The Condor 92:304–312

CONDUCTANCE AND STRUCTURE OF EGGS OF ADELIE PENGUINS, *PYGOSCELIS ADELIAE*, AND ITS IMPLICATIONS FOR INCUBATION[1]

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Abstract. Structure and conductance of eggshells of Adelie Penguins, *Pygoscelis adeliae*, were studied to address the question: How is the eggshell adapted to cope with the extreme aridity of the Antarctic, and in particular, what is the significance and function of the organic cuticle on the eggshell? Adelie Penguin shell structure has a basic avian pattern with relatively straight, unbranched pores that are occluded by an organic cuticle on the outside of the shell. Mean shell conductance of 15.4 $mg \cdot day^{-1} \cdot Torr^{-1}$ of six intact eggs is significantly lower than one would predict on the basis of fresh egg mass, and conductance after cuticle removal (18.6 $mg \cdot day^{-1} \cdot Torr^{-1}$) from three eggs is significantly higher. Theoretical consideration of tensions of O_2 and CO_2 in intact eggs and cuticle-removed eggs indicates that, whereas O_2 tensions inside the egg may not be stressful to the embryo prior to hatching if the cuticle remained intact throughout incubation, CO_2 tensions may be. We conclude that the cuticle reduces loss of water during the early part of incubation, but that its erosion during incubation increases conductance thereby maintaining CO_2 tensions close to levels expected in eggs of this size. Calculations of functional pore radius from conductance measures for cuticle-removed eggs are almost identical to real mean pore radius measured from pore casts.

Key words: Eggshell; conductance; pore structure; Adelie Penguin; Pygoscelis adeliae; *incubation; egg; Antarctic.*

INTRODUCTION

The porosity of avian eggshell is extremely important because the avian embryo is isolated from its environment by the shell, and the only exchanges during incubation occur by diffusion of gases through pores in the shell (Wangensteen et al. 1970/1971). Oxygen is taken up and carbon dioxide and water vapor given off during incubation. Shell conductance is one of the factors which determines the rate at which gases may be transmitted across the shell and is the inverse of resistance (Ar et al. 1974). Conductance depends, in part, on the number and structure of pores (Rahn and Ar 1974). Pore structure may change through incubation by embryonic erosion of the inner surface of the shell (e.g., Booth and Seymour 1987). Conductance is modified by selection in such a way that desiccation does not endanger the embryo but that water loss during incubation is sufficient for proper air space formation and the ability to supply sufficient oxygen and get rid of excess carbon dioxide is not compromised. The eggshell must also be strong enough for the brooding bird not to break it when incubating, yet not so strong that the chick cannot break free (Ar et al. 1979).

As gas exchange through the eggshell occurs by diffusion, conductance is inversely proportional to the partial pressure gradient of the gas across the shell (Paganelli 1980). Selection acts to modify conductance of eggshells of birds at high altitude, where partial pressure of oxygen and water vapor is very different from that at sea level, by acting on functional pore area (Wangensteen et al. 1974, Carey et al. 1983). Thus, it is clear that conductance of avian eggshells matches the physiological requirements of the egg with its normal incubation environment.

As water moves through the shell as vapor (Ar

[1] Received 1 May 1989. Final acceptance 1 February 1990.

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TABLE 1. Physical characteristics of six Adelie Penguin eggs used in the study. (See text for calculation of mass, volume, and surface area.) Thickness measures are means of the mean of four measures at each of 20 or 21 equidistant positions between the blunt and pointed poles of each egg.

	Mass (g)	Volume (cc)	Surface area (cm^2)	Dry shell (g)	Thickness (mm)
$\bar{x}$	117.5	108.66	110.97	14.8	0.57
SD	10.9	10.08	6.95	1.7	0.06
Range	102.0–130.0	94.37–120.26	101.09–118.97	12.7–16.6	0.47–0.64

et al. 1974), nest humidity is an important parameter in determining how much water is lost from an egg during incubation. Eggs incubated in conditions creating unusual vapor pressure gradients, e.g., high altitude (Rahn et al. 1977, Carey 1980, Carey et al. 1983), buried (Seymour and Ackerman 1980), dry (Rahn and Hammel 1982), or in wet environments (Ackerman and Platter-Rieger 1979, Sotherland et al. 1984), have conductances different from those of eggs of similar size from "normal" environments (i.e., in open nests, close to sea level), and in which water loss is maintained within acceptable limits (ca. 15%, Ar and Rahn 1980).

Arguably, one of the driest environments in the world in which birds breed is that of the Antarctic. The dry conditions result from extremely cold temperatures. Adelie Penguins, *Pygoscelis adeliae,* nest at Cape Bird on Ross Island adjacent to the Antarctic mainland in early November (Spurr 1975), when conditions are still very cold. A previous study showed that eggshell of this species is adapted to low humidities with a reduced shell conductance and fewer than predicted pores (Rahn and Hammel 1982). We further studied the significance of the organic cover of the shell (we refer to it as the cuticle), which occurs commonly throughout the Sphenisciformes (Tyler 1965) and was postulated by Rahn and Hammel (1982) to be a factor contributing to the lower than expected shell conductance of Adelie Penguin eggs.

METHODS

Six eggs from different clutches of *P. adeliae* were collected at Cape Bird (70°13'S; 166°28'E) at the very beginning of incubation (9–11 November 1987). They were kept cool (but not frozen) until returned to Wellington in February 1988, when their length and breadth were measured to 0.1 mm with a dial vernier caliper (Table 1).

All eggs were equilibrated to 25.5°C overnight before being placed over silica gel in a bell chamber and maintained in a constant temperature cabinet for 36 hr at 25.5°C. Three copper constantan thermocouples were placed adjacent to the eggs in different parts of the chamber. Eggs were removed from the chamber and weighed to 1 mg on the electronic pan balance after 0.5, 1, 1.5, 2, 3, 6, 12, 24, 30, and 36 hr. They were replaced within 30 sec of removal. Temperature was a constant 25.5°C in the first measurement of conductance and averaged 25.6 ± 0.1°C (n = 30) in the second measurement. Rate of mass loss fell until it was constant after 6 hr, so calculations were based on the rate of movement of water vapor across the shell ($\dot{M}_{H_2O}$) over the final 30 hr of measurement.

Three of the eggs were than washed for 90 sec in Janola (active ingredient 31.5 $g \cdot l^{-1}$ sodium hypochlorite; Reckitt and Coleman [N.Z.], Avondale, Auckland) at 42°C to remove the cuticle (Deeming 1987). Completeness of cuticle removal was checked using a binocular dissecting microscope. The eggs were rinsed in tap water at 50°C for several minutes and then in tap water at room temperature. All six eggs (three washed and three intact) were re-equilibrated to 25.5°C overnight before being placed back into the bell chamber over fresh silica gel. All eggs were weighed at the same 10 time intervals as before.

Conductance to water vapor was calculated using a modification of Fick's first law of diffusion:

$$G_{H_2O} = \dot{M}_{H_2O}/\Delta P_{H_2O} \quad (1)$$

(Ar et al. 1974)

where G_{H_2O} is the conductance of the shell to vapor ($mg \cdot day^{-1} \cdot Torr^{-1}$), $\dot{M}_{H_2O}$ is rate of movement of vapor across the shell ($mg \cdot day^{-1}$), and ΔP_{H_2O} is the partial pressure gradient of vapor across the shell (Torr). P_{H_2O} was assumed to be zero outside the egg (over silica gel) and saturated inside the egg. Thus at 25.5°C P_{H_2O} is 24.5 Torr and at 25.6°C is 24.6 Torr (Weast and Astle 1981).

Eggs had lost mass prior to arrival in Wel-

lington so fresh egg mass (W) was predicted from length (L) and breadth (B) using the equation:

$$W = 0.548L \cdot B^2 \quad (2)$$

(Hoyt 1979).

This value was used to predict shell conductance (G_{H_2O}) using:

$$G_{H_2O} = 0.384\ W^{0.814} \quad (3)$$

(Ar and Rahn 1978).

Egg volume (V) was calculated using:

$$V = 0.507L \cdot B^2 \quad (4)$$

(Hoyt 1979)

and this value was used to calculate surface area (S) of each egg using:

$$S = [4.393 + 0.394 \cdot L \cdot (B^{-1})](V^{0.667}) \quad (5)$$

(Hoyt 1976).

On completion of conductance measures, each egg had 5-mm intervals marked with graphite pencil around its long axis and was cut along this axis with a dental drill. Contents were discarded, inner shell membrane wiped free of fluid, and the shell allowed to dry over silica gel before being weighed. At each 5-mm interval, shell thickness with dried membrane intact was measured to 0.001 mm with a micrometer with one curved surface, which was placed against the inside of the eggshell. The cut edge of each shell was then soaked in water, the shell membrane peeled away (Tyler 1965), and the thickness of the shell alone measured at each 5-mm interval. This gave four independent measures of thickness (with and without membranes) at each 5-mm circumference interval of each egg except at the poles where only two measures were available. We assumed thickness to be constant around one latitude (Tyler 1965), so the four measures were averaged.

Specimens for structural analysis were dried over silica gel, mounted on aluminum stubs with silver colloidal glue, gold coated in a Dynovac sputter coater, and examined using a Philips 505 scanning electron microscope (SEM), with accelerating voltages of 20–30 kV. Micrographs were taken on Ilford FP4 film and prints made using standard techniques.

Fragments of shell from the blunt and pointed ends and equator of each egg were examined using the SEM. Some intact shell, i.e., with cuticle (unwashed) and shell membranes, was examined. Cuticle thickness was estimated from micrographs. Other shell was also boiled in 10% NaOH (by weight) for 10 min to eliminate all organic components (especially shell membranes), rinsed in distilled water, and dried. Some of the NaOH treated shell was examined using the SEM, and some was set in resin for preparation of casts as described by Tompa (1980). Resin blocks were cut to reveal eggshell, which was then etched in 2M HCl, rinsed in distilled water, dried over silica gel, and mounted for SEM analysis as described for the shell. Pore length and diameter at 10 equidistant points along the pore were measured from micrographs of pore casts.

Mean values are given ± one standard deviation. Means are compared using Student's t-test and statistical significance is assumed if $P < 0.05$.

RESULTS

The six eggs averaged 68.6 ± 2.7 mm long (range = 65.5–71.6 mm) and 55.8 ± 1.7 mm wide (range = 53.3–57.9 mm). These values were used to predict initial mass, volume, and surface area from equations 2, 4, and 5 (Table 1).

SHELL STRUCTURE

The shell of each egg tended to be thinnest near the equator and thickest about 15–30 mm from the pointed end (Fig. 1). There was little difference in shell thickness between each end of the egg and the thickness was remarkably similar throughout the entire egg. The between-egg variation was much greater than within-egg variation (Fig. 1).

Combined inner and outer shell membranes were significantly thicker at the pointed end (72 ± 17 μm) of the egg than the equator (49 ± 6 μm) (paired-sample $t = 3.04$, df = 5). Combined membrane thickness could not be measured at the blunt end of the egg because of separation of inner and outer shell membranes over the air space.

Shells were typical of avian eggs with a distinct mammary zone and thick palisade layer (Fig. 2A). The species also had a surface crystal layer as described by Tyler (1965). However, they had a relatively thick outer waxy layer over the entire surface which also covered the external pore openings (Fig. 2D). The waxy layer consisted of individual units arising from the calcareous shell on stalks and expanding to meet the next adjacent unit (Fig. 2E). They formed a uniform surface over the egg (Figs. 2D, E), which from the

surface had the appearance of "dried mud" (Deeming 1987) (Fig. 2C). The whole waxy cuticle was about 48 μm thick. The top half of the units were composed of round globular structures (Fig. 2F) whereas the bottom ("stalk") had a pitted but relatively featureless structure (Fig. 2G).

Pores were hourglass-shaped being slightly wider at the outer surface than the inner surface, although there was more variation in the former (Figs. 2B, 3). The narrowest point was between 20 and 40% of the distance from the inside surface. There was no difference in the shape or dimensions of pores from the blunt or pointed ends or equator of the eggs.

CONDUCTANCE

There was no significant change in conductance of three eggs that were not treated with hypochlorite between measurements ($t = 0.459$, df = 4, $P > 0.6$), but there was a significant increase in conductance of hypochlorite-treated eggs ($t = 3.894$, df = 4, $0.02 > P > 0.01$) (Table 2). Predicted G_{H_2O}'s for each egg (Table 2) (calculated using equation 3) were significantly higher than those measured in pretreated eggs ($t = 3.493$, df = 10, $0.01 > P > 0.001$), but not significantly different from hypochlorite-treated eggs ($t = 1.742$, df = 4, $0.20 > P > 0.10$).

DISCUSSION

STRUCTURE

Eggs used in this study (117.5 ± 10.9 g) were slightly smaller than those examined by Rahn and Hammel (1982) (125 ± 2 g SE) and those reported by Shönwetter (1960). Adelie Penguins usually lay two eggs in a clutch, the second being smaller and having a shorter incubation than the first (Taylor 1962). However, eggs in clutches of one egg only are smaller than the first egg of two-egg clutches. We assume that some of our eggs would have been from single egg clutches because they are smaller than the recorded range for first eggs of two-egg clutches (Taylor 1962).

Mean shell thickness of 0.57 mm (Table 1) is similar to values of 0.61 (Rahn and Hammel 1982), 0.60 (Schönwetter 1960), and 0.58 (Tyler 1965). We found shell thickness to vary in the same way from pole to pole in all eggs (Fig. 1), unlike Tyler (1965) who found variation in this pattern in Adelie Penguins. This anomaly warrants further investigation.

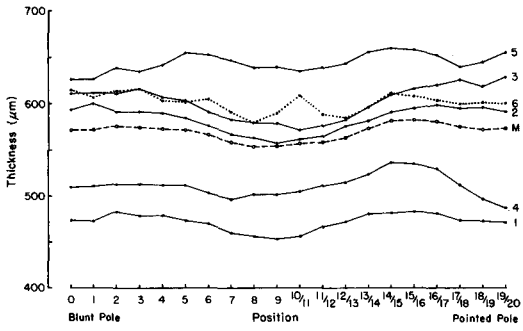

FIGURE 1. Thickness of eggshell of six Adelie Penguin eggs measured at approximately 5-mm intervals from blunt to pointed pole. As eggs were of different sizes, either 20 (eggs 1–3) or 21 (eggs 4–6) positions were measured. Only the 10 measures from each pole to the equator are presented in the figure. Hence, one equatorial measure for eggs 4–6 is not represented on the figure, but it does not influence the overall picture. Each point represents the mean of four measures in different places at the same latitude on each egg, except at the poles, where only two measures were possible.

Our measure of cuticular thickness (48 μm) is much greater than that found by Tyler (1965). Although Tyler found that thickness of cuticle in Adelie Penguin eggs was relatively uniform over the whole egg surface compared to other penguins, he was confused by variation between samples. Perhaps some of his specimens had already undergone some cuticular erosion (see below).

The pore system of Adelie Penguins fits into the arbitrary 3 a i classification of Board et al. (1977), i.e., pores are unbranched and are occluded by an organic cuticle that covers the whole egg. Our pore casts show the same variation as found by Tyler (1965); the main variation between pores is at either end (Fig. 3). We found much more variation, and a widening at the base (inside end) of pores resulting from our different techniques. Included in our pore measurements is the opening to the inner shell between the shell units (Fig. 2B), which is not represented in Tyler's casts. We found no evidence of an organic plug penetrating the pore as found in *Aptenodytes patagonica* (Tyler 1965).

Rahn and Hammel (1982) had shown that the number of pores in Adelie Penguin eggs is significantly lower than predicted for eggs of similar mass (9,108 compared to 10,700 derived from the equation of Tullett and Board [1977]). Using the equation of Rahn and Hammel (1982):

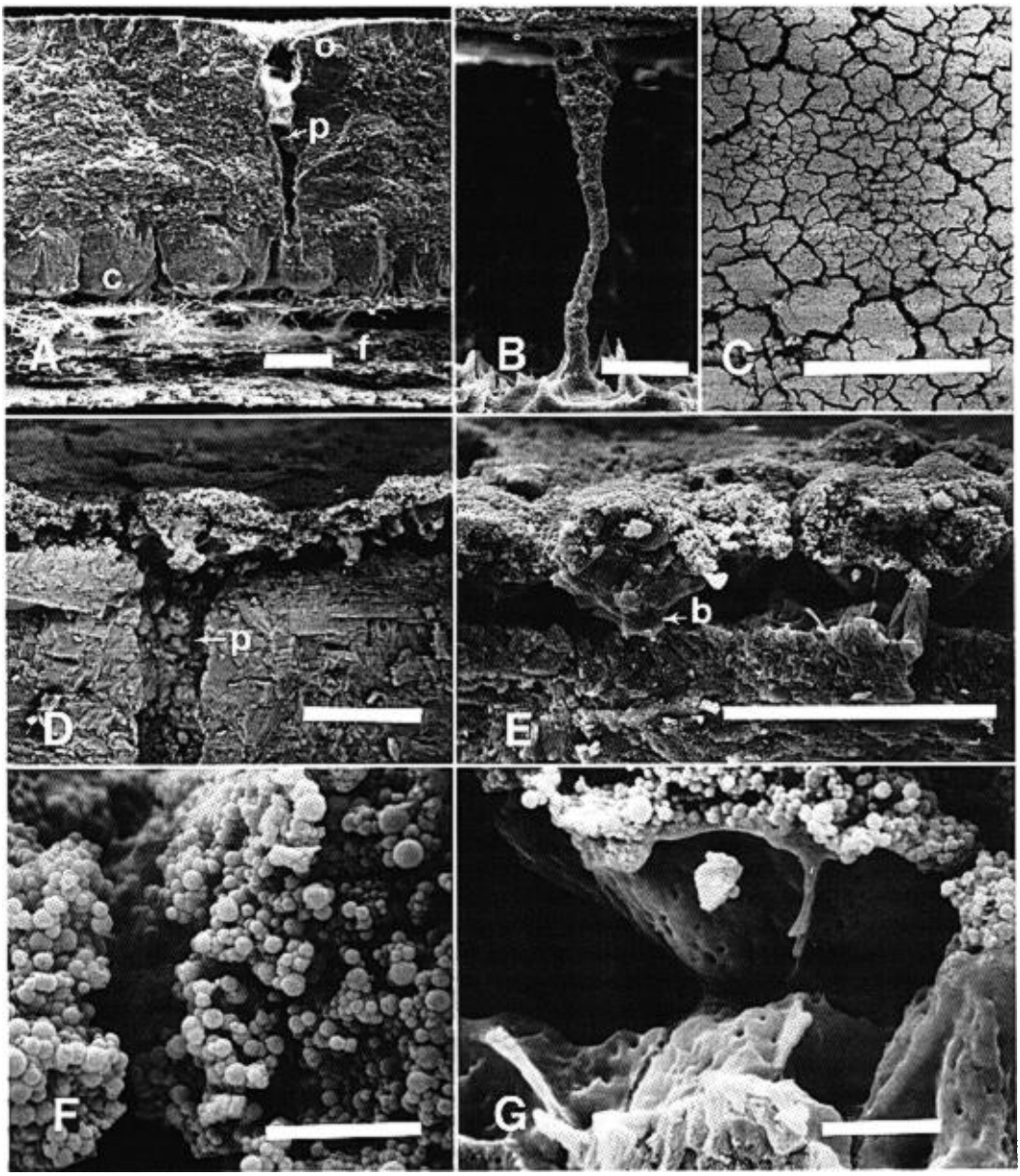

FIGURE 2. A. Radial view of intact Adelie Penguin eggshell showing fibrous shell membranes (f) on the inside of the shell, mammary cones (c), thick spongy layer (s), pore (p), and part of the organic cuticle (o) occluding the pore. Bar = 0.1 mm. B. Cast of pore through Adelie Penguin eggshell. Note expansion of pore to inside of shell (bottom) as well as outside (top). Bar = 0.1 mm. C. Outside surface (tangential) view of cuticle over eggshell showing its appearance described as "dried mud" (Deeming 1987). Bar = 1.0 mm. D. Close up of the outer organic cuticle showing its complete cover of the surface and occlusion of a pore (p). Bar = 0.1 mm. E. Organic cuticle is composed of individual units which arise on a stalk (b) from the calcareous shell, and then mushroom out to meet the adjacent unit. Bar = 0.1 mm. F. Globular structure of the top, expanded portion of the organic cuticle. Bar = 10 μm. G. Relatively smooth stalk of a shell unit. Apart from pitting, no regular structure is visible. Note globular structure of part of top portion of unit (as in Fig. 2E) at top of picture. Bar = 10 μm.

TABLE 2. G_{H_2O} (mg·day^{-1}·Torr^{-1}) for six eggs of Adelie Penguins. Initial values were obtained before treatment. Treated values were obtained after eggs 1–3 were scrubbed with sodium hypochlorite. Eggs 4–6 were not treated with hypochlorite to act as controls.

	n	$\bar{x}$	SD	Range
Pretreatment	6	15.4	1.0	14.2–17.1
Predicted	6	18.6	1.4	16.6–20.2
Treated	3	18.6	—	17.7–20.0
Controls	3	15.7	—	14.9–16.6

$$Ap\ (mm^2) = 0.447 \cdot G_{H_2O} \cdot T \qquad (6)$$

(Ap is functional pore area, T is shell thickness [mm]), and an estimated pore number of 9,108, our mean calculated functional pore radius of 11.7 (±0.9) μm is very close to the 11.3 μm of Rahn and Hammel (1982) and is only a little more than the real mean minimum pore radius (Fig. 3). On the basis of conductance measures on the three eggs before and after treatment with hypochlorite, we know that functional pore radius increases about 12.6%. The functional pore radii estimates in this study and that of Rahn and Hammel (1982) become 12.7 and 13.2 μm, which are almost identical to the mean minimum radius of the major portion of an average pore (Fig. 2B). This supports the finding of Tøien et al. (1987) that it is the minimum pore radius that contributes most to the resistance to diffusion through eggshells. However, unlike the chickens they studied, the intact organic cuticle of Adelie Penguins contributes significantly to total resistance.

Using the equation:

$$Ap = 9.2 \cdot 10^{-5} \cdot W^{1.23} \qquad (7)$$

(Ar et al. 1974)

to predict functional pore area (Ap) for an egg of 117.5 g (Table 1) gives 3.3 mm², which is lower than our value of 3.9 mm² for untreated and 4.6 mm² for treated eggs.

CONDUCTANCE

Conductance clearly increases with removal of the cuticle in eggs of Adelie Penguins, thus confirming that the cuticle is an important means of reducing the rate of water loss, presumably in response to the arid Antarctic environment (Rahn and Hammel 1982). The rate of water loss of Adelie Penguin eggs increases throughout incubation in nature and this is thought to be a result of increased metabolic heating with embryonic development combined with the erosion of the organic cuticle on the surface of the egg (Rahn and Hammel 1982). Since embryonic mass and metabolism is small during the first half of incubation (C. Vleck et al. 1980), an increase in $\dot{M}_{H_2O}$ caused by higher metabolism will not occur until the latter half of incubation. As the circulatory system develops there will be an increase in heat flow from the brood patch through the egg, increasing mean egg temperature, also (Turner 1987). Field data presented by Rahn and Hammel (1982) for the mass of eggs for the first 23 days of an approximately 35-day incubation period actually showed a greater increase in the rate of water loss in the first part of the measuring period than in the last part. As the organic cuticle is a significant contributor to the resistance of the shell to water loss, it seems likely that conductance increases during the first half of incubation by erosion of the cuticle, increasing con-

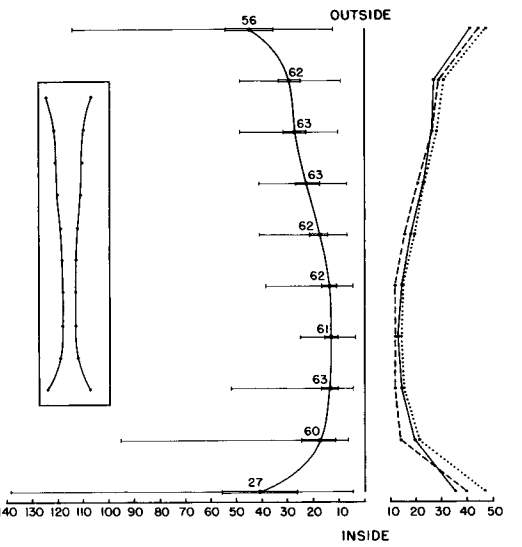

FIGURE 3. Stylized pore through shell of Adelie Penguin egg based on measurements of pore casts at 10 equidistant points from the inside to the outside of the shell. Right: mean values for pores from pointed (dashed) and blunt (solid) ends, and equator (dotted). Left: overall mean value with range and standard deviation at each point; sample sizes are given. Two axes are not to the same scale: x-axis shows pore radius in μm; y-axis has not been given units, but mean shell thickness (= pore length) is 569 ± 60 μm (range = 454–660 μm). Inset shows real proportions of pore.

TABLE 3. Conductance values measured and calculated in Adelie Penguin eggs. $n = 6$ pretreatment eggs and $n = 3$ eggs washed in hypochlorite to remove waxy cuticle. R & H represents data of Rahn and Hammel (1982).

Parameter	G_{H_2O} mg·day^{-1}·Torr^{-1}	G_{H_2O} cm^3·day^{-1}·Torr^{-1}	G_{H_2O} cm^3·day^{-1}·Torr^{-1}	G_{O_2} cm^3·day^{-1}·Torr^{-1}	G_{CO_2} cm^3·day^{-1}·Torr^{-1}
Temperature (°C)	25.5*	25.5*	35	35	35
Pretreatment	15.4	19.2	19.5	15.4	12.6
Range	14.2–17.1	17.7–21.3	18.0–21.6	14.2–17.1	11.7–14.0
Posttreatment[1]	18.6	23.1	23.5	18.6	15.3
Range	17.7–20.0	21.4–24.9	21.7–25.3	17.1–20.0	14.1–16.4
R & H	13.1	16.3	16.6	13.1	10.7

* Posttreatment eggs were measured at 25.6°C.

ductance compatible with the respiratory requirements of the embryo. For an egg in a dry environment like the Antarctic, it is advantageous for the rate of water loss to be as low as possible without compromising the exchange of respiratory gases. One way to maximize this is for conductance to increase to match the respiratory demands as incubation proceeds (Seymour et al. 1986). It seems that Adelie Penguins achieve this by providing the egg with a waxy outer cuticle which reduces conductance, but gradually erodes away. The initial "dried mud" appearance is explained as the junction between adjacent cuticular units. "Mushroom-shaped" cuticular units may trap vapor beneath the cap as suggested by Deeming (1987), and perhaps it is just the caps that break off at the narrow point on the stalk (Fig. 2G). As the cuticle erodes, conductance increases. Although we were unable to obtain shell from incubated Adelie Penguin eggs, those of King Penguins, *Aptenodytes patagonica,* which live in much less severe climates than Adelie Penguins, lose a mean of 48% of their cuticle through erosion during incubation and this results in increasing conductance through incubation (Handrich 1989).

By knowing the conductance, incubation temperature, and pre-IP $\dot{V}_{O_2}$, we can calculate the partial pressure of oxygen inside the egg prior to hatching. Pre-IP $\dot{V}_{O_2}$ is 34.6 cm^3·hr^{-1} in Adelie Penguins (Bucher et al. 1986). This is remarkably close to the value of 32.6 cm^3·hr^{-1} predicted using the relationship between $\dot{V}_{O_2}$ and fresh egg mass and incubation time determined by Hoyt and Rahn (1980). Adjusting the G_{H_2O} measures in Adelie Penguins from mg·day^{-1}·Torr^{-1} to cm^3·day^{-1}·Torr^{-1} (coefficient = 1.244, Paganelli et al. 1978) and adjusting to the incubation temperature of 35°C (Rahn and Hammel 1982) we can calculate G_{O_2} and G_{CO_2} (Table 3) (Paganelli et al. 1978). This calculation assumes that the cuticle is dry. By substituting into equation 1 we calculate ΔP_{O_2} to be 54 Torr for pretreated eggs and 45 Torr for treated eggs which gives pre-IP oxygen tensions of 104 Torr at sea level if conductance did not change from initial values, and 113 Torr if all the cuticle was removed. Predicted pre-IP O_2 tensions of 109 Torr in eggs the size of those of Adelie Penguins (D. Vleck et al. 1980) are similar to that of treated (cuticle removed) eggs. Even if the O_2 tension of 98 Torr calculated from the mean conductance value of Rahn and Hammel (1982) is used, it is unlikely that oxygen would be limiting to the embryo. In fact, it is close to the value found in a variety of birds (Hoyt and Rahn 1980).

By assuming an RQ of 0.71 (Rahn et al. 1974) to calculate $\dot{V}_{CO_2}$ from $\dot{V}_{O_2}$ of 24.6 cm^3·hr^{-1}, P_{CO_2} inside the pre-IP egg would be 47 Torr. If all wax was removed, CO_2 tension would be 39 Torr, close to the predicted value of 34 Torr (D. Vleck et al. 1980). However, levels of 47 Torr are higher than any levels recorded for eggs of this size (Rahn et al. 1974, D. Vleck et al. 1980). Conductance data from Rahn and Hammel (1982) predict internal pre-IP CO_2 tension of 55 Torr, which is higher than the mean value for birds (Hoyt and Rahn 1980) and higher than recorded in any but the smallest avian eggs, and may therefore be stressful to the embryos.

Based on egg mass alone, and on the ratio of egg mass to incubation time, the predicted conductance of eggs of Adelie Penguins is 18 mg·day^{-1}·Torr^{-1} (Rahn and Hammel 1982), which is very close to the value we obtained for eggs in which the cuticle was removed (Table 2). Consequently, we conclude that the cuticle is an adaptation that reduces the rate of water loss in the

early stages of incubation, but that its erosion during incubation facilitates proper respiratory function of the egg late in incubation. We do not know how much of the cuticle erodes during incubation or whether it has any other function. About 50% of the cuticle on eggs of King Penguins is eroded during incubation (Handrich 1989).

Clearly cuticular erosion is not the only way of achieving an increase in conductance as incubation proceeds. In the buried eggs of megapodes, a similar result is obtained by having funnel-shaped pores with extremely narrow openings to the inside of the shell. As the shell is etched by the embryo during incubation, the narrowest part of the pore is obliterated, removing the region of higher diffusion resistance as well as reducing pore length (Booth and Seymour 1987). Adelie Penguins do not have pores of this shape.

The predicted shell thickness for Adelie Penguins (from equation 7 of Ar et al. 1974) is 0.45 mm, 21% thinner than the actual mean thickness (Table 1), and is reflected in the shell being heavier than predicted (Rahn and Hammel 1982). The effect of a thicker than predicted shell on conductance is offset to some extent by a greater than predicted functional pore area. Perhaps a weaker eggshell, or one with more extremely funnel-shaped pores, would be more likely to break in a penguin nest, especially when compared to the protection offered by the mound nest of a megapode. Also, with such a thick shell, it is unlikely that embryonic dissolution of the shell would be sufficient to significantly decrease pore length and influence pore shape as in the thinner megapode eggshells. Consequently, a waxy cuticle may be better able to provide a different solution to the requirement for an increasing conductance through incubation in penguins than a different pore shape would, especially if it has some other function, also.

ACKNOWLEDGMENTS

This study was supported by a New Zealand Universities Grant Postdoctoral Fellowship to M.B.T. and by the Department of Zoology, Victoria University of Wellington. Approval for egg collection was given by Ross Dependency Research Committee, Antarctic Division, New Zealand Department of Scientific and Industrial Research (DSIR), and eggs were kindly collected and returned to Wellington by John Cockrem, Ecology Division, DSIR. Final manuscript preparation was supported by the Department of Zoology, University of Florida.

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