EGGSHELLS OF ARCTIC TERNS FROM FINLAND: EFFECTS OF INCUBATION AND GEOGRAPHY

M. FINNLUND

R. HISSA

J. KOIVUSAARI

E. MERILÄ

AND

I. NUUJA

ABSTRACT.—Seventy-four eggs from seven colonies of Arctic Terns (*Sterna paradisaea*) in the Quark and the Bothnian Bay of Finland were collected in 1981 shortly after laying and immediately before hatching. Shell thickness, weight, thickness index, and egg weight index were determined and compared with the same characteristics of 200 eggs collected between 1874 and 1935.

We found no significant differences in these measures of egg thickness between recent and museum shells from the same geographical areas. Shells of museum specimens from different geographical regions did show significant variations.

The weight and the wing and tarsus length of the embryos correlated negatively and significantly with all measured characteristics of the shell except its thickness when the shell membranes were present. During the incubation period, the shell's thickness (without membranes) decreased 8%; thickness index and weight decreased 4%; and the shell's thickness with shell membranes present decreased 1–2%. In this paper, we discuss reasons for these changes.

Pesticide-related reproductive failures have been reported in both American and European terns (*Sterna* spp.; Switzer and Lewin 1971, Koeman and van Genderen 1972, Switzer et al. 1973, Gochfield 1975, Fox 1976). For example, high levels of chlorinated hydrocarbons were found in the tissues of marine animals from the Baltic Sea (Jensen et al. 1969, Koivusaari et al. 1972, Anderson and Hickey 1974), an area where eggshell thinning of 11–17% was reported in White-tailed Eagles (*Haliaeetus albicilla*) and Ospreys (*Pandion haliaetus*; Koivusaari et al. 1980, Odsjö 1982). In contrast, Lemmetyinen and Rantamäki (1980) reported low pesticide contamination in the eggs of Arctic Terns (*S. paradisaea*) from the archipelago of southwestern Finland. The thickness of eggshells from these terns has recently increased significantly (5.2%, $P < 0.05$) in Finland (Gulf of Bothnia; Pulliainen and Marjakangas 1980).

Several studies concerning geographic variations in eggshells have been published (e.g., Anderson and Hickey 1970, 1972; Sutcliffe 1978; Olsen 1982), but there are almost no studies of this kind from Europe (e.g., Svensson 1978).

Besides effects of pesticides and geography, the mobilization of eggshell calcium for the developing embryo is known to affect eggshell thickness (e.g., Kreitzer 1972). Our objectives, therefore, were (1) to describe recent changes in the thickness and size of Arctic Tern eggshells in comparison to museum material; (2) to check the reliability of available museum material for use as a standard; and (3) to find a method for measuring shell variables that is independent of the shell thinning that occurs naturally during embryonic development.

MATERIALS AND METHODS

We collected Arctic Tern eggs in 1981 from three colonies in Quark (63°10′N, 21°25′E) and from four colonies in Bothnian Bay (65°03′N, 25°10′E) in the Gulf of Bothnia (Fig. 1). At each nest, one egg was chosen randomly at an early stage of incubation (little or no embryonic development). Nine of these nests in the Quark colony were marked and two more eggs were taken from each shortly before hatching was expected. Where Arctic and Common terns (*S. hirundo*) bred in the same colonies, we confirmed identification of Arctic Tern nests by observation from a blind or by flushing a parent from its nest before taking an egg.

Eggs were kept in a refrigerator until prepared. Their length and breadth were measured with a vernier caliper to the nearest 0.1 mm. A piece of shell, 16–18 mm in diameter, was cut out from the equator of each egg. The contents of the egg were then removed, the shells were rinsed with water, and the shell
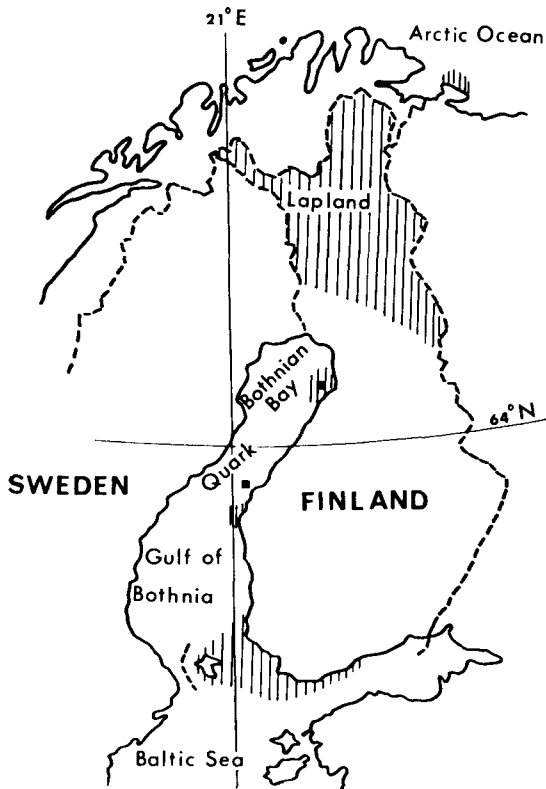
FIGURE 1. Collection sites of Arctic Tern eggs: museum (1874–1935) specimens were collected in the hatched areas; eggs used in the present (1981) study were collected at the Quark and Bothnian Bay (black squares).

membrane under the air space was punctured. The shells and pieces of shell were allowed to dry for two months at room temperature; they were then weighed to the nearest 0.001 g on an electric precision balance. The shell membranes were softened by boiling the pieces of eggshells in 2.5% NaOH for 3 min (see Vanderstoep and Richards 1970). This procedure caused no perceptible changes in the calcium structure of the shell's outer surface, and probably did not change the inner surface of the shell since it was protected by the shell membranes. The membranes were then freed under running tap water with the aid of forceps and a soft brush. The pieces of shell were then rinsed with distilled water and allowed to dry.

In order to estimate the geographical variation in the eggshells of Arctic Terns from Europe, Greenland, and North America, we calculated weight and thickness indices for museum eggs using published information about their dimensions and weight (Makatsch 1974). In addition, eggshells from various regions of Finland and the Arctic Ocean were measured at the zoological museums in Helsinki and Oulu, Finland, and Leningrad,

U.S.S.R. The eggs in these collections represented specimens obtained between 1874 and 1935. For purposes of measurement, we assumed that museum eggs with small emptying holes had not contained embryos of any considerable size, and, hence, had shells that had not been depleted of calcium by the embryo.

To determine the developmental stages of embryos in recently-obtained eggs, we removed them from the shell, weighed them to the nearest 0.01 g, and measured their manus lengths to the nearest 0.1 mm with a vernier caliper (see Ryder and Somppi 1977). Eggs containing dead embryos were disregarded. In eggs collected at early stages of incubation, the chorioallantoic membrane was not attached to the shell membranes, and, hence, shell calcium had not been depleted (see Dunn et al. 1981). In order to calculate an "egg weight index," we filled shells with distilled water and weighed the water (ww). The water's weight was then used to calculate the egg's weight index constant (K_w) from the relationship: $K_w = wwLB$, where L is the egg's length (cm), B is its maximum breadth (cm), and ww is in g. This equation gave the empirical value 0.466 for K_w, which we used to calculate the egg weight index (WI) described by the equation $WI = K_wLB^2$. This equation is much like the commonly used volume index $V = K_vLB^2$, where K_v (0.478) is the volume index constant (Coulson 1963, Coulson and Horobin 1976).

We also calculated eggshell thickness indices (in mg/mm²) defined by Ratcliffe (1970) as shell weight/LB. We ignored weight loss due to the emptying holes (maximum diameter: 4 mm) in museum shells. The thickness of shell pieces with and without membranes and some loose membranes were measured to the nearest 0.01 mm using a dial micrometer. The museum eggs were measured through their blowing holes with the aid of a specially adapted measuring pin. The pin had a round ball of 2.0-mm diameter on the end and a measuring load of 77.7 g (SD = ±1.4 g). The thickness used in our calculations is the arithmetic mean of six measurements per shell. The mean thickness for eggs from different geographical areas, populations, or other groups is based upon values of individual eggs, not on clutches.

We analyzed the data with Student's t-tests and linear regression analyses.

RESULTS

EGGSHELL PARAMETERS AND THEIR
GEOGRAPHICAL VARIATION

Eggshells that we collected from colonies in the Quark and the Bothnian Bay did not differ statistically from each other for any parameters investigated, so we pooled the samples.

TABLE 1.   Characteristics of Arctic Tern eggs collected at various times and from various parts of the species' breeding range. Values in each row of the table are $\bar{x} \pm$ SD, range, and n.

Sample	Characteristic of the egg[a]			
	SMT (μm)	Thickness index (mg/mm²)	Shell weight (g)	Egg weight index
Quark and Bothnian Bay (1981)	184 ± 14 (147–216) 57	0.882 ± 0.061 (0.710–0.986) 57	1.054 ± 0.099 (0.825–1.287) 57	16.62 ± 1.26 (14.39–19.05) 74
Museum samples combined (1874–1935)	178 ± 16 (134–216) 193	0.846 ± 0.076 (0.612–1.023) 198	1.014 ± 0.131 (0.644–1.292) 198	16.48 ± 1.81 (13.07–21.34) 200
Quark and Bothnian Bay (1887–1934)	184 ± 10 (160–202) 32	0.870 ± 0.050 (0.769–1.023) 31	1.068 ± 0.068 (0.811–1.219) 31	17.07 ± 1.81 (14.14–20.44) 32
Archipelago of SW Finland (1919–1935)	185 ± 15 (135–212) 50	0.883 ± 0.069 (0.751–1.002) 48	1.076 ± 0.101 (0.796–1.270) 48	17.00 ± 1.67 (13.62–20.16) 48
Arctic Ocean (1899–1926)	183 ± 15 (153–215) 20	0.836 ± 0.071 (0.724–0.975) 21	1.032 ± 0.141 (0.820–1.276) 21	17.27 ± 2.64 (13.07–22.69) 21
Lapland (1874–1935)	173 ± 16 (134–216) 99	0.823 ± 0.077 (0.612–0.971) 107	0.964 ± 0.136 (0.644–1.293) 107	15.88 ± 1.72 (13.07–20.61) 108

[a] SMT = thickness of the eggshell with the shell membranes attached; "thickness index": shell weight/LB; "egg weight index": $0.466LB^2$ (L = length, B = breadth of the egg).

The thickness of shells with tightly attached membranes (SMT) was 184 μm (SD = ±14 μm, $n = 57$), and without membranes (ST) was 146 μm (SD = ±10 μm, $n = 57$). "Membrane thickness," derived from the difference between SMT and ST, was 38 μm (SD = ±10 μm, $n = 57$), and thickness measured from loose membranes was 55 μm (SD = ±4 μm, $n = 12$). Thus, we assumed that in unincubated eggs, the mammillae in the mammillary layer of the calcified shell projected into the membranes to a depth of 17 μm (31% of 55 μm).

For the 1981 sample, mean thickness index, shell weight, and WI were 0.882 (SD = ±0.061, $n = 57$), 1.054 g (SD = ±0.099 g, $n = 57$), and 16.62 (SD = ±1.26, $n = 74$), respectively (see Table 1). The ranges of mean eggshell weights, and thickness and weight indices among different collections from Europe and North America, were 0.99–1.10 g, 0.85–0.90, and 15.7–17.3, respectively (see Table 2). The respective ranges in four museum subsamples from Finland and the Arctic Ocean were 0.96–1.08 g, 0.82–0.88, and 15.9–17.3, i.e., the ranges in our museum eggshells considerably overlapped those in all other samples. This was mainly due to the exceptional Lapland sample, characterized by small, variable, thin-shelled eggs.

Compared with all the museum material, the 1981 sample of Arctic Tern eggs had significantly thicker shells, both in terms of SMT ($P < 0.02$) and thickness index ($P < 0.005$). Also, their shells were significantly heavier than those of museum eggs ($P < 0.05$). When the

museum material was grouped according to collection sites, however, there were no significant differences between the 1981 sample and museum specimens from about the same areas of Quark and Bothnian Bay (see Fig. 1 and Table 1). For instance, the SMT (184 μm) was identical in both groups.

On the other hand, geographic groups of museum eggs varied considerably. The most extreme group was from Lapland (an inland population). Compared with the two southern, mainly archipelagic marine groups, the Lapland shells had both smaller SMT ($P < 0.001$) and thickness index ($P < 0.005$). The eggshells were also lighter ($P < 0.001$) and WI smaller ($P < 0.001$) than those of the marine groups. Eggs in a small ($n = 20$–21) sample from the Arctic Ocean closely resembled those in the two southern marine groups.

We also found a significant positive correlation between SMT and WI in the Lapland subgroup ($r = 0.571$, $P < 0.001$, $n = 98$). This correlation indicated that smaller eggs tended to have thinner shells and larger eggs, thicker shells. Such a trend was not noted in any other geographic subgroups of museum specimens, even when they were pooled, or in our present material. We found a similar correlation ($r = 0.408$, $P < 0.001$, $n = 187$), however, in all of the museum material, partly owing to the dominance of the Lapland specimens.

EMBRYONIC EFFECT ON EGGSHELL THICKNESS AND WEIGHT

The effect of the embryo on eggshell variables was clear: shells became thinner and lighter

TABLE 2. Egg weight indices, shell weights, and thickness indices of various museum samples of Arctic Tern eggs reviewed by Makatsch (1974).

Collection sites	n	Egg weight index[a]		Shell weight (g)		Thickness index[a] (mg/mm²)
		$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$
North America	123	16.6	(12.6–21.9)	—	—	—
Greenland	54	15.7	—	—	—	—
Iceland	115	16.0	(11.9–18.9)	0.99	(0.80–1.22)	0.85
Spitzbergen and Bear islands	147	17.2	(13.4–22.3)	1.07	(0.86–1.28)	0.87
Arctic Ocean and White Sea	1,443	16.5	—	—	—	—
Great Britain	100	16.2	(10.3–19.2)	—	—	—
Central Europe	88	16.9	(15.9–20.2)	1.07	(0.82–1.23)	0.86
Sweden	244	16.9	(10.4–20.7)	1.10	(0.69–1.39)	0.90

[a] Calculated from values in Makatsch (1974). See Table 1 for definitions of "egg weight index" and "thickness index."

during incubation (Tables 3 and 4). This was verified in two ways.

First, developmental stages of the eggs, expressed in terms of the weight, or the wing or tarsus length of the embryos, correlated significantly with most of the shell thickness parameters (ST, thickness index, and shell weight; Table 3).

We found highly significant (P < 0.001) correlations between ST and all three developmental parameters. Eggshell weight and thickness index had weaker, but still significant (P < 0.05) negative correlations with these developmental parameters. Surprisingly, SMT did not correlate significantly with any of them (P > 0.1).

Second, the thickness of the eggshell decreased between early and late stages of incubation (Table 4). Comparing each unincubated reference egg from nine nests with two incubated eggs from the same clutch showed a 7.4% (SD = ±3.5%) decrease in ST and a 4.4% (SD = ±3.4%) decrease in thickness index. Mean thickness parameters of 18 incubated vs. 9 and 54–57 reference eggshells (Table 4) varied as follows: SMT, 1.1–2.2% (NS); ST, 7.6–8.2% (P < 0.05–0.001); thickness index, 3.4–4.4% (NS); and shell weight, 4.3–4.4% (NS).

The mean difference between SMT and ST in the sample of incubated eggs was 46 µm (=180−134), whereas in the reference groups it was only 37 µm (=182−145) or 38 µm (=184−146). This 8- or 9-µm difference (representing a change of 17.4–19.6%) was highly significant (P < 0.001). The difference between the actual thickness of loose membranes (55 µm) and the SMT-ST "membrane thickness" (46 µm) of incubated eggs indicates that shell mammillae projected into the membrane to the depth of 17–18 µm in unincubated eggs, but only to 9 µm in incubated eggs (a change of 50–53%).

DISCUSSION

EGGSHELL THICKNESS PARAMETERS: CHANGE WITH TIME AND GEOGRAPHICAL VARIATION

The eggshell must be protective and permeable to allow for successful embryonic growth and hatching. Hence, it is not surprising that eggshell thickness does not vary greatly within a species, even though the properties of the shell are adapted to different environments (Rahn et al. 1977, Carey 1980, Visshedijk and Rahn 1981).

Contamination by DDE exceeding 2.5 ppm in eggs of DDE-sensitive birds may cause shell thinning (Fox 1979). Lemmetyinen et al. (1982) reported very low DDE-contamination (0.6 ppm) in eggs of Arctic Terns from Finland. Our results are consistent with that finding because shell thickness in 1981 was the same as that of museum eggs collected before DDT began to be used. The SMT values were identical in both groups, if comparisons were made between eggs from the same geographical areas (Quark and Bothnian Bay).

Pulliainen and Marjakangas (1980) collected hatched eggshells of Arctic Terns from Both-

TABLE 3. Relationships between characteristics of the eggshell and the stage of embryonic development in Arctic Terns. Values in the table are correlation coefficients (r).

Characteristic of the eggshell	Embryo[4]		
	Weight	Wing length	Tarsus length
SMT[1]	−0.241[N.S.]	−0.239[N.S.]	−0.234[N.S.]
ST[2]	−0.518***	−0.570***	−0.566***
Thickness index[3]	−0.292*	−0.294*	−0.288*
Shell weight	−0.316*	−0.317*	−0.310*

[1] SMT = thickness of the eggshell with membranes attached.
[2] ST = thickness of the eggshell without membranes.
[3] Shell weight/LB (mg/mm²; L = length, B = breadth of the egg).
[4] N.S. = not significant, * = P < 0.05, *** = P < 0.001 of linear regression analysis (n = 48).

TABLE 4.   Changes in eggshell thickness between early and late incubation in the eggs of Arctic Terns from the Quark colony. Values in each row of the table are $\bar{x} \pm$ SD, range, and n.

Measures of eggshell thickness	Early incubation (all samples)	Early incubation (reference eggs from test nests)	Late incubation (incubated eggs from test nests)
SMT[1] (μm)	184 ± 14 (147–216) 57	182 ± 11 (162–196) 9	180 ± 11 (156–196) 18
ST[1] (μm)	146 ± 10[3] (118–162) 57	145 ± 10[4] (128–157) 9	134 ± 10 (110–147) 18
$SMT - ST$[2] (μm)	38 ± 6[3] (28–54) 57	37 ± 3[3] (33–40) 9	46 ± 7 (32–64) 18
Thickness index	0.882 ± 0.062 (0.710–1.006) 54	0.891 ± 0.064 (0.805–1.006) 9	0.852 ± 0.062 (0.706–0.934) 18
Shell weight (g)	1.055 ± 0.099 (0.825–1.287) 55	1.054 ± 0.100 (0.878–1.160) 9	1.009 ± 0.087 (0.787–1.121) 18

[1] See footnotes in Table 3.
[2] $SMT - ST$ = "shell membrane thickness" expressed as the difference between SMT and ST.
[3] Difference between variables $P < 0.001$.
[4] $P < 0.05$.

nian Bay in 1977–1978. Their measurements yielded an ST of 124 μm (SD = ±7 μm, n = 15), which is 7.5% smaller ($P < 0.005$) than ST (134 μm) in our study, a difference possibly due to our use of a different technique for measuring the thickness of the eggshell. They found a statistically significant ($P < 0.05$) difference of 6 μm between the thickness of their eggs and museum eggs from "northern Europe," as we did using the entire museum sample as a reference group. We agree with them that the "increased" thickness of present-day eggshells may be due to several factors including the geographic origin of the eggs.

Egg size and shell thickness are related to each other both within and among species, smaller eggs tending to have thinner shells (Asmundson et al. 1943, Ar et al. 1979). We found statistically significant correlations between these variables in the entire Finnish museum material and separately in the Lapland subsample. Consequently, the thinness of the shells and the small size of the eggs in the Lapland sample may have a similar cause.

Much circumstantial evidence indicates relationships between the nutritional status of egg-laying females and eggshell thickness, egg size, and clutch size (Polin and Sturkie 1954, Verheyen 1972, Cooke 1973, O'Connor 1979, Otto 1979, Högstedt 1981). In the Common Tern, the male's capacity for courtship-feeding affects egg and clutch size (Nisbet 1973). Lemmetyinen (1973) found a relationship between food supply and clutch size of Arctic Terns breeding in southwestern Finland. Coulson and Horobin (1976) reported a 3% reduction of egg size of Arctic Terns breeding in England, due to a reduction of available food. They con-

cluded, however, that when the quantity of material which is put into egg production is reduced, the change is primarily expressed in clutch size rather than in the size of individual eggs.

Unlike marine breeding areas that exhibit more stable and predictable weather, Lapland often experiences sharp changes in weather, which reduce the foraging success of the terns. There, Arctic Terns breed by smaller bodies of water that are exposed and covered by ice during cold periods. The thin-shelled, small eggs from Lapland may reflect the nutritional stress on females which nest there. The clutch size, however, was quite normal. Egg characteristics are known to vary with heredity (e.g., Romanoff and Romanoff 1949, Väisänen et al. 1972), and we regard the "exceptional" characteristics of the Lapland eggs as "ecotypic," i.e., partly due to genetic adaptations of Arctic Terns to local circumstances on their breeding grounds. More investigation is needed to confirm this hypothesis, and to search for similar examples of egg size and shell thickness among other species which have both inland and coastal breeding areas.

On the basis of our work, we recommend that when studying temporal changes in eggshell parameters, ornithologists should compare samples that have the same geographic origin and, hence, were laid under similar environmental conditions.

THE EFFECT OF EMBRYONIC CALCIUM RESORPTION ON EGGSHELL THICKNESS PARAMETERS

An avian embryo gets about 80% of the calcium needed for mineralization of its skeleton

from the eggshell (Simkiss 1961, 1967). Simkiss (1967) calculated that this calcium is 5% of a hen's eggshell, by weight. The chorioallantoic membrane begins to grow after only a few days of incubation and covers the entire inside of the eggshell after about the middle of the incubation period (Rahn et al. 1979). It is capable of resorbing calcium from the shell (Romanoff 1960, Terepka et al. 1969, Dunn et al. 1981). After the middle of incubation, in fact, the eggshell significantly weakens because of thinning (Vanderstoep and Richards 1970) and the activity of carbonic anhydrase (an enzyme participating in calcium resorption) in the embryo's blood and chorioallantoic membrane rises concomitantly (Gay et al. 1981).

For Arctic Terns, we found a 4.3–4.4% decrease in shell weight during incubation (Table 4). Our value is somewhat smaller than the 5% reported by Simkiss (1967), possibly because the embryos that we obtained during incubation were not fully grown (ready to hatch) and, thus, calcium resorption was not yet complete. The percentage decrease of thickness index (3.4–4.4%) corresponds well with the percentage change in shell weight.

Vanderstoep and Richards (1970, calculated from the authors' graph) and Pulliainen and Marjakangas (1980) reported a decrease in ST of 6.4 and 7.9% for the eggs of chickens (*Gallus gallus*, var. *domesticus*) and 8.2% for those of Black-headed Gulls (*Larus ridibundus*) during incubation. Our 7.4–8.2% decrease in the shells of Arctic Terns corresponds well with these values. Comparable values for SMT are: Japanese Quail (*Coturnix coturnix japonica*), 7.3%; Cedar Waxwing (*Bombycilla cedrorum*), 5.6%; White-faced Ibis (*Plegadis chihi*), 4.3%; Osprey, 2.4% (Kreitzer 1972, 1973; Rothstein 1972, calculated from author's graph; Capen 1977; and Odsjö 1982, respectively). All values, except that of Osprey, exceed those of the Arctic Tern.

Calcium mobilization begins at the tips of the mammillae in the mammillary layer of the shell (Simkiss 1961), and, during advanced incubation, the connection between this layer and the shell membranes weakens. According to Tyler and Simkiss (1959), the membranes come away from the shell usually carrying the ends of the mammillae with them. This was not obvious, however, in incubated eggs of Arctic Terns, from which the membranes were never totally free. The 17–20% increase of the difference between SMT and ST during incubation shows that the main site of change is the connection between shell and shell membranes. Despite erosion of most of the tips of the mammillae, some unaffected areas may be left holding the parts together, as suggested by our finding that the SMT was smaller than ST plus membranes in incubated Arctic Tern eggs (see Becking [1975] or Parsons [1982] for a detailed description of the ultrastructure between shell and membrane surfaces). The organic core at the center of each mammilla is connected with the outer shell membrane by fibers that penetrate the calcified mammillary tips (Simkiss 1968, Parsons 1982); they too may hold the shell and shell membranes together after calcium mobilization. If such connections rupture, however, the shell membranes may also collapse on the inner surface of the eggshell, thereby decreasing SMT values, as was obvious in most studies cited above. Also, the measuring and drying procedures may break such connections if the measuring load is too great or the drying method too rapid. In a preliminary study we tested rapid methods of drying shells, e.g., in an oven (40–60°C) or with a hair dryer, and found abnormal bending of the shell pieces and partial or complete loosening of the membranes. Nonetheless, we found that SMT changed little during incubation, as shown by the insignificant 1–2% decrease (Table 4) and lack of correlation between it and parameters of embryonic growth (Table 3).

Why do different thickness variables change in differing degrees during incubation? For example, our statistically significant 7.4–8.2% decrease in ST during incubation was roughly double the relatively insignificant decrease in shell weight (4.3–4.4%) or thickness index (3.4–4.4%). Since calcium resorption (shell thinning) begins at the tips of mammillae (Simkiss 1961), estimates of thinning (such as thickness index) are very sensitive to the amount (weight) of calcium mobilized by the embryo. The mammillary layer of the shell, however, because of its cone-structure, is not solid like the palisade layer of the shell. Consequently, when calcium resorption shortens the cones of the mammillary layer (ST becomes thinner), the effective weight loss of the cones is relatively smaller than if the thinning had taken place in the solid calcium (palisade) region of the shell.

Having compared several methods, we conclude that SMT measurement is the parameter least affected by incubation and, hence, is most reliable for measuring eggs collected at various stages of incubation. We also regard the thickness index as a suitable alternative measurement that can be used with museum specimens, provided eggs with large blowing holes (and, hence, large embryos) are disregarded.

ACKNOWLEDGMENTS

U.S.S.R. for access to egg collections at the Zoological Museums in Helsinki, Oulu, and Leningrad. We also thank L. Barber, Department of Biology, McMaster University, Hamilton, Canada, for editing the manuscript.

LITERATURE CITED

ANDERSON, D. W., AND J. J. HICKEY. 1970. Oological data on egg and breeding characteristics of Brown Pelicans. Wilson Bull. 82:14–28.

ANDERSON, D. W., AND J. J. HICKEY. 1972. Eggshell changes in certain North American birds. Proc. XV Int. Ornithol. Congr. (1970):514–540.

ANDERSON, D. W., AND J. J. HICKEY. 1974. Eggshell changes in raptors in the Baltic region. Oikos 25:395–401.

AR, A., H. RAHN, AND C. V. PAGANELLI. 1979. The avian egg: mass and strength. Condor 81:331–337.

ASMUNDSON, V. S., G. A. BAKER, AND J. T. EMLEN. 1943. Certain relations between the parts of birds' eggs. Auk 60:34–44.

BECKING, J. H. 1975. The ultrastructure of the avian eggshell. Ibis 117:143–151.

CAPEN, D. E. 1977. Eggshell thickness variability in the White-faced Ibis. Wilson Bull. 89:99–106.

CAREY, C. 1980. Adaptation of the avian egg to high altitude. Am. Zool. 20:449–459.

COOKE, A. S. 1973. Shell thinning in avian eggs by environmental pollutants. Environ. Pollut. 4:85–102.

COULSON, J. C. 1963. Egg size and shape in the Kittiwake and their use in estimating age composition of population. Proc. Zool. Soc. Lond. 140:211–227.

COULSON, J. C., AND J. HOROBIN. 1976. The influence of age on breeding biology and survival of the Arctic Tern, Sterna paradisaea. J. Zool. (Lond.) 178:247–260.

DUNN, B. E., J. S. GRAVES, AND T. P. FIZHARRIS. 1981. Active calcium transport in the chick chorioallantoic membrane requires interaction with the shell membranes and/or shell calcium. Dev. Biol. 88:211–227.

FOX, G. A. 1976. Eggshell quality: its ecological and physiological significance in DDE-contaminated Common Tern population. Wilson Bull. 88:459–477.

FOX, G. A. 1979. A simple method of predicting DDE-contamination and reproductive success of populations of DDE-sensitive species. J. Appl. Ecol. 16:737–741.

GAY, C. V., H. SCHAER, D. J. SHARKEY, AND E. RIEDER. 1981. Carbonic anhydrase in developing avian heart, blood, and chorioallantoic membrane. Comp. Biochem. Physiol. A Comp. Physiol. 70:173–177.

GOCHFELD, M. 1975. Developmental defects in Common Terns of western Long Island, New York. Auk 92:58–65.

HÖGSTEDT, G. 1981. Effect of additional food on reproductive success in the Magpie (Pica pica). J. Anim. Ecol. 50:219–229.

JENSEN, S., A. G. JOHNELS, M. OLSSON, AND G. OTTERLIND. 1969. DDT and PCB in marine animals from Swedish waters. Nature (Lond.) 224:247–250.

KOEMAN, J. H., AND H. VAN GENDEREN. 1972. Tissue levels in animals and effects caused by chlorinated hydrocarbon insecticides, chlorinated biphenyls and mercury in the marine environment along the Netherlands coast, p. 428–435. In Marine pollution and sea life. Fishing News (Books), Surrey, England.

KOIVUSAARI, J., A. LAAMANEN, I. NUUJA, R. PALOKANGAS, AND V. VIHKO. 1972. Notes on the concentrations of some environmental chemicals in the eggs of the White-tailed Eagle and the Osprey in the Quarken area of the Gulf of Bothnia. Work-Environ. Health 9:44–45.

KOIVUSAARI, J., I. NUUJA, R. PALOKANGAS, AND M. FINNLUND. 1980. Relationships between productiv-

ity, eggshell thickness and pollutant contents of addled eggs in the population of the White-tailed Eagles (Haliaeetus albicilla L.) in Finland during 1969–1978. Environ. Pollut. Ser. A Ecol. Biol. 23:41–52.

KREITZER, J. F. 1972. The effect of embryonic development on the thickness of the egg shells of the Coturnix quail. Poult. Sci. 51:1764–1765.

KREITZER, J. F. 1973. Thickness of the American Woodcock eggshell, 1971. Bull. Environ. Contam. Toxicol. 9:281–286.

LEMMETYINEN, R. 1973. Clutch size and timing of breeding in Arctic Terns. Ornis Fenn. 50:18–28.

LEMMETYINEN, R., AND P. RANTAMÄKI. 1980. DDT and PCB residues in the Arctic Tern (Sterna paradisaea) nesting in the archipelago of southwestern Finland. Ann. Zool. Fenn. 17:141–146.

LEMMETYINEN, R., P. RANTAMÄKI, AND A. KARLIN. 1982. Levels of DDT and PCB's in different stages of life cycle of the Arctic Tern Sterna paradisaea and the Herring Gull Larus argentatus. Chemosphere 11:1059–1068.

MAKATSCH, M. 1974. Die Eier der Vögel Europas. Teil 1. Verlag J. Neumann-Neudamm, Melsungen-Berlin-Basel-Wien.

NISBET, I. C. T. 1973. Courtship-feeding, egg-size and breeding success in Common Terns. Nature (Lond.) 241:141–142.

O'CONNOR, R. J. 1979. Egg weights and brood reduction in the European Swift (Apus apus). Condor 81:133–145.

ODSJÖ, T. 1982. Eggshell thickness and levels of DDT, PCB and mercury in eggs of Osprey (Pandion haliaetus (L.)) and Marsh Harrier (Circus aeruginosus (L.)) in relation to their breeding success and population status in Sweden. Ph.D. diss., Univ. of Stockholm, Stockholm, Sweden.

OLSEN, P. D. 1982. Ecogeographical and temporal variation in the eggs and nests of the Peregrine, Falco peregrinus (Aves: Falconidae) in Australia. Aust. Wildl. Res. 9:277–291.

OTTO, C. 1979. Environmental factors affecting egg weight within and between colonies of Fieldfare Turdus pilaris. Ornis Scand. 10:111–116.

PARSONS, A. H. 1982. Structure of the eggshell. Poult. Sci. 61:2013–2021.

POLIN, D., AND P. D. STURKIE. 1954. Effects of starvation on diffusible and non-diffusible calcium in the fowl. Poult. Sci. 33:1077.

PULLIAINEN, E., AND A. MARJAKANGAS. 1980. Eggshell thickness in eleven sea and shore bird species of the Bothnian Bay. Ornis Fenn. 57:65–70.

RAHN, H., A. AR, AND C. V. PAGANELLI. 1979. How bird eggs breathe. Sci. Am. 240:38–47.

RAHN, H., C. CAREY, H. BALMAS, B. BHATIA, AND C. PAGANELLI. 1977. Reduction of pore area of the avian eggshell as an adaptation to altitude. Proc. Natl. Acad. Sci. USA 74:3095–3098.

RATCLIFFE, D. A. 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. J. Appl. Ecol. 7:67–115.

ROMANOFF, A. L. 1960. The avian embryo. Macmillan, New York.

ROMANOFF, A. L., AND A. J. ROMANOFF. 1949. The avian egg. Wiley, New York.

ROTHSTEIN, S. I. 1972. Eggshell thickness and its variation in the Cedar Waxwing. Wilson Bull. 84:469–474.

RYDER, J. P., AND L. SOMPPI. 1977. Growth and development of known-age Ring-billed Gull embryos. Wilson Bull. 89:243–252.

SIMKISS, K. 1961. Calcium metabolism and avian reproduction. Biol. Rev. Camb. Philos. Soc. 36:321–367.

SIMKISS, K. 1967. Calcium in reproductive physiology. Reinhold, New York.

SIMKISS, K. 1968. The structure and formation of the shell and shell membranes, p. 3–25. *In* T. C. Carter [ed.], Egg quality: a study of the hen's egg. Oliver and Boyd, Edinburgh, Scotland.

SUTCLIFFE, S. A. 1978. Pesticide levels and shell thickness of Common Loon eggs. Wilson Bull. 90:637–640.

SVENSSON, B. W. 1978. Clutch dimensions and aspects of the breeding strategy of the Chaffinch *Fringilla coelebs* in northern Europe: a study based on egg collections. Ornis Scand. 9:66–83.

SWITZER, B., AND V. LEWIN. 1971. Shell thickness, DDE levels in eggs, and reproductive success in Common Terns (*Sterna hirundo*) Can. J. Zool. 49:69–73.

SWITZER, B., V. LEWIN, AND F. H. WOLFE. 1973. DDE and reproductive success in some Alberta Common Terns. Can. J. Zool. 51:1081–1086.

TEREPKA, A. R., M. L. STEWART, AND N. MERKEL. 1969. Transport functions of the chick chorioallantoic membrane. II. Active calcium transport in vitro. Exp. Cell Res. 58:107–117.

TYLER, C., AND K. SIMKISS. 1959. Studies on eggshells. XII. Some changes in the shell during incubation. J. Sci. Food Agric. 10:611–615.

VÄISÄNEN, R. A., O. HILDEN, M. SOIKKELI, AND S. VUOLANTO. 1972. Egg dimension variation in five wader species: the role of heredity. Ornis Fenn. 49: 25–44.

VANDERSTOEP, J., AND J. F. RICHARDS. 1970. The changes in egg shell strength during incubation. Poult. Sci. 49: 276–285.

VERHEYEN, R. F. 1972. Observations on egg-laying in starlings (*Sturnus v. vulgaris*). Proc. XV Int. Ornithol. Congr. (1970):699–700.

VISSCHEDIJK, A. H., AND H. RAHN. 1981. Incubation of chicken eggs at altitude: theoretical consideration of optimal gas composition. Br. Poult. Sci. 22:451–460.

Department of Zoology, University of Oulu, Box 191, SF-90570 Oulu 57, Finland. Address of third author: Department of Applied Zoology, University of Kuopio, Box 6, SF-70211 Kuopio 21, Finland. Address of fifth author: Erämiehenkatu 18, SF-40630 Jyväskylä 63, Finland. Received 5 December 1983. Final acceptance 22 September 1984.

RECENT PUBLICATIONS

The birdwatcher's companion; an encyclopedic handbook of North American birdlife.—Christopher Leahy. 1982. Hill and Wang, New York. 917 p. $29.50. An entertaining, informative, and authoritative encyclopedia of facts and lore about North American birds. More than 1,200 entries, including definitions and pronunciation of terms, mini-essays on important topics, sketches of birders and ornithologists, and practical advice on interaction with birdlife. Appendices on taxonomy, common or irregularly occurring birds of North America, and regional timing of migration with best periods for observation. Thorough bibliography arranged by major subject. Excellent monochrome and color illustrations by Gordon Morrison. If a birder wants one good reference book in addition to a field guide, this may be it.—J. Tate.

Eastern birds of prey.—Neal Clark. 1983. Thorndike Press, Thorndike, ME. 174 p. $6.95 paperback. Source: Thorndike Press, P.O. Box 157, Thorndike, ME 04986. A broadbrush review of the more common raptors of eastern North America, in an environmental conservation format. Illustrated with photographs of uneven quality, from a variety of sources. List of references.—J. Tate.

North American game birds and mammals.—A. Starker Leopold, Ralph J. Gutiérrez, and Michael T. Bronson. 1984. Charles Scribner's Sons, New York. 198 p. Paper cover. $12.95. A reprint edition of a book first published in 1981 (noted in Condor 84:196). The same large format is used and the illustrations are reproduced as well as before. At this price, it's a good buy.

A functional and evolutionary analysis of rhynchokinesis in birds.—Richard L. Zusi. 1984. Smithsonian Contributions to Zoology No. 395, Smithsonian Institution Press, Washington, DC. 40 p. Paper cover. When a bird opens its mouth, not only is the lower jaw dropped but also the upper jaw, or some portion of it, is raised. Movement of the upper jaw occurs in three basic patterns in modern birds, depending on the configuration of the bony hinges. This technical yet clearly written paper examines those conditions, emphasizing that in which bending within the upper jaw accompanies kinetic motion of the jaw as a whole. (This pattern appears in many families of birds, notably the palaeognathous groups, gruiforms, charadriiforms, Columbidae, Trochilidae, and Furnariidae). From a study of skulls and manipulation of simple mechanical models, Zusi describes the pertinent morphology of the upper jaw and analyzes the functional properties of cranial kinesis. On this basis, he constructs a series of hypotheses about the origin and evolution of the different forms of kinesis. His findings and ideas offer stimulation for further studies of anatomy, paleontology, systematics, and feeding behavior. Drawings, references, index.