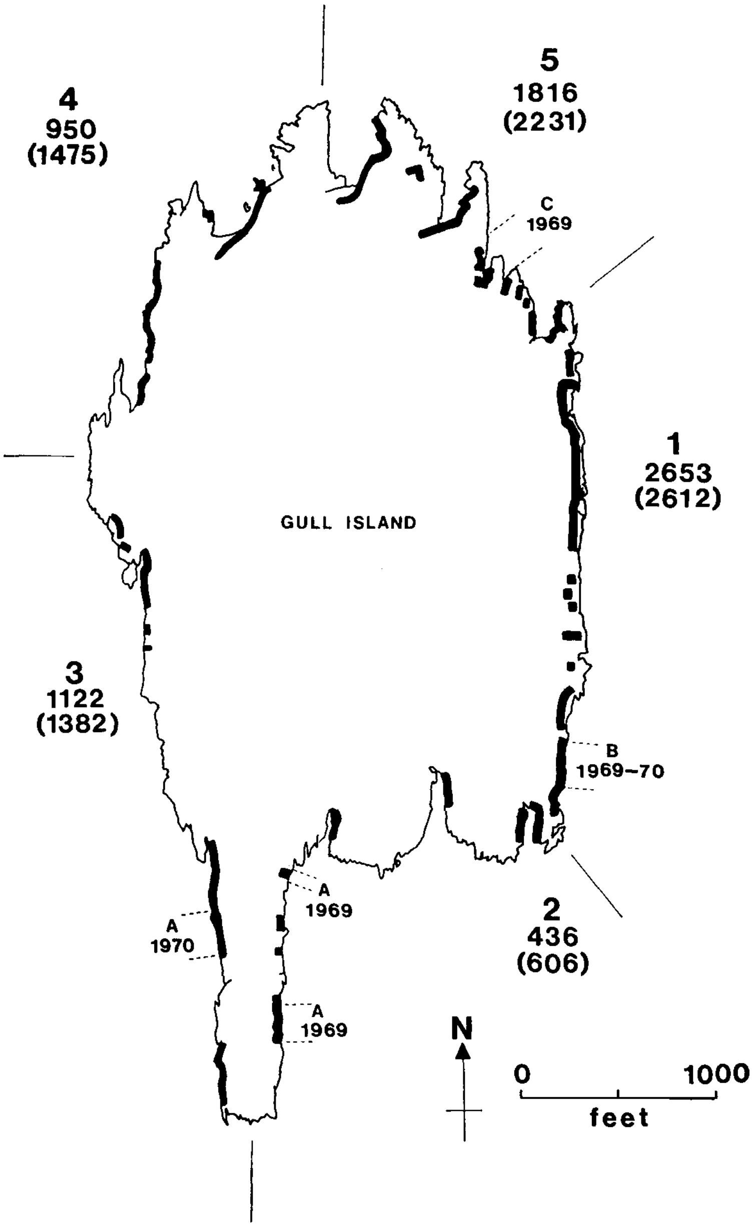

Figure 2. Gull Island, Witless Bay, Newfoundland, showing census and study areas, numbers of nests per area (1970 figures in parentheses), and cliffs occupied by kittiwakes in 1969 and 1970.

and usually slant outwards and downwards. They represent the edges of upthrust strata and are usually overhung by the layers above. Usually weathered cracks of varying width lie between the strata that form the ledges and those that form the overhanging rock faces.

Approximately 3,725 nests (54%) in 1969 and 5,100 nests (62%) in 1970 were on westward-facing cliffs. The remainder in both years were on eastward-facing cliffs. Of the latter, approximately 1,300 nests (40%) in 1969 and 1,150 nests (36%) in 1970 were on the northeast corner of the island in an area where huge sheets of rock have fallen from the cliff and produced many good nesting sites. The portion of east-facing ledges suitable for kittiwakes seem to be almost fully occupied, the population change from 1969 to 1970 being a decrease of 50 nests (1.5%). The increase on west-facing ledges for the same period was 1,375 nests (27%). Extremely few cliffs on Gull Island face directly north or south.

The small decrease in the number of kittiwake nests on the eastern ledges may have been partly attributable to an increase in the number of Common Murres (*Uria aalge*) breeding there in 1970 (62 pairs in 1969, 180 pairs in 1970). In 1970 one part of the large northeastern cliff mentioned above was almost devoid of kittiwake nests in the vicinity of a completely new murre concentration of approximately 50 pairs; this area in 1969 contained 200 kittiwake nests. The kittiwake population on the entire cliff dropped from 970 pairs in 1969 to 755 pairs in 1970. Belopol'skii (1961) gives a similar account of murre-kittiwake relations in Russia.

None of the cliffs on Gull Island are more than 35 m high, and the birds show no visible height preference for nesting, as Coulson (1963a) found in Britain. Nest-site height appeared to be determined by the availability of ledges. Nests were found from 2 m above the high tide mark to rock outcrops on the lower "puffin slopes" approximately 15 m above the level of the cliff tops. This is despite the fact that on the west-facing cliffs, where both extremes occurred, many apparently suitable ledges at medium heights remained vacant. When extremely crowded, as by murres on Green Island 1 mile south of Gull Island, kittiwakes will nest in atypical locations, e.g. murres and kittiwakes share caves in several places. Kittiwakes may also take locations in the midst of the murre colony, on top of boulders 1–4 m high and on the sides of oddly shaped blocks and pillars of gravel and concretions that have escaped erosion by the murres and weather. Murres seem to be important agents of erosion in seabird colonies; apart from the considerable amounts of gravel being continuously thrown about by beating wings and scratching feet, Belopol'skii (1961) states that Murres expanding their territory destroy the grassy vegetation and actively destroy the peat by digging it up with their bills.

Nest building and materials.—Nest building starts early in the year. Sporadic watch of the islands was kept from the mainland in late winter (February-April in 1969 and 1970) with a 15–60X spotting telescope. On 27 February 1969 small flocks of kittiwakes were present on the water and on the ledges of Gull Island. On 22 March 1969 most of the visible ledges were occupied and the birds appeared to have paired. The first observation made in 1970 (27 March) showed nests in various stages of construction on Great Island, 6 miles south of Gull Island. On 5 April 1969, almost all birds present on Gull Island occupied well-advanced nests with white flags of excrement developing on the cliffs below each site. The building of nests continued until the first week in June 1970, after which time only a few birds, presumably inexperienced ones (Coulson and White, 1956), started bulding. One nest was begun on 18 June 1969 and completed 2 days later.

The methods and behavior involved in nest construction in this study were similar to those described by Cullen (1957) and Paludan (1955). Nest construction is executed in a series of stages, each stage corresponding to a day's activity. This results in the formation of a number of horizontal layers that are easily separable and can usually be lifted off as discrete units.

The lower foundations are usually unconsolidated wedges of wet grass and loose peat. The main adhesion to the cliff is maintained by the slanting base of the body of the nest. The main layers are predominantly wet peat chunks mixed with grass and straw, (all references to grass in this paper mean fresh green material, while straw means dried grass from a previous year's growth).

During the first half of the nest building season in 1970 material used for the foundations of many nests consisted of loose, heterogeneous pellets containing a mixture of seaweed, feathers, straw, and the bodies (exclusive of calcareous plates) of barnacles (*Balanus balanoides*). Nests built later in the nesting season were usually constructed with drier peat and straw mixed with a great variety of miscellaneous substances.

Most of the nest materials were obtained on the island. The peaty material was gathered during the early morning when flocks of kittiwakes congregated on the numerous puffin slope washouts or during and after a rain at the edges of trickles of water cutting through these areas. During these periods the water-eroded peat is soft and workable (it is hard and crumbly when dry). The correlation of nest building with rain has been noted previously in kittiwakes by Cullen (1957). The mosses, ferns, and flowering plants, including the grasses, were gathered in wet parts of the puffin slopes. The algae, except for *Prasiola crispa* which grows on the cliffs, came mostly from the intertidal zone. Considerable use was made of material that heavy rains washed down onto the rocks from the grass slopes, as well as debris floating on the sea. We often saw kittiwakes flying between the island and the mainland with nest material, some of which they doubtless obtained from the mainland shores. The lichen *Cladonia rangiferina* and the conifer *Juniperus horizontalis*, which were found in one nest, do not grow on the island, but do occur on nearby headlands. All locally obtained material found in the nests occurred within 100 m of the island's edge.

The nest material used may be related to the spring growth of the vegetation, early nests being built almost entirely of peat and straw, while later nests contained large amounts of fresh grasses and a great variety of other plants. These other plants were used when they had a growth sufficiently large (different size for each plant species) to be useful to the builder. Material was usually obtained at several different places on the island at a varying distance from the nest, and consequently the composition of the nests was unaffected by local abundance of one type of plant. Nests throughout the colony were very similar in composition. For approximately a month after each nest was built, some repairs and improvements were carried out, this activity usually involving the addition of materials to the top of the nest and the building up of the edges of the nest cup. Material was regularly inserted beneath the eggs. Stealing of nest material was noted many times during the late nesting period, as Cullen (1957) also reported. One nesting kittiwake removed so much of the lower portion of a nest just above it to incorporate into its own nest that the damaged nest was in danger of collapsing.

The opportunity to investigate rebuilding of totally destroyed nests presented itself on 29 May 1969 when waves generated by a violent storm washed eight marked and many unmarked nests from their ledges. These nests were 6.5–9.5 m above the high tide mark and 7–10 m inland. One of the marked nests contained two eggs when destroyed. While the birds that had occupied the nests were not marked, the lateness of the date and the speed with which the nests on these sites were rebuilt suggest that these were indeed the same individuals. Seven of the eight nests were rebuilt. All were started within 2 days after the storm and took from 2 to 9 days to rebuild. One nest was built in a very haphazard fashion and was soon deserted. All six nests that remained after rebuilding later contained eggs.

While no detailed series of measurements were made, the nests had an outside diameter of approximately 20–25 cm at the top and a height of 20–25 cm on the side away from the cliff. Nests weighed 2.5–5 kg. Dement'ev and Gladkov (1969) in the U.S.S.R. give a cup diameter of 25–30 cm, a height of 15–20 cm or more, and a weight of approximately 5 kg., Swartz (1966) in an Alaskan study reports an inside diameter of 20–30 cm, an outside diameter of 40–50 cm, and a height of 50 cm or more. Belopol'skii (1961) in the U.S.S.R. noted the average weight of a nest as 2.5–3.0 kg.

In at least three cases, single eggs were laid in depressions on bare rock, possibly by young birds. In such cases nests were successfully constructed around and beneath the eggs within a few days after laying.

Nests vary in size and shape according to location. Some nests, built on large flat ledges, resemble the "very big. . .slovenly" (Belopol'skii, 1961: 123) nests of the larger gulls. One such kittiwake nest measured 34 × 24 × 5 cm and contained only loose straw.

In isolated cases nest material was added to a nest for no apparent reason and covered up the eggs. In such cases, the eggs were usually at least partially uncovered from one to several days later (though few (< 10%), hatched), and rarely the nest was completely destroyed and deserted 2–3 days after the eggs were covered. This phenomenon occurred in nests containing both one and two eggs.

Egg laying.—Eggs were laid over a 32-day period (21 May–22 June) in 1969 and a 47-day period (15 May–1 July) in 1970. The mean dates were 3 June 1969 (SD = 6.8 days) and 29 May 1970 (SD = 7 days). Eggs were laid in 92 percent of 112 marked nests in 1969 and in 91 percent of 134 marked nests in 1970. The high rate of nest utilization indicated that marking nests and making daily visits did not lead to their desertion.

The mean clutch size of 1.85 we found was similar to that reported by other workers, e.g. 1.84 (Swartz, 1966), 2.05 (Coulson and White, 1958b), 1.89 (Uspenski, 1956), 1.96 (Belopol'skii, 1961), and 1.94 (Cullen, 1957).

The percentage of one-, two-, and three-egg clutches (sample 225 nests: total 1969 and 1970: 16%:82%:2% respectively) was similar to that found by Swartz (1966) in Alaska and Uspenski (1956) in Novaya Zemlya. Studies in the Murmansk area (Belopol'skii, 1961) indicated that the number of eggs per clutch is related to the availability of food through the level of intraspecific strife, (i.e. clutch size is smaller in years or areas of food scarcity).

Coulson and White (1958a) stated that average clutch size was largest in clutches begun during the first part of the breeding season, and this was related to the fact that older birds have larger clutches and nest earlier. While 1969 data for Gull Island appear to be in basic agreement with this (mean clutch size 23–29 May = 1.93, 13–19 June = 1.13), 1970 data showed no significant decrease in clutch size with time (mean clutch size 23–29 May = 1.96, 13–19 June = 1.66). Coulson (1963b) found that normally eggs laid toward the end of the season were somewhat smaller than those laid at the beginning and related it to the early laying by the older birds, which tend to lay larger eggs. The present study produced similar results. The mean period between the laying of the first and second eggs of a clutch was 2.67 days (SD = 0.7 days). In the case of three-egg clutches, the third egg in one instance was laid 3 days after the second, while in two other cases it was laid 2 days after the second.

Eggs appear to be laid at random times during both the day and night. A check of 134 nests for new eggs on 26 May 1971 (3 days before the peak of laying activity) showed six eggs laid during the night between 19:30 and 06:30 and seven eggs laid during the day between 06:45 and 16:00. Unfortunately bad weather curtailed further observations. Paludan (1951) noted that in the Lesser Black-backed Gull (*Larus fuscus*) and the Herring Gull (*Larus argentatus*) the first egg appeared to have been laid during the early part of the day, while the second and third eggs appeared to have been laid during the evening and at night. In the present study 66.7 percent of the overnight eggs and 57.2 percent of the daytime eggs were first eggs.

Belopol'skii (1961) and Dement'ev and Gladkov (1969) both mentioned that the kittiwake is capable of replacing lost clutches if gonad regression has not progressed too far. Of 19 nests that were emptied of eggs in 1970 on Gull Island, relaying occured in six (31.6%), one egg to a nest. Of these, three (50%) were fertile. The tendency to replace a clutch and the success of replaced eggs decreases as time from peak laying activity increases. In all cases, except the 1969 example when two eggs were replaced, only one egg was laid in each new clutch. Of the seven clutches (including one from 1969) replaced two were begun 13 days after the old clutch was lost, three were 14 days after, and two were 15 days after, (mean = 14 days after old clutch was lost).

The Egg.—Coulson (1963b) gives a detailed account of egg size and shape in the kittiwake and the usefulness of such data in estimating population age composition. The weights of 176 freshly laid eggs in the present study ranged from 40.0 to 63.0 g (mean = 51.7). A summary of egg measurements is contained in Table 1. A comparison of mean egg volumes calculated from studies in various areas shows for the Murman Coast, 49.1 cc (Gorchakovskaya, 1944); for England, 43.0 cc

TABLE 1
SUMMARY OF EGG MEASUREMENTS TAKEN AT GULL ISLAND, 1969[1]

	Egg from 1-egg nest	Egg #1 of 2-egg nest	Egg #2 of 2-egg nest	Total
Number of eggs	22	77	77	176
Measurement range				
Breadth	34.5–42.5	38.5–43.5	35.0–44.5	34.5–44.5
Length	51.5–60.5	52.0–61.5	51.0–59.5	52.0–61.5
Measurement mean				
Breadth	39.9	40.8	40.1	40.3
Length	55.7	56.1	55.5	55.8
Volume range	35.0–48.0	37.6–54.2	34.6–52.6	34.6–54.2
Volume mean	43.0	45.4	43.3	44.2
Shape index range	57.0–79.7	65.3–77.6	60.4–81.7	57.0–81.7
Shape index mean	71.8	72.8	72.6	72.4

[1] Measurements in mm, volume in cc.

(Witherby et al., 1941) and 43.0 cc (Coulson, 1963b); for America, 45.5 cc (Bent, 1921) and 44.2 cc (this study).

The second egg in a two-egg clutch is smaller on the average than the first and has a slightly lower shape index. The egg in a one-egg nest is smaller than either from a two-egg nest, but has a lower shape index than either from the two-egg nest (Table 1).

Egg colors are extremely variable. Base colors vary through Brown, Tan, Olive, and Sky Blue to Gray (Munsell, 1946), the markings usually being a dark brown or a gray color. The base color of the eggs changed abruptly from one of a definite brownish cast to one of a definite gray, green or bluish cast during the first 3 days of June 1969. This may have been due (Welty, 1962) to a changeover from predominantly hemaglobin derivative pigmentation (porphyrins) to predominantly bile derivative pigmentation (cyanins). One explanation for this phenomenon might be the rapid change in food habits at this time. Spawning capelin (*Mallotus villosus*) first appeared on or near the beaches of the mainland on 1 June 1969 and the kittiwakes began feeding on them instead of various intertidal materials and marine crustacea. In 1970 the color was predominantly green, gray, or blue from the beginning of the laying season, and it may be noted that this year the capelin shoals were being utilized as a food source during the whole laying period and already constituted approximately 20 percent (by occurrence, or approximately 90% by weight) of their diet in the 2 weeks before 1 June.

Data on color obtained from 110 eggs in 1969 and from 98 eggs in 1970 showed that 65.6 percent of the eggs laid before 1 June 1969 and 21 percent of eggs laid after this date were brownish in color. In

1970 only 39.8 percent of the eggs laid before 1 June were brownish, and while specific data are lacking, substantially fewer than 50 percent of the small number of eggs laid after this date were brown.

Incubation period.—Much confusion exists over the term "incubation period." The present study uses Heinroth's (1922) definition as translated in Thompson (1964: 396), namely "the time from laying of the last egg of a clutch to hatching of that egg." The mean length of incubation for 66 clutches in 1970 was 27.2 days (SD = 1.05 days) as compared with 27.3 days (119 clutches, Coulson and White, 1958b), 28.0 days (15 clutches, Swartz, 1966), and 24.25 days (6 clutches, Uspenski, 1956). The mean period between the laying of the first and second eggs of a clutch was 2.67 days (SD = 0.7 days) while that between hatching of the first and second eggs was 1.3 days (SD = 0.7 days). Barth (1955) accounts for the difference in the times the first and second eggs need to hatch by pointing out that effective incubation in gulls does not begin until about the time the last egg is laid. Data from the present study show that incubation for the first few days is ineffective in maintaining a high egg temperature, but examination of growth curves of the parts of the embryos that start developing first (i.e. shoulder to tail length) shows that development apparently begins on the day of laying.

The temperatures of eggs being incubated increased rapidly from an average of 6.0° C above the ambient 0–1 days after laying, to an average of 10.6° above the ambient 4–5 days after laying (ambient remained steady). The increase after this period appeared relatively slow and was probably due to thermogenesis of the embryo (Drent, 1970) and a higher ambient temperature. The steady rise in egg temperature during the first few days of incubation was probably due to the increasing attentiveness of the adults (Drent, 1970). The temperature of pipped eggs was 2–3° lower than for unpipped eggs of the same age, possibly as a result of rapid evaporation (Drent, 1970) through the pierced shell. The temperatures of eggs being incubated from the 6th day after laying onward ranged from 11.9° to 24.2°. This is very low compared to the average egg temperature of 34.0° ± 2.38 for other wild birds under natural conditions (Huggins, 1941).

Low ambient temperatures and exposure of nests to wind influence egg temperature. Measurements taken with a strong wind blowing were consistently lower than those taken on a calm day with similar ambient temperatures. Egg temperatures taken at lower ambient temperatures and similar wind conditions also are considerably lower. No significant cooling at the point of measurement below the eggs was noted when adult birds were frightened off their nests for periods up to 45 minutes.

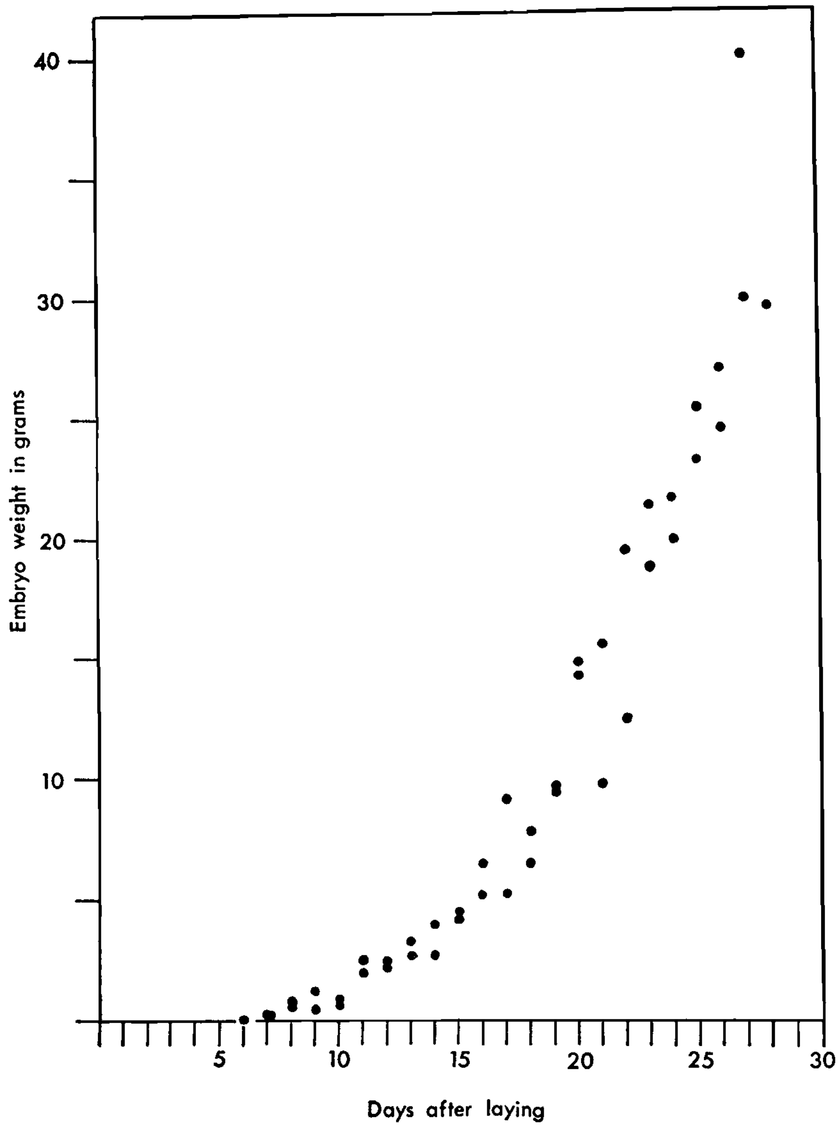

Figure 3. Weight increase of kittiwake embryos, 1970.

The specific gravity (SG = wt(g)/volume (cc)) of 10 marked eggs was calculated at several points during incubation. The specific gravity decreased from 1.17 at laying to 0.95 at 29 days after laying, a decrease of 19 percent of the original weight. This may be compared with a

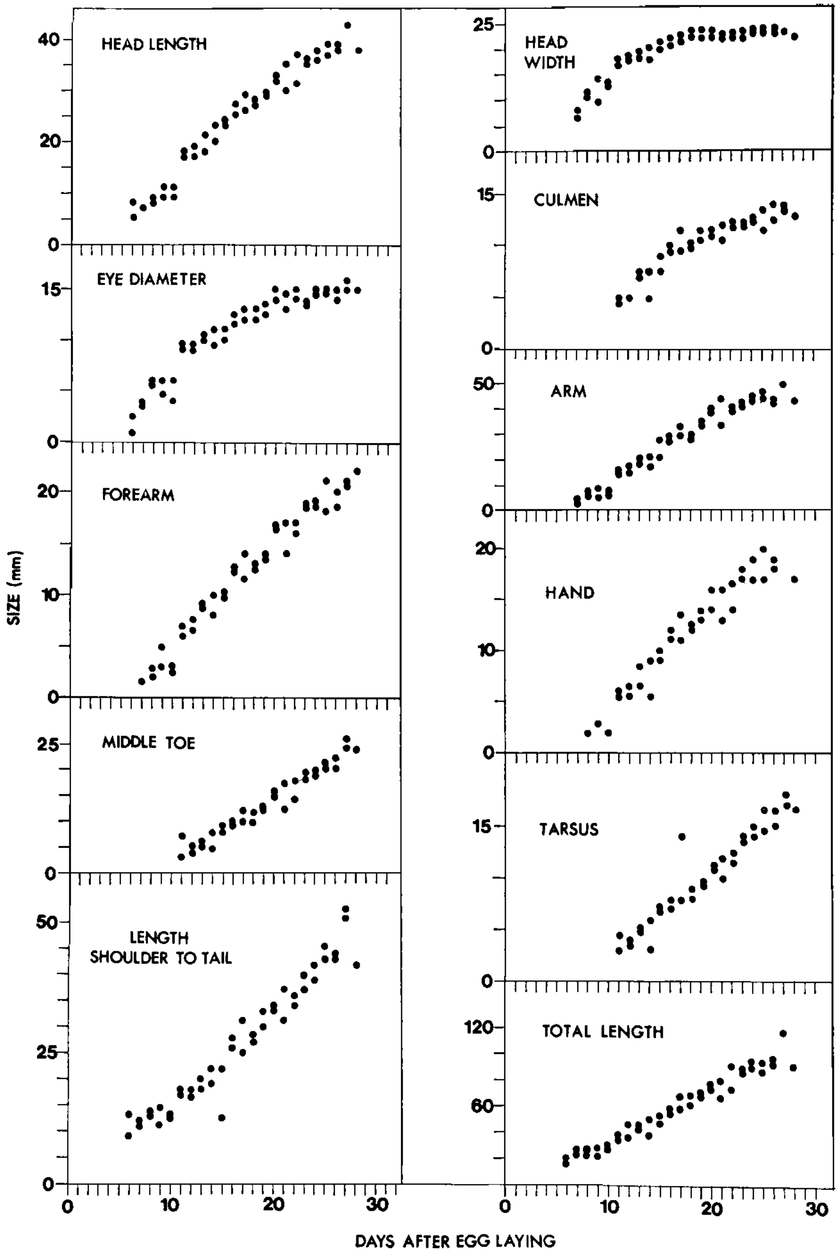

Figure 4. Growth of body parts of kittiwake embryos, 1970.

loss of 18.5 percent in the Common Gull (*Larus canus*), 13.0 percent in the Lesser Black-backed Gull (Barth, 1952), and 15 percent in the Herring Gull (Harris, 1964). The amount of weight lost, mainly in the form of water, is inversely related to the size of the egg (Drent, 1970).

Growth of embryos.—Very few workers have studied seabird embryo growth. Harris (1964) gives weight increases of Herring and Great Black-backed Gull (*Larus marinus*) embryos, but no measurements of the various parts of the developing organism. We took embryo measurements from the 6th day after laying until the time of hatching (Figures 3 and 4). Measurements of embryos from the first and second eggs were best compared when age was taken to be the number of days after the laying of each egg. Embryo weight reaches 50 percent of the embryonic maximum 22 days after laying, 5 days before hatching.

The first embryos examined were from eggs that had been laid for 6 days. These individuals had very small wing and tail buds with slightly broadened tips, a small head with prominent midbrain, and small, slightly pigmented eyes (Figure 4). The midbrain loses its prominence on the 9th day after laying and the head begins to broaden, chiefly as a result of the rapidly enlarging eyes. The eyes are well-pigmented by the 10th day after laying, and gradually close between the 17th and 23rd days, then gradually open again before hatching. Eye diameter reaches 50 percent of the embryonic maximum on the 10th day. The bill is first evident by the 8th day and grows rapidly, the egg tooth being faintly visible 3 days later. The egg tooth is fully developed by the 20th day. The bill gradually becomes horny between the 18th and 24th days and reaches 50 percent of embryonic maximum on the 13th day. The shoulder to tail (i.e. body) length reaches 50 percent of embryonic maximum on the 16th day. The yolk sac is still prominent at hatching, but becomes a mere button (5 mm in diameter) within 24 hours. The digits of both fore and hind limbs are rudimentary, but visible, on the 9th day. The feet are well formed by the 16th day, and nails first become visible at this time. The forearm length reaches 50 percent of embryonic maximum on the 15th day, while the middle toe length reaches this point on the 19th day and the tarsus length reaches it on the 18th day.

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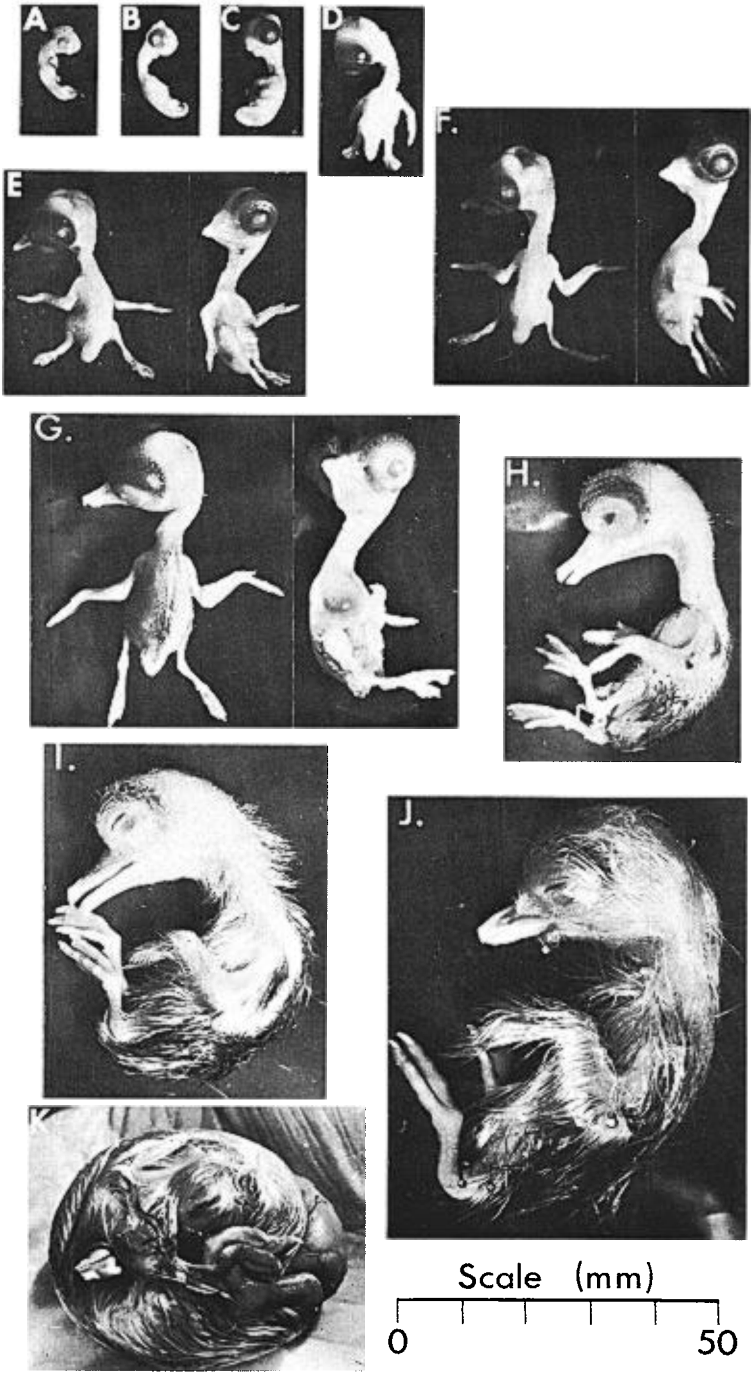
Figure 5. A series of known-age kittiwake embryos, 1970. Ages are given as days after laying. A, 6 days; B, 7 days; C, 8 days; D, 9 days; E, 11 days; F, 13 days; G, 15 days; H, 17 days; I, 19 days; J, 22 days; K, 27 days (pipping—note intact yolk sac).


A
B
C
D
E
F.
G.
H.
I.
J.
K
Scale (mm)
0
50

Hatching.—The egg is first broken by hairline fractures encircling the larger end. The shell is then pipped and the chick cuts the end of the egg. The two sections are almost always undamaged, so that it is often possible to fit them together again with only a few missing pieces. Of the 192 chicks that hatched in the study areas in 1969 and 1970, two cases (1%) were noted where the chick's position in the egg was reversed so it had to emerge through the small end. One of these chicks hatched successfully, the other did not.

The mean time periods between appearance of hairlines and pipping, and between pipping and hatching, were 2.3 (SD = 0.92 days) and 1.0 days (SD = 0.62 days) respectively. As stated earlier, the mean period between hatching of the two eggs of a clutch was 1.3 days (SD = 0.7 days). The mean dates of hatching were 28 June 1969 (SD = 4.07 days) and 25 June 1970 (SD = 4.78 days).

Weather may modify the hatching dates of individual eggs. In 1970 the eggs hatched during a period of warm weather, which in itself is not significant, but a short period of colder weather within the warm spell was accompanied by a temporary decrease in the hatching rate. Possibly cold days may affect the metabolism of the still essentially cold-blooded chick enough to prevent some individuals temporarily from making the strenuous hatching effort. Pipping and subsequent egg-breaking activities were always accomplished with the bill projecting from the right wing axil (Figure 5, 27-day chick).

Chick Growth.—Chick weight continued to increase without interruption during and after hatching (Figures 3 and 6). This is unlike the case reported by Harris (1964) for the Herring Gull, in which chicks lost up to 15 percent of their weight in the first day after hatching and before the first meal. Apparently kittiwake parents feed their chicks immediately after hatching for newly hatched chicks were usually found to have food in their foregut.

Chick weight peaked at 420 g on the 29th day after hatching (Figure 6), and then decreased steadily until the birds flew at approximately 42 days of age. The peak of chick weight is approximately 96 percent of adult weight (436.8 g SD = 39.0 g). The loss of weight before fledging may result from a lack of feeding by adults at the end of the nestling period. Older chicks (30–40 days old) had food in their foregut far less often than younger chicks, and toward the end of the breeding season there were days when no food was observed anywhere on the cliffs containing predominantly older chicks.

Growth of various body parts is shown in Figures 6–9. These parts reach 90 percent of adult size in the following times after the chick

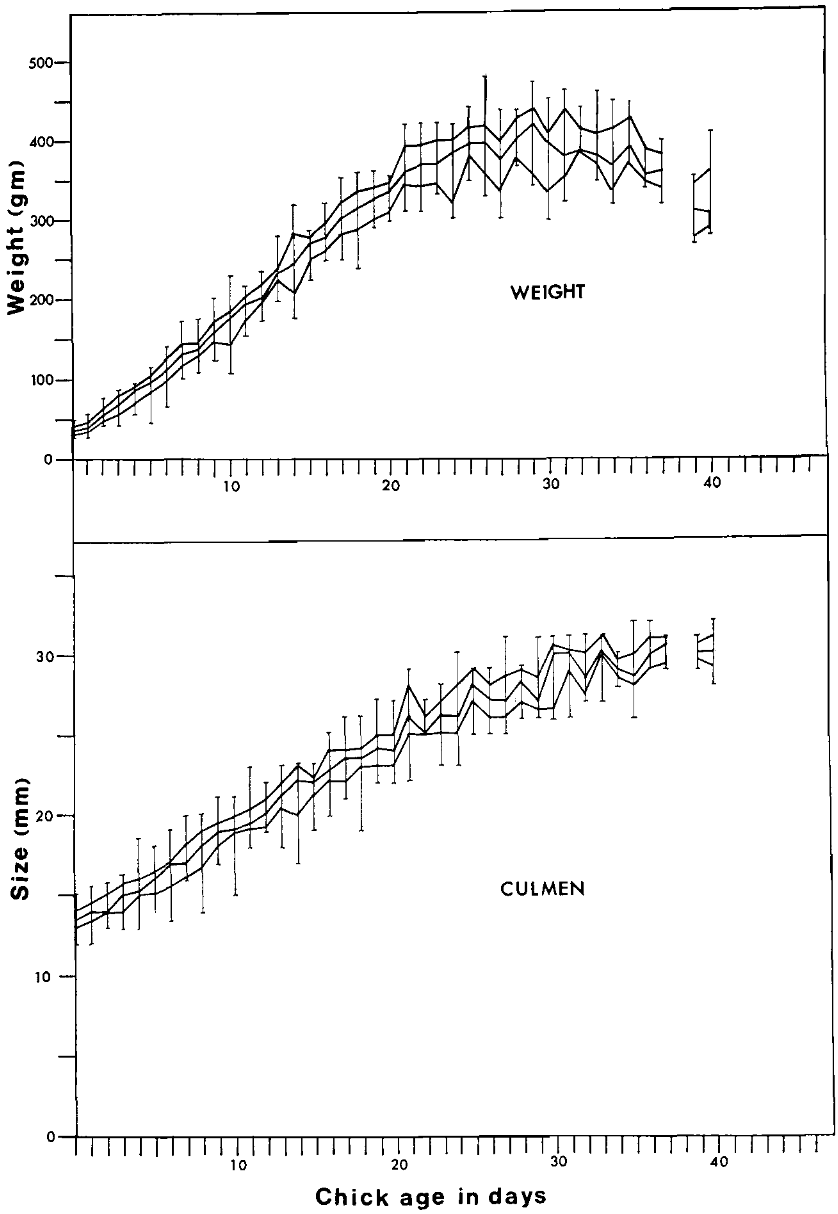


Figure 6. Growth in weight and culmen length of kittiwake chicks, 1970. Curves represent Q_1, median, Q_3 of measurements and vertical lines represent range.

hatches: culmen, 55 (estimated) days; wing (hand plus primary), 48 (estimated) days; tarsus, 12 days; tail, 42 days.

Means for adult measurements (from fresh sample of 31 birds taken at Witless Bay) are as follows: wing = 311.5 mm (SD = 9.4 mm), tail = 129.4 mm (SD = 5.9 mm), culmen = 36.6 mm (SD = 1.6 mm), tarsus = 34.9 mm (SD = 1.0 mm).

It can be seen that the rate of growth of the various parts of the chicks is related to the usefulness of these members at a given age. Cullen (1957) states that the strongly developed claws and toe musculature of chicks are an adaptation for holding onto the cliff nests. The bill grows much more slowly than the leg components because food is provided by the adults in a soft, semidigested state by regurgitation, so that a large, strong bill is not needed at this time. The wing and tail attain almost maximum size at the time the chicks are advanced enough to leave the nest.

The wing measurement of the chicks used in the above comparison was not measured directly, but obtained by summing the hand and primary measurements. This gives a figure that is almost the same as the wing measurement along the natural bow of the feathers, which was used on all adult measurements. The more widely used measurement was not taken in this study because the hand/primary junctions in young chicks are so flexible that varying the angle between the sections can produce large errors ($\geqslant$ 20%). In addition the growth of the wing is a compound process including simultaneous growth of the hand and the flight feathers.

The use of measurements of parts, or combinations of these measurements, appears to be a more accurate method of determining growth and age than weight, at least in older chicks, as chicks may eat up to one third of their own weight of food at one feeding.

In kittiwakes the data for forearm growth is most useful from hatching to an age of 20 days, while length of primary feathers, and to a slightly lesser extent, tail feathers, are useful from the age of 7 days through fledging ($\geqslant$ 42 days). The accuracy of ageing birds using this method is approximately $\pm$ 1 day.

The newly hatched chick is relatively weak for the first 24 hours but can tumble around with difficulty. The eyes are open and the egg tooth is present. The bill is pinkish, while the feet are a pale pinkish-gray color with whitish webs. The egg tooth remained until the 7th day after hatching in most cases. Approximately 50 percent of egg teeth had been lost by the 10th day after hatching, and 90 percent by the 16th day.

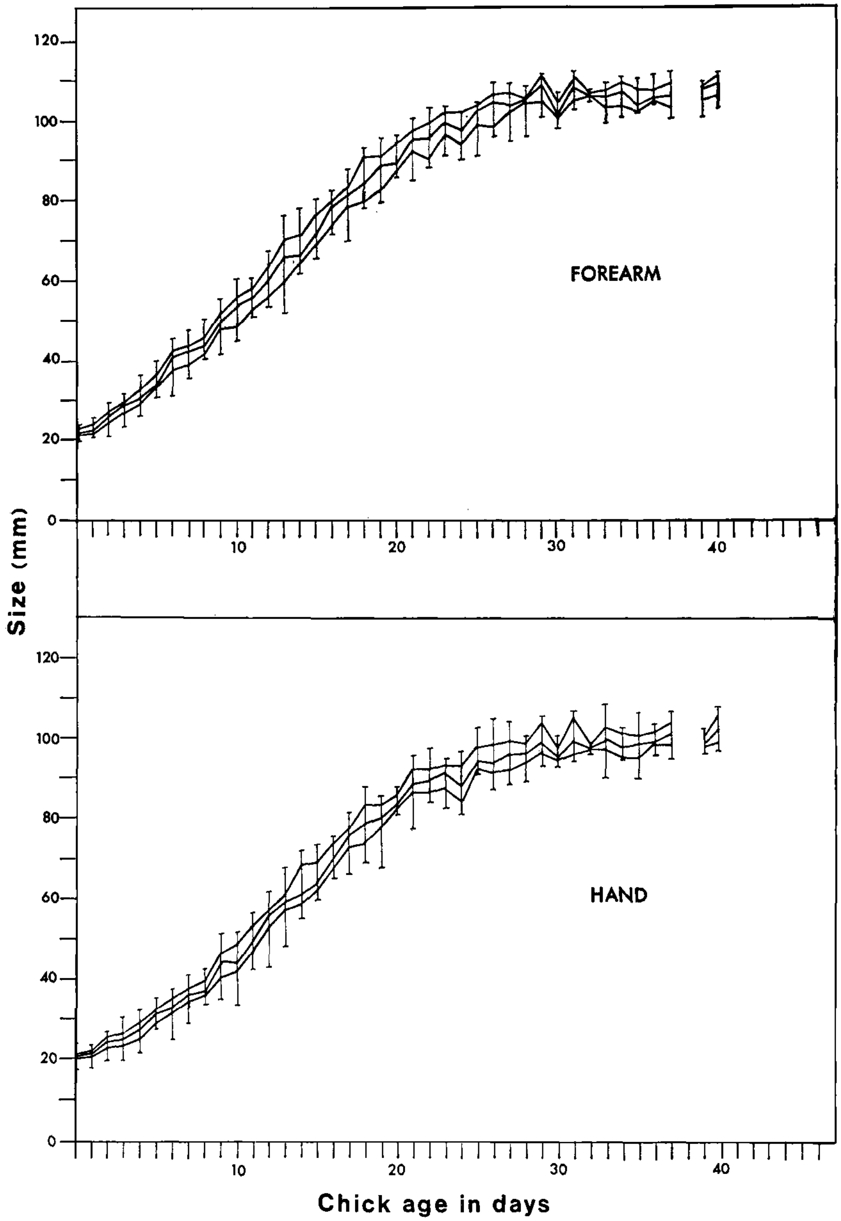


Figure 7. Growth in length of forearm and hand of kittiwake chicks, 1970. Curves represent Q_1, median, Q_3 of measurements and vertical lines represent range.

Flapping motions of the wings began in the first week of life, probably as stretching motions, and about 17 days after hatching became more definite and coordinated. The legs had developed sufficiently for the chick to stand firmly at an age of 6 days, and the feet, exclusive of the webs, had become black. By the 8th day after hatching, the webs had also become black.

Body temperatures.—The body temperature of kittiwake chicks rises rapidly after hatching, from approximately 21° C on the last day in the egg to 35.0° within 3–4 hours after leaving the egg. A further rise occurs at a slower rate until the normal adult temperature of 41.5° C (Simpson, 1912) is reached. Average temperatures for four consecutive 2-day periods ranging from 1–8 days after hatching were: 35.3°, 36.0°, 37.0°, 38.6°.

Dement'ev and Gladkov (1969) claim that thermoregulation becomes operative on the 6th day after hatching in kittiwakes. Our data show that chicks apparently are partially homoiothermic on the hatching day, but their temperature regulating mechanism remains weak for the first 7 days. The hatching temperature of 35° C increases steadily, as indicated above, and by extrapolation, the adult temperature of 41.5° is reached on the 10th or 12th day after hatching. A similar pattern was shown in the European Capercaille (*Tetrao urogallus*) by Hoglund and Borg (1955).

Pterylography.—The following account deals with only the phenology of feather development in the kittiwake embryos and chicks

Tracts of feather buds became visible in the embryo on the 11th day after laying. Color appeared in the buds on the 13 days, feathers erupting from the humeral, spinal, crural, and anal tracts on the 15th day. The feathers on the front of the head and on the ventral surface of the body emerged on the 16th day. Spinal tract feathers were approximately 9 mm long on the 17th day, and by the 20th day the embryo was well covered with down (Figure 5).

The newly hatched chick is fully feathered with down, which is grayish on the back with suffusions of tan on the shoulders and wings, and white elsewhere. The juvenile plumage begins to develop about 5 days after hatching, though some down feathers remain on the head and back until the chick is 25–30 days old.

Feathers of the head first begin to develop in the forehead region and spread backwards from there. Neck feathers erupted approximately 5 days after hatching, the black tips of the vanes being first visible at the tips of the disintegrating keratinized feather sheaths on the 9th day, and the longest feathers reaching a length of 25 mm by the 16th day. Scapular and flank feathers became evident on the 4th or 5th days, the

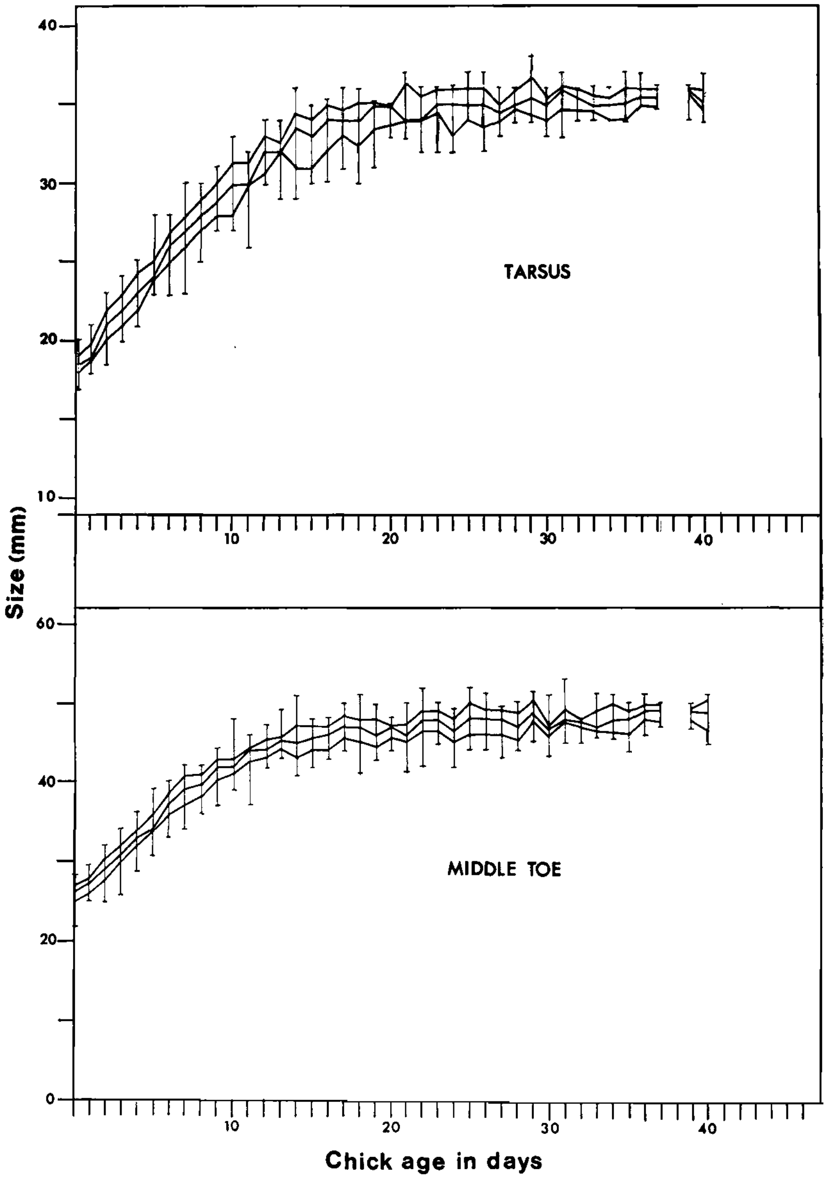


Figure 8. Growth in length of tarsus and middle toe of kittiwake chicks, 1970. Curves represent Q_1, median, Q_3 of measurements and vertical lines represent range.

longest feathers in both regions reaching a length of 25 mm by the 12th day. Remiges usually emerged on the 5th day after hatching, the vanes being first visible beyond the sheaths by the 11th day, as were the black tips of the vanes of the upper wing coverts. The primary length reached 100 mm by the 26th day and 150 mm by the 36th day. The rectrices erupted on the 10th day, the black tips of the vanes becoming visible about the 16th day, and the tail feather length reached 100 mm by the 35th day.

A useful character for aging chicks from a distance is by the relative backward projection of the tail and wings when the chick is standing. The two are almost equal at 30 days of age, while at 36 days the primaries project 1–2 cm beyond the tail, and at 40–45 days, the difference is 3–4 cm.

Fledging period and nest leaving.—Thompson (1964: 299) defines fledging as the "acquisition by a young bird of its first true feathers; when the process is complete the bird is 'fledged'." For our purposes this is not a particularly useful definition, as kittiwakes leave the nest several days before their flight feathers stop growing. Nor is the date of first leaving the nest very useful as an indication that chicks have fledged, because kittiwake chicks return to the nest after they have flown, and are fed there by the parents. Coulson and White (1958b) define the fledging period as "the time between hatching and the final vacating of the nest by the chick," but young birds may return to their nests and perch there after all adult-chick ties have been broken. Swartz (1966) argued that the first departure was probably the most significant. This is difficult to understand, because most chicks can fly acceptably at the age of 30 days if forced to, and chicks of 34–36 days are often made to leave the nest for short periods by disturbance, either of human or other origin. These older birds usually return and continue their nestling period. Thus the fledging period defined by Swartz may depend to a large extent on the level of disturbance in the colony. Therefore we define fledging as the time between hatching and the vacating of the nest for a period longer than 4 consecutive days.

Coulson and White (1958b) in Britain obtained figures of 42.7 days for the mean fledging date with early and late dates of 32–34 and 53–55 days respectively. Keighley and Lockley (1947) recorded that two chicks first flew in 44 (± 1) and 45 (± 1) days respectively. We found the average fledging age to be 41.6 days (SD = 3.12). The two areas on Gull Island investigated in 1970 showed a 2-day difference in fledging age, 40.6 ± 3.00 on the east side, 42.6 ± 2.90 on the west side. A possible explanation for this may be that the eastward-facing nests are higher and on the windward side of the island. Chicks of 30–35 days or older

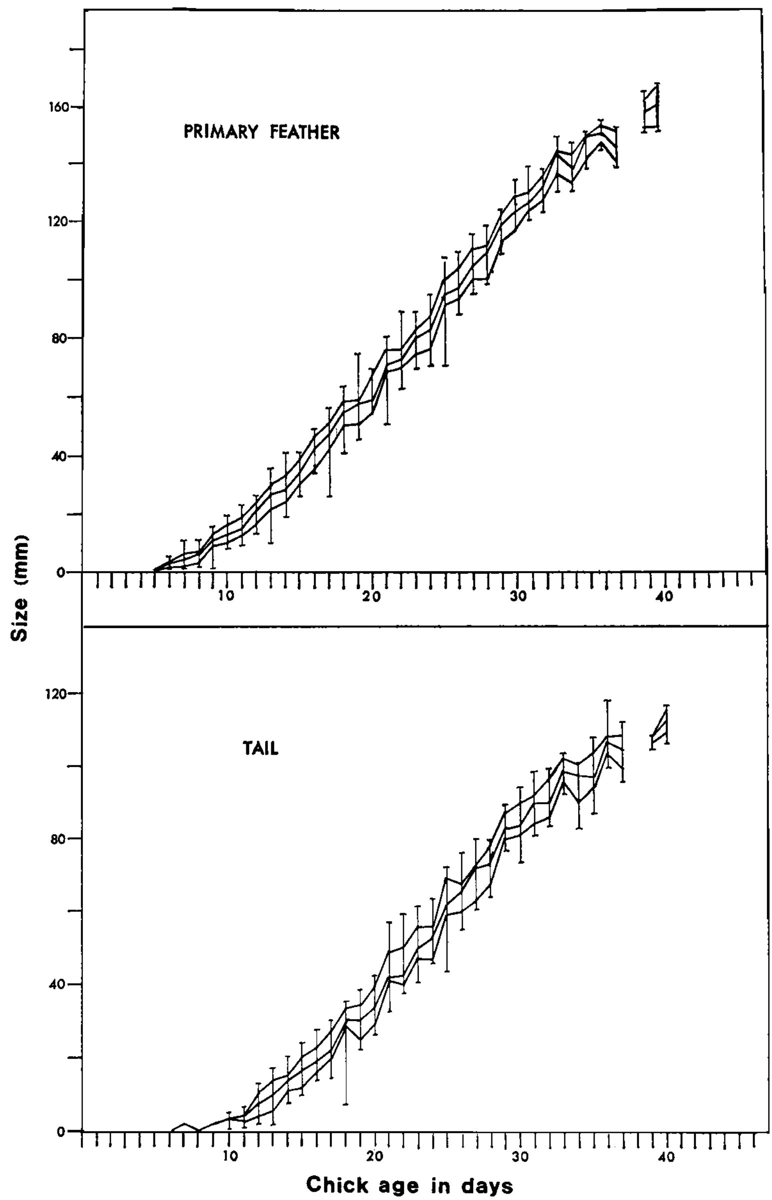


Figure 9. Growth in length of primaries and tail of kittiwake chicks, 1970. Curves represent Q_1, median, Q_3 of measurements and vertical lines represent range.

exercise their wings often, and the strong updrafts on the east side of the island probably encourage them to fly a few days earlier than those reared where the air is relatively calm.

Large numbers of young birds usually move to the mainland shores a few days after flying for the first time. Here they congregate near the fish plants and in the water along the beaches where they eat capelin and fish offal.

Food and feeding.—Cullen (1957) in describing kittiwake feeding behavior points out that chicks take food from the throats of the adult birds rather than picking up regurgitated items from the ground as other gull chicks do. However we recorded many cases where whole capelin (*Mallotus villosus*) and lance fish (*Ammodytes americanus*) were deposited on the nest and later eaten by the chicks. This food on the nest is separate and distinct from the half-digested food the chicks themselves often regurgitate.

The food of the chicks and the adults is chiefly pelagic organisms (Threlfall, 1968). Belopol'skii (1961) states that the kittiwake collects its food from the surface water, though it is able to dive to depths of 0.5–1.0 m, dropping into the water directly from the air, its chief foods being pelagic fish and some crustaceans. It occasionally eats mollusks and other invertebrates on the shore.

In 1969 food found on nests, both deposited by adults and regurgitated by chicks, was almost exclusively capelin. Pellets containing *Mytilus edulis* shells and filamentous algae were seen once, as were lance fish, while squid (*Illex illecebrosus*), were seen in four nests. In 1970 capelin was again the main food item. Flocks of kittiwakes gathered frequently in the intertidal zones of the island and gathered barnacles by smashing the conical cases with thrusts of their beaks and extracting the soft bodies. Toward the end of the breeding season lance fish were taken to a greater extent than earlier in the season, as was offal from the fish-meal plant on the mainland.

Mortality.—The egg mortality of the Gull Island kittiwakes was 28.4 percent (sample of 81) in 1969 and 27.1 percent (sample of 181) in 1970. Chick mortality as defined here is the loss of individuals up to the 35th day after hatching. It is very difficult to keep track of the birds after this age because of their wandering and flying. Chick mortality in 1969 was 19 percent (sample of 58) and in 1970 it was 26.3 percent (sample of 141). In 1970 chicks died on the nests after the 35th day of age. Overall egg to fledging mortality at Witless Bay was 42 percent in 1969, 46 percent in 1970. Coulson and White (1958b) noted 31 percent egg mortality and 14 percent nestling mortality (44% overall mortality) in their studies.

TABLE 2
CAUSES OF EGG MORTALITY AT GULL ISLAND, 1970[1]

Cause of egg mortality	Number lost
Unknown-missing	15
Hole pecked in egg	3
Infertile	11
Knocked from nest	6
Buried and rejected	2
Laid outside nest	1
Nest collapsed	3
Dead pip	3
Predation	5
TOTAL MORTALITY OF EGGS	49

[1] Sample from study areas, 181 eggs.

The causes of egg mortality on Gull Island in 1970 are given in Table 2. In the "unknown-missing" category, some eggs were probably taken by Ravens (*Corvus corax*), others probably were knocked out of their nests accidently, rejected as infertile, or deserted after the loss of another egg in the nest.

While the data in Table 2 do not show it, marauding Ravens took a large proportion of the eggs laid in one part of the colony in 1970 during the first week of laying and substantial numbers during the next fortnight. The great loss of eggs to Ravens during the first part of the laying season is probably the result of a lack of attentiveness and cooperation of the parents, which effectively mob the predators later in the breeding season. In only one instance was a Herring Gull seen to take an egg. Several eggs were lost in 1969 when storm waves washed nests from the cliffs.

The known causes of chick mortality in 1970 were few. Chilling was apparently the cause of 10 known chick deaths in the study areas. Falling from the nest accounted for two more deaths. (Only in cases where chicks fall directly into another nest and are accepted are they reared out of the home nest. In all other cases the chicks are ignored and starve to death or are killed by the larger gulls.) One chick was pecked to death on the nest, and 24 were in the unknown missing category, which probably includes many that fell or were pushed from the nest. Chilling resulted from extremely high air temperatures followed by cool nights or heavy rain. Gordon (1928) records that all chicks of a colony in Scotland were killed by 2 weeks of rain. Predation on chicks is rare, but it does occur, usually involving gulls (noted twice).

In one case a Raven, which was suffering from old gunshot wounds, ate two chicks on a nest before being knocked from the cliff by adult kittiwakes. Premature attempts to fly and resulting chilling when chicks land in sea is common. Collapsing nests claim some chicks, others are driven from their nests by wandering Herring Gull chicks.

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SUMMARY

The topography of Gull Island, Witless Bay, Newfoundland was examined and major Black-legged Kittiwake cliffs were mapped. The breeding population of kittiwakes increased from 6,977 pairs in 1969 to 8,306 pairs in 1970. The birds showed no visible height preference for nesting sites. Birds returned to the colony in February, the nest building season extending from March to early June. Nest construction, materials, and gathering areas are described. Mean egg laying dates were 3 June 1969 and 29 May 1970. Mean clutch size was 1.85; the eggs laid toward the end of the breeding season were smaller. Mean period between laying of first and second eggs of clutch was 2.67 days. Eggs were laid at random times during day and night. Clutches were replaced after loss in 31.6 percent of cases. Relaying success decreased rapidly after the laying peak. New clutches were begun an average of 14 days after the old clutches were lost. Egg weights and measurements and color changes with changing food habits are discussed. Incubation period in 1970 averaged 27.2 days. Time between hatching of first and second eggs was 1.3 days. Egg temperatures were correlated with weather conditions. The temperature of incubating eggs was between 6.0° C and 24.2° C. Specific gravity of eggs decreased from 1.17 at laying to 0.95 just before hatching. Embryo growth is described. Hatching is described and correlated with ambient temperatures. Chick growth is described. Adult body temperature was reached approximately the 12th day after hatching. Pterylography of embryos and chicks is described. Fledging age was about 41.6 days. Food and feeding habits are discussed. Total mortality to fledging was 42 percent in 1969 and 46 percent in 1970.

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