Notes

Thickness of Common Murre (*Uria aalge*) Eggshells in Atlantic Canada

DONALD W. PIRIE-HAY and ALEXANDER L. BOND[1]

Department of Biology, University of Saskatchewan, and Environment Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan S7N 3H5 Canada
[1]Corresponding author: alex.bond@usask.ca

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Reported values for eggshell thickness in Common Murre (*Uria aalge*) are few, and even fewer since the decline in use of organochlorine pesticides and other environmental pollutants that caused significant thinning of shells. The eggshells of Common Murres and Thick-billed Murres (*Uria lomvia*) are among the thickest and heaviest, proportionately, of any bird and this represents a non-trivial maternal investment. We measured the length and breadth of Common Murre eggs collected from Machias Seal Island, New Brunswick, in 2006, and Gull Island, Newfoundland and Labrador, in 2012, and we measured the thickness of the eggshells. Shell thickness was not related to egg size or volume, and it varied in individual eggs. The shells of Common Murre eggs from Machias Seal Island (mean and standard deviation [SD] (0.767, SD 0.078 mm) and Gull Island (0.753, SD 0.057 mm) were significantly thicker than any previously reported value and among the thickest of all birds. Such thickness is likely a result of nesting on rock substrate with no nesting material and, perhaps, high breeding densities.

Key Words: Common Murre; *Uria aalge*; eggshell thickness; egg size; Atlantic Canada; Bay of Fundy; Gull Island; Machias Seal Island; Witless Bay; New Brunswick; Newfoundland and Labrador

Introduction

The integrity of avian eggshells, which are composed mainly of calcium carbonate, is critical for successful breeding (Gill 2007). Eggshell thickness depends on the dietary intake of calcium of the egg-laying female (Uspenski 1958); thus, the need to produce thick shells creates high calcium demand. Thickness is also affected by organochlorine pesticides, introduced in the 1940s. These compounds caused widespread eggshell thinning in birds (Bitman *et al*. 1969; Ratcliffe 1970; Lundholm 1997), and the most detrimental, dichlorodiphenyltrichloroethane (DDT), was banned in North America in the 1970s.

Common Murres (*Uria aalge*) are cliff-nesting seabirds that typically breed in high-density colonies (Tuck 1961). They build no nest. The shells of their ovate-pyriform to elliptical-ovate eggs are thicker at the narrow end, a characteristic shared with Razorbills (*Alca torda*) and presumably an adaptation to nesting on bare rock (Belopolskii 1961; Ainley *et al*. 2002). Given the conditions of the nesting habitat, thick shells prevent egg loss and breakage and, therefore, thickness is an important factor in breeding success. The shape of Common Murre eggs is adapted to maximize the surface area in contact with the brood patch to facilitate incubation (Harris and Birkhead 1985; Ainley *et al*. 2002), and the small roll radius, which further decreases as the egg develops, helps prevent the egg from rolling off the ledge (Uspenski 1958). Murres, along with penguins (Spheniscidae), cormorants (Phalacrocoracidae), and guillemots (Alcidae: *Cepphus* spp.), have the heaviest eggshells relative to whole egg mass of any flying bird (Schönwetter 1960-1992).

The purpose of our study was to determine eggshell thickness and its relation to egg size of Common Murres in contemporary samples from two sites in Atlantic Canada and to compare eggshell thickness with previously published values. We also investigated the relation between eggshell thickness and other physical characteristics (colour and speckling pattern).

Methods

We collected Common Murre eggs from two sites in Atlantic Canada: Machias Seal Island, New Brunswick (44°30'N, 67°06'W), where about 100 pairs of Common Murre breed beneath large boulders (Diamond and Devlin 2003; Bond and Diamond 2006) and Gull Island (47°16'N, 52°46'W) in the Witless Bay Ecological Reserve, Newfoundland and Labrador, which supports approximately 10 000 breeding pairs of Common Murres (S. I. Wilhelm, Canadian Wildlife Service, unpublished data, 2012).

We collected 10 whole eggs from Machias Seal Island in June 2006 and 69 intact and partly broken shells from eggs depredated by gulls (*Larus* spp.) on Gull Island in July 2012. Because gulls could be targeting younger inexperienced breeders, which have thinner eggshells (Hipfner *et al*. 2003), we also collected 20 eggs from known established breeders near the centre of nesting cliffs on Gull Island in June 2013.

For mostly intact eggs from Gull Island, eggshell thickness (including the egg membrane) was measured at six locations: four equidistant points at the equator (i.e., largest circumference) and one at each end of the egg. Thickness was measured to the nearest 0.0025 mm using a spring-loaded micrometer. Measurements at the ends of the eggs were taken on the flattest part to avoid measuring a strongly curved surface, especially at the narrow end. Any obvious exterior or interior surface or shell irregularities were avoided. Average thickness of the egg membrane was determined by measuring the difference in shell thickness with and without the membrane at a sample of adjacent spots on the egg (n = 10, selected randomly from all eggs). The mean of the four thickness measurements at the equator (minus mean egg membrane thickness) was recorded as middle eggshell thickness. We assessed measurement error by measuring 21 eggs twice on different days. A single observer made all measurements.

We measured the length and breadth of intact eggshells (n = 50 from Gull Island, not including any collected in 2013) with dial callipers, to the nearest 0.1 mm. Because eggs were depredated by gulls, both measurements could not be made on all eggs (breadth n = 44, length n = 40). Ground colour and speckling pattern of eggs were sorted into one of five classes, as defined by Gaston and Nettleship (1981), with higher numbers indicating more base and speckling pigmentation in the eggs. As depredated eggs might be more likely to come from young or inexperienced females and, therefore, have thinner shells (Hipfner *et al.* 1999), eggshell thickness measurements from Gull Island in 2012 should be taken as a minimum estimate.

Statistical methods

We used repeated-measures analysis of variance (ANOVA) to examine within-egg variation in shell thickness between the bottom (round end), middle (largest circumference), and top (narrow end) of eggs collected from Gull Island in 2012. Only eggs with measurements for all locations were included.

We used Tukey's honest significant difference (HSD) post-hoc test for pairwise comparisons. To determine whether shell thickness at the top (the measurement with the largest sample size, n = 58) increased with increasing ground colour and speckling pattern, we used Kruskal-Wallis rank-sum test.

We tested relations between egg size (length, breadth, and volume) and shell thickness using linear regression. A volume index was calculated as length × breadth^2 (Hipfner and Gaston 1999).

Finally, we compared the thickness of our shell samples with previously published values (Gress *et al.* 1971; Henny *et al.* 1982; Pyle *et al.* 1999; Zimmerman and Hipfner 2007) and tested differences using ANOVA and Tukey's HSD. All tests were performed in R 3.0.2 (R Development Core Team 2013), and differences were considered significant when $P < 0.05$. Data are presented as the mean and standard deviation (SD).

Results

Differences between repeated measurements of the thickness of the same shells were small (0.016, SD 0.021 mm) and ranged from zero to 0.145 mm or 0.0–8.6% of shell thickness. The membrane measured 0.070 mm (SD 0.049), or 8.2% of the combined thickness of the shell and membrane. Among the 21 eggs assessed twice on different days, categorization of ground colour and speckling pattern differed for two and five eggs, respectively; in all cases, the assessment differed in a single category.

Shell thickness varied within each egg at both sites (Table 1). At Gull Island in 2012, repeated measures (ANOVA, $F_{2,44} = 310.3$; $P < 0.001$) showed that the mean thickness of the shell at the bottom (0.687, SD 0.066 mm) was thinner than at the middle (0.753, SD 0.057 mm, $P < 0.001$), and the mean thickness of the shell at the middle was thinner than at the top (0.906, SD 0.062 mm, $P < 0.001$). We observed a similar pattern in shells from Machias Seal Island (repeated meas-

TABLE 1. Shell thickness and size of Common Murre (*Uria aalge*) eggs from Gull Island, Newfoundland and Labrador (2012) and Machias Seal Island, New Brunswick (2006).

Shell thickness	*n*	Range (mm)	Mean (mm)	SD (mm)
Gull Island				
Top	58	0.761–1.040	0.906	0.062
Middle*	56	0.664–0.822	0.753	0.057
Bottom	54	0.568–0.860	0.687	0.066
Machias Seal Island				
Top	9	0.780–0.932	0.829	0.058
Middle*	8	0.726–0.907	0.767	0.078
Bottom	7	0.653–0.866	0.684	0.064
Egg size				
Gull Island				
Length	40	74.2–90.8	82.2	3.6
Breadth†	44	47.6–53.9	50.7	1.4
Machias Seal Island				
Length	10	79.0–91.0	84.6	3.3
Breadth†	10	49.4–52.9	50.0	3.5

*At the "equator" or largest circumference.
†Largest diameter.

ures ANOVA, $F_{2,8}$ = 9.29, P = 0.008); although the mean thickness of the shell at the top and at the middle did not differ ($P > 0.05$), both were thicker than at the bottom ($P < 0.05$). On Gull Island, mean shell thickness in 2012 did not vary with ground colour ($\chi^2 = -1.91$, df = 4, P = 0.75) or speckling pattern ($\chi^2 = -1.31$, df = 4, P = 0.86; Table 2).

The mean length and mean diameter of Gull Island eggs in 2012 were 82.2 mm (SD 3.7) and 50.7 mm (SD 1.4), respectively; these measures for Machias Seal Island eggs were 84.6 mm (SD 3.3) and 50.0 mm (SD 3.5). At both sites, there was no detectable correlation between eggshell thickness at the six measured locations and length (all $P > 0.08$ and $r^2 < 0.08$), diameter (all $P > 0.23$ and $r^2 < 0.04$), or volume index (all $P > 0.58$, and $r^2 < 0.01$).

Common Murre eggs collected from Gull Island in 2012 and Machias Seal Island in 2006 were significantly thicker than any previously reported value ($F_{8,283}$ = 57.55, all pairwise comparisons $P < 0.05$; range of means: 0.54–0.716 mm; Figure 1). The mean thickness of the shells of the 20 eggs collected from known established breeders on Gull Island in 2013 was significantly greater than the mean thickness of eggshells measured in 2012 on Gull Island (middle: 0.811, SD 0.040 mm, $P < 0.001$), but was not significantly greater than the mean thickness of eggshells on Machias Seal Island (middle: 0.767, SD 0.078 mm, P = 0.58).

TABLE 2. Ground colour and speckle pattern on Common Murre (*Uria aalge*) eggs from Gull Island, Newfoundland and Labrador (2012).

Ground colour	No. of eggs
Class 1 (lighter)	14
Class 2	23
Class 3	12
Class 4	10
Class 5 (darker)	7
Unclassified	3
Speckle pattern	
Black speckles with blotches at large end	14
Brown spots with a few scribbles	4
Faint brown scribbles	7
Black scribbles	18
Black blotches	24
Unclassified	2

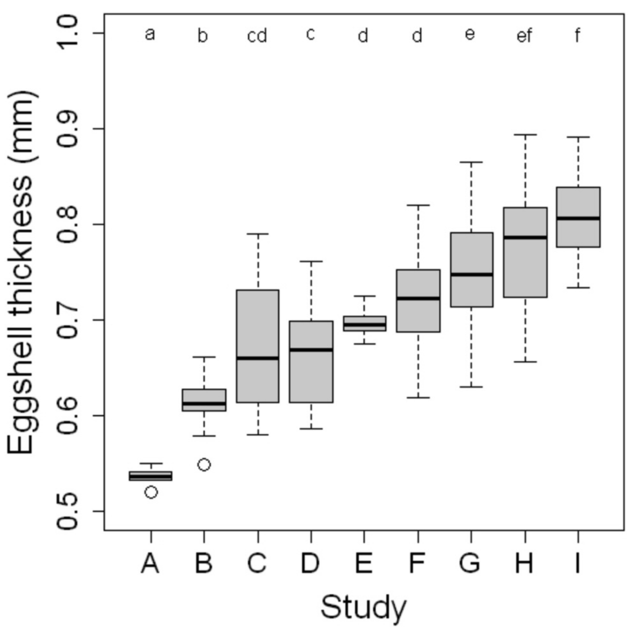

FIGURE 1. Shell thickness at the equator of Common Murre eggs in Atlantic Canada (G–I) compared with that reported in other studies (A–F). Groups not sharing the same lowercase letter above are significantly different (Tukey's HSD, $P < 0.05$). Black horizontal lines indicate the mean, shaded boxes are the first and third quartiles, whiskers are the 5–95% data range, and open dots are extremes. A, Triangle Island, British Colombia (Zimmerman and Hipfner 2007); B, Farallon Islands, California, 1968 and 1970 (Gress *et al*. 1971); C, Island Rock and Gull Island, Oregon, 1979 (Henny *et al*. 1982); D, Southeast Farallon Island and Ano Nuevo Island, California, 1993 (Pyle *et al*. 1999); E, Farallon Islands, California, 1913 (Gress *et al* 1971); F, Pacific Coast, northern California to Queen Charlotte Islands, British Columbia, pre-1947 (Henny *et al*. 1982); G, Gull Island, Newfoundland and Labrador, 2012; H, Machias Seal Island, New Brunswick, 2006; and I, Gull Island, 2013.

Discussion

Like those of Thick-billed Murres (Uspenski 1958), eggs of Common Murres are not of uniform thickness. Greater thickness at the top allows the egg to withstand the same amount of pressure there as at the bottom, but over a smaller surface area. Egg size was not related to shell thickness at any location on the egg, nor was there any relation between thickness and level of pigmentation.

The eggs collected in Atlantic Canada had the thickest shells ever recorded for Common Murres. In the comparison, we excluded eggs measured at Gull Island in 1977 and 1978 (0.43 mm, measured by vapour conductance; Mahoney and Threlfall 1981), because they were measured by a different method: vapour conductance.

The only other record of shell thickness after the rapid decline in use of organochlorine pesticides (Zimmerman and Hipfner 2007) also differs significantly from our measurements. These eggs, collected from Triangle Island, British Columbia, had a lower average shell thickness (0.54, SD 0.005 mm), but egg length (85.5, SD 3.5 mm) and diameter (50.5, SD 1.2 mm) were similar despite a small sample size (n = 6 for thickness, n = 15 for length and breadth; Zimmerman and Hipfner 2007). The thicker eggshells in the Atlantic region suggest population differences between the two oceans, where birds are known to experience different ecological pressures (Ainley *et al*. 2002). Differences in contemporary eggshell thickness could be related to salinity (Dyck and Kraul 1984) or the availability of calcium in pre-breeding diets (Bientema *et al*. 1997; Brenninkmeijer *et al*. 1997).

Our study is the first to examine the relation between egg size and shell thickness in this species. Although we found no such relation, this is the first investigation of its kind among Common Murres, and similar research is recommended at other colonies, particularly those where shell thinning is known to have occurred as a result of environmental pollutants.

Williams *et al*. (1982) found that, among Charadriiformes, eggshell mass, as a proportion of total egg mass, is highest among murres (13.7% for Common Murres and 14.4% for Thick-billed Murres), compared with terns (Sternidae: 4.8–10.7%) and gulls (*Larus* spp.: 5.9–11.8%); this progression corresponds to decreasing rigidity of nest sites (bare rock [murres], sand and gravel [terns], and plant material [gulls], Williams *et al*. 1982). Penguins, cormorants, and murres have the heaviest proportional eggshells among seabirds (Williams et al. 1982). Although Razorbills (*Alca torda*) nest on substrates similar to those used by Common Murres, they aggregate much less densely (Birkhead 1978), and their eggshells are proportionally less massive (8.66 ± 0.36%; Birkhead and Nettleship 1984). It is possible that species breeding on a rigid breeding substrate without nesting material and in dense aggregations (relative to other seabirds) combine to produce some of the relatively thickest and heaviest eggshells.

Conclusions

Our results show that Common Murres from Atlantic Canada have the thickest eggshells recorded for this species and that even the eggshells of supposedly inexperienced breeders are thicker than those found elsewhere. Thickness varied with location on the egg, and thickness was not related to egg size or volume. Eggs of established breeders had thicker shells than those depredated by gulls, possibly produced by younger murres. This is one of only a few studies to investigate eggshell thickness in seabirds since the decline of organochlorine pesticide use. We recommend further research to investigate contemporary murre eggshell thickness throughout the breeding range and possible ecological, toxicological, or phylogenetic influences.

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