NOTES ON THE EGGS, EMBRYOS AND CHICK GROWTH
OF COMMON GUILLEMOTS *URIA AALGE* IN NEWFOUNDLAND

The eggs and growth of the chicks of the Common Guillemot *Uria aalge*, which is Holarctic in its distribution, have been briefly described by various workers (e.g., Tuck 1961, Hedgren & Linnman 1979). This paper reports on comparative data collected in Newfoundland.

MATERIALS AND METHODS

Eggs, embryos and chicks were obtained from Gull Island, Witless Bay, Newfoundland (47° 15' N, 52° 46' W) in 1977 and 1978. Egg dimensions were recorded using dividers and a millimetre ruler. Weights were taken daily to note any losses during incubation. Egg shapes were described by reference to Preston (1953) and Palmer (1962). Shell surface area, shell weight and egg density were determined by the methods of Paganelli, Olszowka & Ar (1974) and Preston (1974), and by the volumetric method of Groebells (1927). Recent investigations into various aspects of egg weight loss (Drent 1973, Ar et al. 1974) indicate incubation time for a given egg weight to be inversely proportional to the water vapour conductance of the egg shell, with all eggs, regardless of size, losing approximately 18% of their initial weight during incubation. Water vapour conductance (WVC) of Common Guillemot eggs was determined utilizing the formula of Rahn & Ar (1974). WVC is in turn set by the pore area and thickness of the egg shell. The latter parameters were obtained using the method outlined in Ar et al. (1974).

Fifty known-age eggs (6th day after laying until just before hatching) were injected with 10% formalin. Later shells and extra-embryonic membranes were dissected from the embryos, which were dried on paper towels and weighed (Ohaus 2610 g capacity triple beam balance) to 0·1 g. Measurements taken on 26 embryos were the same as those detailed in Haycock & Threlfall (1975; fig. 2). Forty-seven known age chicks were weighed (Pesola spring balance, 300 g capacity, sensitivity ± 1 g) and measured every second day in 1977, with a further 20 chicks being similarly treated in 1978. In the latter season chicks were handled less frequently in an effort to reduce losses due to human interference. Measurements, taken with a millimetre ruler and dividers, included culmen length and depth, tarsus, hand, forearm and middle toe length. Wing chord length was taken along the outstretched contour of the wing, the tenth (longest) primary was measured from the point the fleshy sheath emerged from the skin to the tip of the feather. A record of feather development from hatching to fledging was also kept. Data were collected on the amount of food (weight in g) fed to chicks daily, and the conversion rate calculated.

Rectal temperatures of known-age chicks were recorded using a YSI model tele-thermometer with a #423 insert probe, over a range of ambient temperatures.

RESULTS AND DISCUSSION

Eggs

The mean weight of 287 eggs in 1977 was 108·39 g (s.d. 9·24), this being approximately 9% of the adult female weight (see Threlfall & Mahoney, in press. *n* = 117, mean wt 979 g, s.d. 76, range 815-1187 g). The maximum length and breadth averages were 82·67 mm, s.d. 3·58 and 50·87 mm, s.d. 2·16 respectively, with these figures being similar to eggs measured elsewhere (see Tuck 1961). Eggs laid as replacements after the first was lost, were smaller than initial layings (average wt of replacements = 10·43 g or 9·6% less, *n* = 30). The latter figure is considerably higher than the 6% recorded for Brunnich's Guillemots *U. lomvia* by Birkhead (1980). Eggs collected on Gull Island showed great variability in shape [Alcid ovoid (Preston 1953) to long pyriform and long

oval (Palmer 1962)], colour and pattern. The background varied from white (Munsell notation* N9.5) to an intense blue-green (5BG 8 4), with pale yellows (10Y9.1) and pale greens (5G9.1) also occurring. Complementing the background, the entire surface of the egg is frequently strewn with streaks and blotches (black (N2.0)-medium brown (5YR4 4)-very dark brown (10YR2 1), of different shapes and sizes. The markings are often concentrated on the blunt end of the egg, a not uncommon phenomenon in bird's eggs (Welty 1975). The colouration of the eggs is undoubtedly of survival value, a contention supported by Tuck (1961) who reported that Great Black-backed Gulls *Larus marinus* preyed selectively on plain white Atlantic Puffin *Fratercula arctica* eggs in preference to coloured Guillemot eggs.

With the degree of variation shown it is surprising that Guillemots do not appear capable of distinguishing their own eggs, and while numerous authors provided evidence to the contrary, Tschanz (1959) stated that members of a pair behave selectively toward their own egg on the basis of colour and pattern. However, in the same study, birds were seen to adapt to eggs of a new colour and pattern if the appearance of the egg was changed gradually. Tschanz (1959) also stated that there was a combined effect of area and egg, the two factors performing mutually to produce the strongest inhibitions against incubating a foreign egg. During the present study four Guillemot eggs were given very differently coloured, shaped and sized eggs, and one a Herring Gull *Larus argentatus* egg. All the Guillemots unhesitatingly incubated the new egg, including the gull egg which hatched successfully.

The average surface area of the eggs was 107·5 cm², with egg density averaging 1·07 g cm⁻³. Average shell weight was 9·70 g and shell density averaged 2·08 g cm⁻³.

Egg volume varied according to the method of calculation that was used, i.e., 95·19 cm³ (Bergtold), to 111·89 cm³ (Preston), with the Paganelli *et al.* equation yielding a value of 100 cm³. The volume, as determined by water displacement of ten eggs was 95·88 cm³ (s.d. 11·37).

Water vapour conductance for common guillemot eggs was calculated to be 16·62 mg H_2O day⁻¹ torr⁻¹ H_2O, with an average pore area of 3·01 mm² and shell thickness of 0·43 mm. The predicted incubation time for Guillemots, based on the equation of Rahn & Ar (1974) where incubation time (I) is equal to 5·2 times the quotient of initial weight of the egg (W) divided by the WVC of the egg (G H_2O), is 33·9 days, which is quite close to the 32-day actual value determined during the present study.

Embryo growth

Embryo weight attained 50% of the embryonic maximum at 25 days (approximately six days before hatching). Figure 1 shows that weight increase is slow until day 20, after which time a rapid growth phase occurs (days 21–28). The general shape of the curve closely approximates those given for Herring Gulls and Kittiwakes *Rissa tridactyla* by Haycock & Threlfall (1975) and Maunder & Threlfall (1972) respectively. The average rate of weight increase recorded was 1·9 g per day, which is the same as that recorded for Herring Gulls by Haycock & Threlfall (1975). Embryonic growth proceeded as follows:

Day 6   Head prominent, beak just starting to develop. Pronounced cerebral development, especially mesencephalon. Fore and hind limbs visible, flattened with no digits. Eye pigmented, lens well formed.

Day 11   Mid-brain loses prominence. Protruberances, marking future follicles, now visible. Pollex, and three hind limb digits noticeable. Beak lengthened, bears egg-tooth. The latter is white and surrounded by a pigmented area. Eyelid covers 50% of eye.

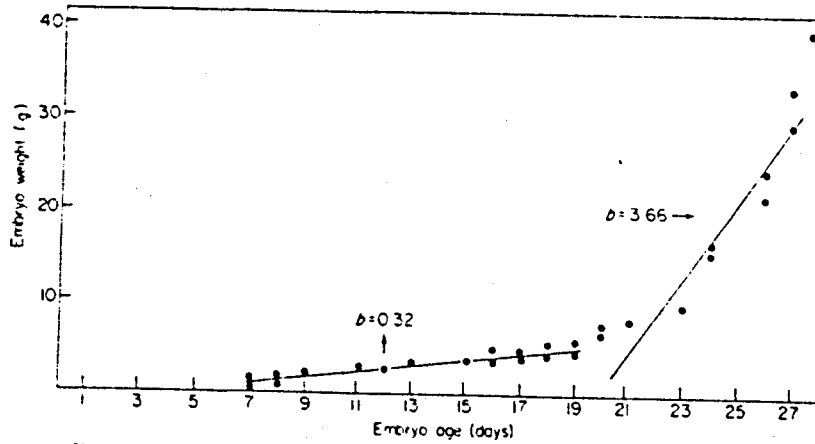* *Munsell Book of Color—Glossy Finish Collection.* 1974 edition. Munsell Color, Baltimore, Md., 21218.

FIGURE 1. Weight of Common Guillemot embryos during development.

Day 17 Follicle protruberances now on limbs and head. Feather eruption in humeral, alar, spinal and femoral tracts. Eyes almost shut. Claws visible on hind digits. Bill, shoulder to tail, arm dimensions 50% of embryonic maximum. Upper mandible hooked in appearance. Egg-tooth more prominent.

Day 21 Eyes completely closed. Feathers in all tracts, ear openings visible, bill hardens, hook on upper mandible and egg-tooth more prominent. Lower mandible with slight swelling in distal region. Tarsus over 50% of embryonic maximum, thin web developed on undersurface. Claws on toes white, well-developed.

Day 25 Entire body surface covered in down feathers (approximately 10 mm long). These neossoptiles were dark on the dorsum, light on the belly, with a gradation of shades along the sides. The 'silvering' evident in newly-hatched chicks was seen at this time, with numerous dark down feathers having a lighter aspect along their surface. Distal portions of claws were darker as was the distal one third of the upper mandible. Pigmentation just appearing on lower mandible, with a reduction in the swelling seen on day 21. Lower mandible contour with a drooping at the extreme distal end over which fitted the hook of the upper mandible. Scaling apparent (scutellate anteriorly, reticulate posteriorly).

Day 28 Tarsus and foot greyish, with scaling fully developed. Bill dark. Hook still present.

Figure 2 shows increase in size of the various body parts at different stages of growth.

Chicks

Chicks emerged from the egg with remnants of the yolk sac still attached and relied on these nutrients for the first two days. The chicks were ptilopaedic, hatching with a complete covering of down, with a mean hatching length of 8 mm on the head and 11 mm on the back (*n* = 30). They were charcoal-grey on the dorsum with a white ventral aspect and suffusions of tan appearing in the neck region. The belly white extended as an inverted 'V' into the darker throat region and the egg-tooth was very prominent at this stage. The head feathers had a silver-tipped appearance which extended to the neck and throat region.

By six days of age neossoptiles had disappeared from large portions of the wing (and other body regions) and contour feathers were emerging over the general body surface. By this time the egg tooth had faded and the yolk sac was completely resorbed.

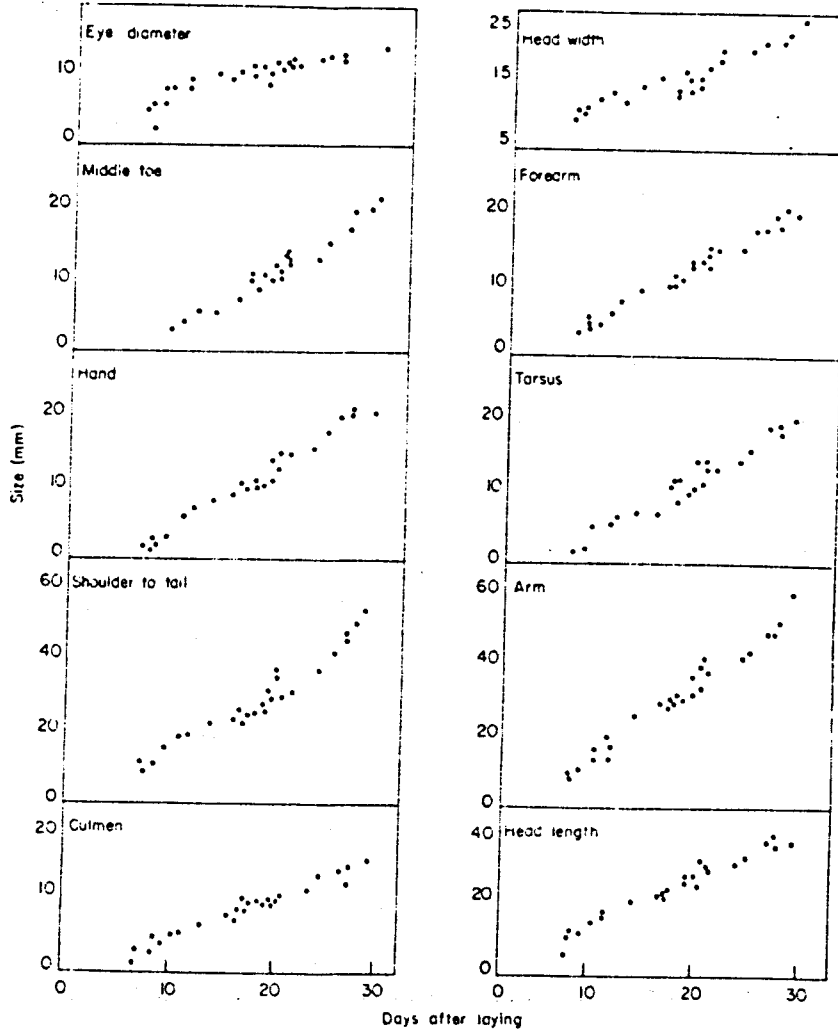The development of the 'mesoptile' plumage (Bédard 1969) continued, and at about

1981

FIGURE 2. Measurements of embryos of Common Guillemot at different stages of development.

12 days of age contour feathers were well developed everywhere, except on the head and neck. In the latter area the tawny band of neossoptiles remained.

At approximately 15 days of age advanced development of the mesoptile plumage was noted with the white of the belly being almost continuous with the more recently developed white of the throat and cheek regions. A sparse band of dark neossoptiles usually remained in the throat region at this stage. Feathering-in of the culmen and eye regions had been completed and in many chicks a prominent black stripe could be observed running from the culmen, through the eye and into the dark plumage at the back of the head and neck. This strip was very conspicuous as it ran between the white area along the cheek and the grey area on the head. The egg-tooth, when present, had become very scale-like and often rubbing the "tooth" would cause it to flake off. Major plumage developments had all been completed by this time and from this point until fledging energy allotted to plumage was presumably invested only in growth of the feathers (and possibly conditioning them for continuous immersion in water).

TABLE 1

Weight (g) increments per 48 h of Guillemot chicks at different localities

Age in days	Gull Island			Skomer Island			Farne Islands		
	Mean wt	Wt change (% adult wt)	r	Mean wt	Wt change (% adult wt)	r	Mean wt	Wt change (% adult wt)	r
1	74·5	— —	—	67·3	— —	—	55·5	— —	—
3	92·1	17·6 (1·7)	0·105	91·0	23·7 (2·7)	0·118	83·2	27·7 (3·0)	0·202
5	112·0	19·8 (1·9)	0·097	104·8	13·8 (1·5)	0·108	129·5	46·2 (4·9)	0·220
7	149·0	37·0 (3·7)	0·142	135·7	30·9 (3·5)	0·112	148·0	18·5 (2·0)	0·066
9	153·0	4·0 (0·4)	0·014	155·8	20·1 (2·3)	0·071	166·5	18·5 (2·0)	0·058
11	195·0	42·0 (4·2)	0·119	179·4	23·6 (2·7)	0·069	185·0	18·5 (2·0)	0·054
13	193·3	−1·7 (−0·1)	0·004	208·0	28·6 (3·2)	0·042	203·5	18·5 (2·0)	0·047
15	215·7	22·4 (2·2)	0·054	200·6	−7·4 (−0·8)	0·008	212·7	9·2 (0·9)	0·022
17	223·0	7·3 (0·7)	0·016	217·3	16·7 (1·9)	0·047	220·0	9·3 (1·0)	0·016
19	236·0	13·0 (1·3)	0·028	216·7	−0·6 (−0·0)	−0·001	249·7	27·7 (2·9)	0·061
21	247·0	11·0 (1·1)	0·022	217·4	0·6 (0·0)	0·006	—	— —	—
23	260·5	13·5 (1·3)	0·049	—	— —	—			

Gull Island Mean r = 0·062   Skomer Island Mean r = 0·058   Farne Islands Mean r = 0·041

Notes: Adult weights: (a) Gull Island = 992·5 g   (b) Skomer Island = 875·0 g   (c) Farne Islands = 925·0 g
Data for Skomer is from Birkhead (1976); that for Farne Islands is from Pearson (1968).

Chick growth, calculated using the formula given by Banks (1959), was 0·063 in 1977 and 0·062 in 1978. Table 1 compares the patterns of weight increase for three populations, namely: Gull Island, Newfoundland (this study), Skomer Island, Great Britain (Birkhead 1976) and the Farne Islands (Pearson 1968). While different patterns of weight increase are indicated for the three groups during particular days, the overall growth rates (r) are not significantly different ($t = 0.65$ df = 7, $P > 0.05$). The different patterns of weight increments probably reflect day to day variations in chick feeding rates which may be influenced by weather and/or prey distribution in the different areas. The chicks that were weighed in this study were located on high density (4–5 pairs per m²) ledges, with a high breeding success.

Between one and 16 days of age chicks gained 144 g, or 8·8 g per day with a mean daily food intake of 75·5 g of fish, this giving a conversion rate of 11·6%. Chicks on Skomer (Birkhead 1976) had a mean increase of 9·3 g per day, and a conversion rate of 31·3%. These discrepancies may be due to internal constraints set by the design of the growing organism (Ricklefs 1969), or to the relative energy requirements for maintenance and growth of chicks in different geographical localities. Energy drains due to thermoregulatory processes can be quite substantial (see Royama 1966). Tuck (1961) considered increased demands for thermoregulation to be responsible for the smaller size of fledging Brunnich's Guillemots at Cape Hay as compared to those at Akpatok Island farther south. Skomer is warmer than Gull Island in June and July, with mean temperatures and mean minimum temperatures being approximately 4° C and 5° C (respectively) warmer on the former than the latter. The majority of chicks hatched in the last two weeks of June on Gull Island, and it was not until the end of the first week of life that their thermoregulatory mechanism became established. Gull Island chicks probably had to expend more energy to stay warm than was the case for birds on Skomer. Which of the above hypotheses best explains the differences between the two populations is difficult to say, although it may well be an interaction of both factors which surfaces as an underlying cause.

The development of various body regions for 65 Guillemot chicks is depicted in Figure 3. The graph differs from those of other workers in that a pre-fledging weight recession is absent. For the six body regions presented in Figure 3, a pronounced division
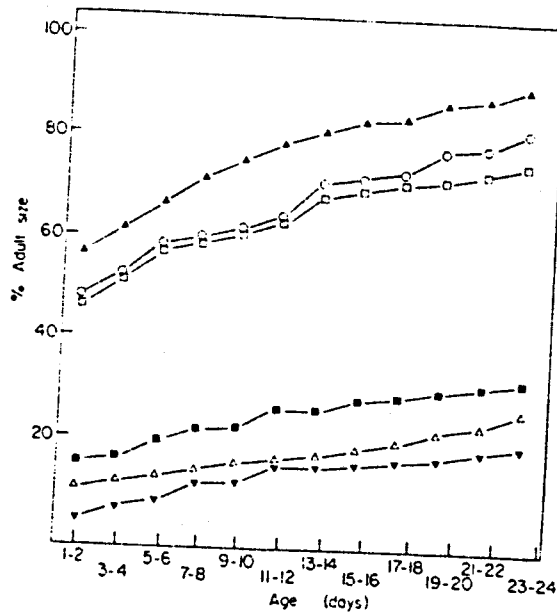
FIGURE 3. Development of various body regions of 65 Common Guillemot chicks expressed as a percentage of the adult size. ▲, Middle toe, ○, tarsus, □, claw length, ■, culmen length, △, wing chord, ▼, weight.

is immediately apparent between the development of the foot (= foot and tarsus) region generally and all other body areas. Tarsus, middle toe and claw lengths all have mean value at hatching of greater than 40% of their average adult values. Culmen length, weight and wing chord, on the other hand, do not attain 40% of adult values even at fledging. By the time chicks are ready to go to sea the tarsus, middle toe and claw are all in excess of 75% of their adult dimensions.

Such non-uniform allotment of energy is found in many species e.g., ground-nesting altricial passerines (Maher 1964). Those attributes which afford the greatest survival value to the developing organism are selected for and, at this critical stage, rather than evenly distribute its energy, the organism allows for rapid growth of those essential body parts and functions which allow for continued development of the chick under less hazardous conditions.

TABLE 2

Fledging and adult values of growth parameters for Gull Island Common Guillemots

	W	H	F	WL	T	MT	C	CL	CD
Adult	992·5	88·8	174·7	481	39·6	45·2	11·2	43·3	14·2
Fledging	240·5	26·6	31·5	135·2	31·3	41·5	8·1	14·6	9·3
% Adult	24·2	29·9	18·0	28·1	78·4	91·8	72·3	33·8	65·8

Notes:
W = Body weight
H = Hand
F = Forearm
WL = Wing length
T = Tarsus
MT = Middle toe
C = Claw (on middle toe)
CL = Culmen length
CD = Culmen depth

Summary values (% ± 1 s.d.):
(a) For all wing parameters: 25·3 ± 6·4
(b) For all tarsus and foot parameters: 80·8 ± 9·97
(c) For all bill parameters: 49·8 ± 22·62.

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In Guillemots the feet provide stability while on the ledge, may be important in the leap from the cliffs at fledging, and are used by the chick to swim away from the colony. Thus strong selection for development of the tarsus and foot probably occurs for life on the ledge as well as in the water, while claw dimensions are of functional significance only while the chick is on the ledge. The percentage of adult dimensions attained for each parameter at fledging is given in Table 2.

Chick temperatures and the ages at which they were recorded are given in Table 3. The appearance of an asymptote at approximately day *10* and the conspicuous reduction in deviations about the mean for chicks of this age and older both indicate that at this

TABLE 3

Rectal temperatures (°C) of developing Guillemot chicks on Gull Island, Newfoundland, in 1978

Age in days	Mean temperature	%. Adult temperature[1]	s.d.	n
1	22·7	54·5	17·0	9
2	29·7	71·2	9·1	26
3	35·1	79·4	5·4	7
4	31·9	76·5	7·7	12
5	36·1	86·5	4·5	8
6	37·0	88·8	3·2	12
7	36·5	87·6	2·7	12
8	36·7	88·1	2·2	26
9	37·5	90·1	1·9	9
10	37·8	90·7	1·4	10
11	37·7	90·5	1·5	12
12	37·8	90·7	0·6	6
13	37·8	90·7	0·6	6
14	37·9	90·8	1·5	8
15	38·6	92·6	1·5	5
16	38·2	91·8	0·6	10
17	38·5	92·5	1·5	7
18	38·4	92·3	1·6	8
19	38·4	92·1	0·9	6
20	38·4	92·1	1·0	10
21	38·7	93·0	1·6	4
22	38·9	93·5	—	1
23	38·9	93·5	—	1

Note: [1] Adult body temperature was considered to be the same as that recorded by Iversen and Krog (1947) for *U. a. californica* (range 40·7 °C–42·5 °C, mean 41·7 °C).

stage chicks are exerting a great deal of control over their body temperatures. These data show marked similarity with those of Johnson & West (1975) who discovered, via much more stringent experimentation, that sustained homeothermy developed in the Guillemot *U. a. inornata* at between six and eight days of age. Tuck (1961) suggested that complete homeothermy in Guillemot chicks was not attained until nearly sea-going.

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