Interrelationships between egg dimensions, pore numbers, incubation time, and adult body mass in Procellariiformes with special reference to the Antarctic Petrel *Thalassoica antarctica**

F. MEHLUM, H. RAHN, C. BECH AND S. HAFTORN

Mehlum, F., Rahn, H., Bech, C. & Haftorn, S. 1986: Interrelationships between egg dimensions, pore numbers, incubation time, and adult body mass in Procellariiformes with special reference to the Antarctic Petrel *Thalassoica antarctica*. *Polar Research 5 n.s.*, 53—58.

Dimensions of eggs and eggshells and pore density are reported for eggs of the Antarctic Petrel *Thalassoica antarctica* (as well as eggs of the Snow Petrel *Pagodroma nivea)*. Allometric relationships are used to estimate the initial egg mass, total number of pores and incubation time. The initial egg mass for Antarctic Petrel was estimated to 83 g, and the incubation time to 55 days. The total pore number in Antarctic Petrel was estimated to 4212 and in Snow Petrel 2654 pores per egg. Using data from 8 species of Procellariiformes, the relationship between total pore counts, initial egg mass and incubation time is described.

Fridtjof Mehlum, Norsk Polarinstitutt, P.O. Box 158, N-1330 Oslo Lufthavn, Norway; Hermann Rahn, Department of Physiology, State University of New York, Buffalo, N.Y. 14214, USA; Claus Bech, Department of Zoology, University of Trondheim, N-7055 Dragvoll, Norway; Svein Haftorn, The Museum, University of Trondheim, Erling Skakkesgate 47A, N-7000 Trondheim, Norway; October 1986 (revised February 1987).

The initial egg mass at the time of laying is an important reference point because of its correlation with various egg parameters, e.g. eggshell dimensions, number of pores in the eggshell, incubation time, and adult body mass. Allometric relationships that have been established allow one to predict many of these, and other functions, once the initial egg mass is established.

Initial egg mass and various egg dimensions of the Antarctic Petrel have only scarcely been reported. Schönwetter (1960) presents data based on a single egg only, and Orton (1968) gives values of mass, length and width, but do not list the number of specimens nor provide data for eggshell dimensions. The data presented here were collected at the end of the incubation period and do not represent initial egg mass. Eggs of the order Procellariiformes lose water during their incubation period (Grant et al. 1982a), which is similar in amount to that of other birds (n = 81), and average 15% of the initial egg mass (Ar & Rahn 1980).

In this study we report dimensions for 21 eggs and eggshells and pore density for 9 eggs of the Antarctic Petrel (as well as 16 and 3 eggs for dimensions of eggs and eggshells, respectively, of the Snow Petrel *Pagodroma nivea)*, which allow one to estimate the initial egg mass based on allometric relationships of egg dimensions versus egg mass established for 69 species of Procellariiformes. Once the initial egg mass is known, one can calculate the total number of pores per egg and, furthermore, predict from other allometric relationships the incubation time and adult body mass for this species. The eggs were collected during the Norwegian Antarctic Research Expedition 1984/85 at the breeding colony Svarthamaren (71°53'S, 5°10'E) located in Dronning Maud Land (Mehlum et al. 1985).

Methods

Length and width dimensions were obtained with calipers and read to the nearest 0.1 mm.

* *Publication No. 87 of the Norwegian Antarctic Research Expeditions (1984/85).*

Shell thickness was measured in each egg at twenty different points, using a ball-point caliper which could be read to 0.01 mm. The shell thickness measurement included the dried membranes adhering to the shell.

Pore density was etablished as follows: Pieces of eggshell from various regions were boiled in 5% (g/l) KOH solutions for several minutes to remove all proteinaceous material. They were then etched by being dipped briefly in concentrated nitrid acid for a predetermined period of about 15 seconds, which enlarges the pores. After drying, the inside of the shell was painted with a concentrated water solution of Evans Blue dye. By capillary action this solution fills the pores which now become visible at the outer shell surface as blue spots against a white background and can now be counted with a dissecting scope. The counting field was 0.25 cm^2, and twenty fields representing various regions of each egg were counted (see Fig. 1). These averaged values where multiplied by 4, expressing the pore density per cm^2. The latter value is factored by the total surface area of the egg derived from the relationship $A(cm^2) = 4.835\ W^{0.662}$ (Paganelli et al. 1984) where W = initial egg mass (g).

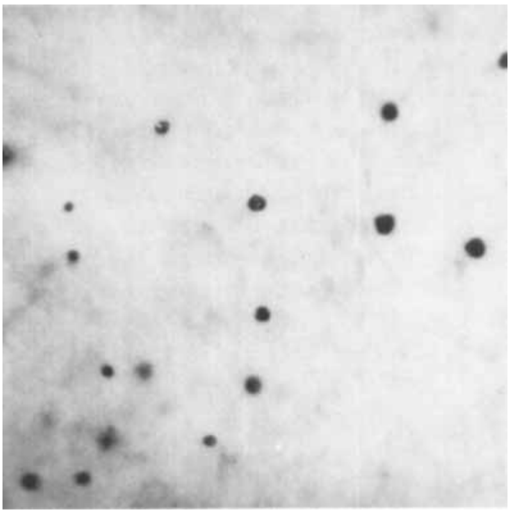

Fig. 1. Photograph of a 0.25 cm^2 shell area showing typical distribution of dye-stained pores which had previously been enlarged by acid etching.

Results and discussion

Prediction of initial egg mass

Table 1 shows egg mass, egg and shell dimensions previously reported, and those obtained in this study. We have estimated the initial egg mass from the regression of length and width dimensions as a function of egg mass based on 88 correlates (69 species) listed by Schönwetter (1960) for the order Procellariiformes shown in Fig. 2. The $\dot{X}$SEE is 1.03 and 1.02 for the length and width correlates, respectively, where $\dot{X}$SEE is the antilog of SEE (standard error of estimate) = value by which Y is multiplied or divided. The projection of 70 mm length and 48 mm width (from Table 1) on Fig. 2 predicts an initial egg mass of 80 and 86 g, respectively. Thus, an average value of 83 g is a reasonable prediction for the initial egg mass from this particular nest site.

The pore density and number of pores

The average pore density for nine eggs was 11.7/0.25 cm^2, or 46.8 cm^{-2} (Table 2). The total egg surface calculated (see Methods) on the basis of an egg mass of 83 g = 90 cm^2. Thus, the total number of pores = (46.8 × 90) or 4212 pores per egg.

Table 3 gives egg and eggshell dimensions for the Snow Petrel and a pore density of (10.7/0.25 cm^2) or 42.8 cm^{-2} for three eggs. The surface area for the 47 g egg is 62 cm^2 and the total pore number = (42.8 × 62) or 2654 pores per egg.

In Table 4 are listed the egg mass, incubation time, and pore number of nine species of the order Procellariiformes, including the two reported from this study. They have been ranked according to egg mass. The number of pores is only 50–60% of that predicted from the regression established for 161 species (Ar & Rahn 1985). Thus, for a given egg mass the pores of the order Procellariiformes are significantly fewer, which appears to be related to their prolonged incubation time (see below). When pore numbers in Table 4 are regressed against the relative growth rate of embryos, expressed as egg mass divided by incubation time ($g.day^{-1}$), the slope is essentially 1.0, a relationship that describes the pore number for birds in general (Ar & Rahn 1985).

Table 1. Egg mass, egg and shell dimensions of the Antarctic Petrel *Thalassoica antarctica*.

	Egg				Shell			Reference
Area	Mass g	Length mm	Width mm	n	Mass g	Thickn. mm	n	
Antarctic Continent	95	71.4	50.0	1	7.14	0.35	1	Schönwetter 1960
Wilkes Station	90	70.0	48.0	—	—	—	—	Orton 1968
Dronning Maud Land	—	70.1	48.6	21	7.29	0.406	9	This study
S.D		(3.1)	(1.5)		(1.01)	(0.032)		

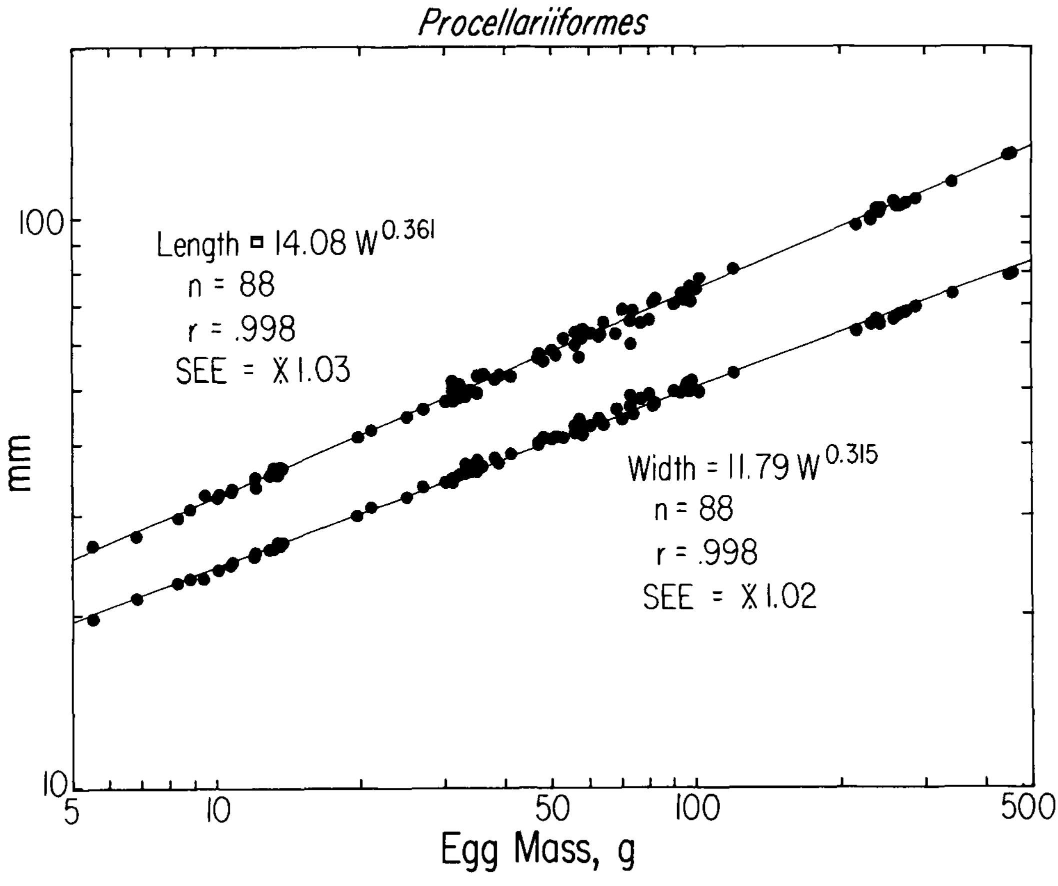

Fig. 2. Regression of egg length and egg width upon egg mass for 69 species and 19 subspecies of the order Procellariiformes taken from the tables of Schönwetter (1960).

Setting aside the unusally high pore count of *Pterodroma hypoleuca* in Table 4, the pore count of Procellariiformes is best described by the relationship, the number of pores, $N = 3100$ (W/I), S.D. 440, where W = initial egg mass, g, and I = incubation time, days.

Incubation time

In Fig. 3 are plotted the incubation times against egg mass for 475 species excluding the order Procellariiformes (Grant et al. 1982a). The dotted lines mark the limits for ± SEE. The shaded

Table 2. Pore density (number of pores per field of 0.25 cm^2) for nine eggs of the Antarctic Petrel *Thalassoica antarctica*. For each egg 20 fields were counted and averaged.

Egg No.	2	3	4	5	7	8	9	10	11	Grand Mean
Pore density	10.1	12.0	13.3	15.3	9.8	10.4	11.7	13.5	8.8	11.7
S.D.	2.0	2.2	3.8	2.8	2.1	2.6	2.7	3.4	2.2	2.1

Table 3. Egg mass, egg and shell dimensions, and pore density of the Snow Petrel *Pagodroma nivea*.

	Egg				Shell			
Area	Mass g	Length mm	Width mm	n	Mass g	Thickn. mm	n	Reference
S. Georgia, S. Orkney	47.0	56.5	40.2	15	3.40	0.27	15	Schönwetter 1960
Davis Station	47.4	55.5	39.4	21	—	—	—	Brown 1966
Dronning Maud Land	–	56.7	39.2	16	3.42	0.28	3	This study
S.D		(2.1)	(1.0)					

Pore density (number of pores per 0.25 cm^2)

Egg No.	1	4	7	Grand mean
Pore density	11.3	11.7	9.2	10.7
S.D.	2.8	2.8	2.2	1.3

Table 4. Egg mass, incubation time, and number of pores per egg in 9 species of the order Procellariiformes.

Species	Egg mass g	Incubation days	No. pores	Reference
Diomedea exulans	500	78	19.698	1
» *nigripes*	305	66	16.700	2
» *immutabilis*	285	65	15.753	2
Fulmarus glacialis	101	49	5.210	3
Thalassoica antarctica	83	(55)	4.212	4
Pterodroma phaeopygia	77	55	4.544	5
Puffinus pacificus	57	52	3.747	6
Pagodroma nivea	47	45	2.654	4
Pterodroma hypoleuca	39	49	4.159	7

References:
(1) Tullett & Board 1977; (2) Grant et al. 1982a; (3) Rahn et al. 1984a; (4) this study; (5) Whittow et al. 1984; (6) Whittow 1984; (7) Grant et al. 1982b.

region above shows the regression ± SEE for 38 species of the Procellariiformes where the incubation times were taken from Watson (1975) and other sources, and the corresponding egg weight from Schönwetter (1960). For the Procellariiformes the regression is incubation time, $I = 31\ W^{0.130}$, $r^2 = 0.82$ and $\dot{X}SEE = 1.11$. For an 83 g egg of the Antarctic Petrel one would predict an incubation time of 55 days (range 50—61 days for ± 1 SEE). This predicted value is larger than the reported incubation period of 40 —45 days (Orton 1968; J.A. van Franeker pers.comm.). The shortening of the incubation period compared to other Procellariiformes may be an adaptation for breeding in the hostile climate on the Antarctic continent.

Adult body weight and egg mass

From the egg weight (Schönwetter 1960) and adult body weight (Warham 1977; Lack 1968) the regression in Fig. 4 is plotted for 67 correlates representing 50 species of the order Procellariiformes. The regression for egg mass, $W = 0.713\ BW^{0.735}$, $r^2 = 0.98$, $\dot{X}SEE = 1.17$. For non-passerine birds (n = 557) a similar regression was reported (Rahn et al. 1985) where $W = 0.399\ BW^{0.723}$, $r^2 = 0.89$, and $\dot{X}SEE = 1.48$.

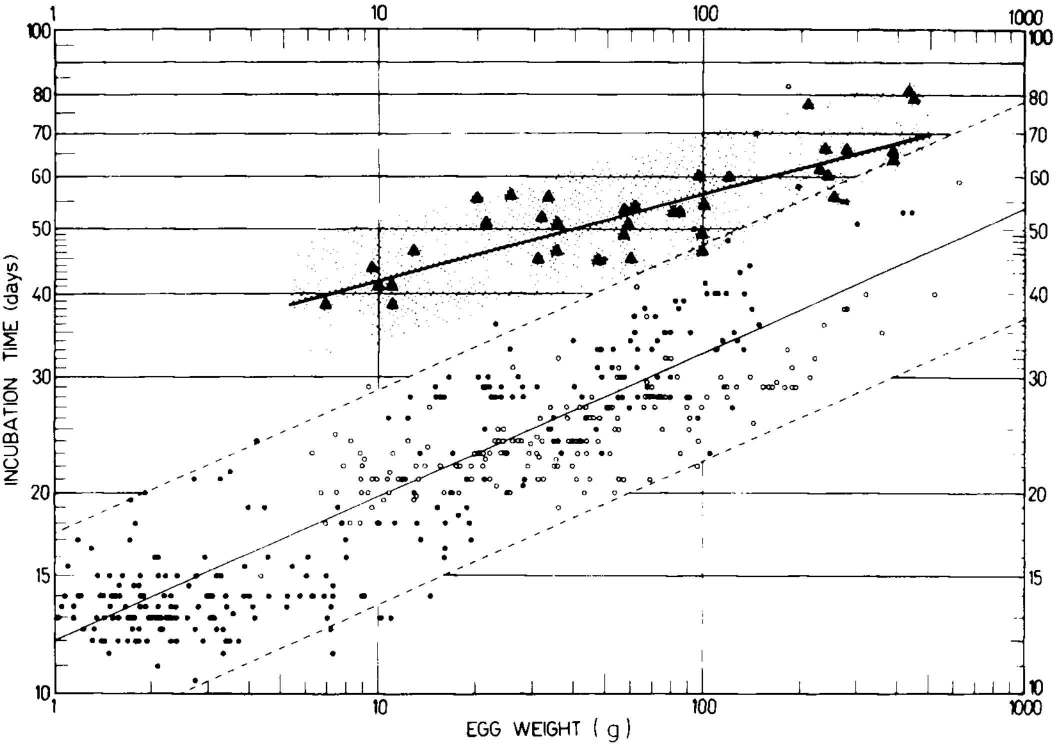

Fig. 3. Regression of incubation time upon egg mass. Upper shaded region for 38 species of the order Procellariiformes. Lower regression for 475 non-passerine birds. For details see text. (From Grant et al. 1982a).

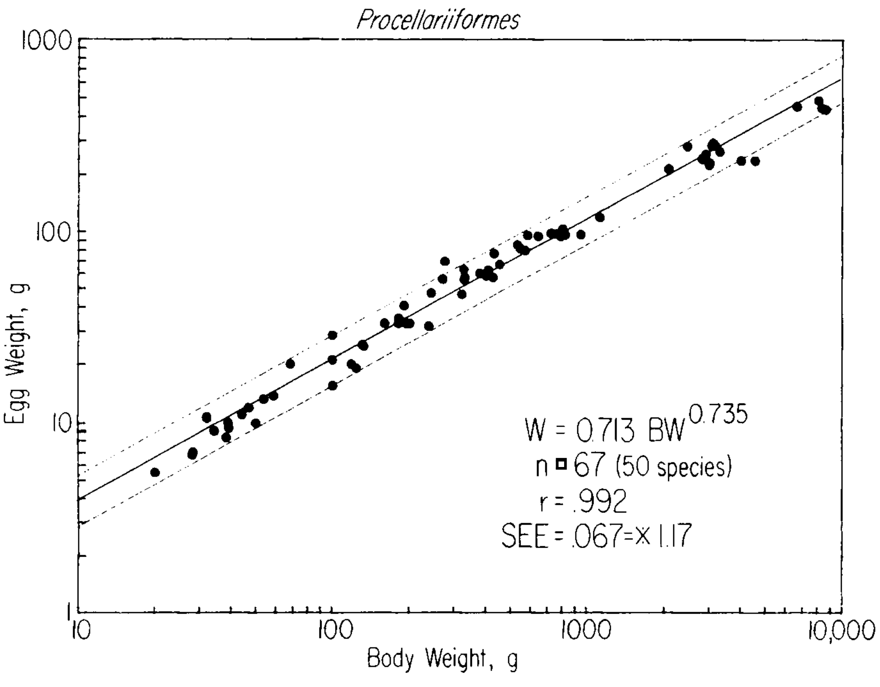

Fig. 4. Regression of egg mass upon adult body mass for 50 species (n = 67) of the order Procellariiformes.

While the exponents of these two regressions are not significantly different, the intercept for the Procellariiformes is (0.713/0.399), or 1.8 times larger than in non-passerine birds. The relatively larger eggs of this order have been described previously (Rahn et al. 1975; Rahn et al. 1984b).

We have also regressed adult body mass against egg mass for the Procellariiformes using the same correlates as above. This regression is adult body mass, BW = $1.73\ W^{1.34}$, $r^2 = 0.98$, and $\dot{X}SEE = 1.23$. Solving this equation for an 83 g egg mass of the Antarctic Petrel predicts an adult body weight of 645 g, which can be compared with 641 g (n = 34) given by Bierman & Voous (1950), cited by Warham (1977), and 609 g (n = 20) obtained in this study.

References

Ar, A. & Rahn, H. 1980: Water in the avian egg: overall budget of incubation. *Amer. Zool. 20,* 373—384.

Ar, A. & Rahn, H. 1985: Pores in avian eggshells: gas conductance, gas exchange and embryonic growth rate. *Respir. Physiol. 61,* 1—20.

Bierman, W.H. & Voous, K.H. 1950: Birds observed and collected during the whaling expeditions of the Willem Barends in the Antarctic, 1946—1947 and 1947—1948. *Ardea 37,* 1—123.

Brown, D.A. 1966: Breeding biology of the Snow Petrel *Pagodroma nivea* (Forster). *ANARE Scientific Reports Ser. B(1) 89.*

Grant, G.S., Pettit, T.N., Rahn, H., Wittow, G.C. & Paganelli, C.V. 1982a: Water loss from Laysan and Black-footed Albatross eggs. *Physiol. Zool. 55,* 405—414.

Grant, G.S., Pettit, T.N., Rahn, H., Whittow, G.C. & Paganelli, C.V. 1982b: Regulation of water loss from Bonin Petrel *(Pterodroma hypoleuca)* eggs. *Auk 99,* 236—242.

Lack, D. 1968: *Ecological adaptations for breeding in birds.* Methuen, London.

Mehlum, F., Bech, C. & Haftorn, S. 1985: Ornithological investigations in Mühlig-Hofmannfjella, Dronning Maud Land. Pp. 27—34 in Orheim, O. (ed.): Report of the Norwegian Antarctic Research Expedition (NARE 1984/85). *Nor. Polarinst. Rapport. 22.* 138 pp.

Orton, M.N. 1968: Notes on Antarctic Petrels *Thalassoica antarctica. Emu 67,* 225—229.

Paganelli, V.C., Olszowka, A. & Ar, A. 1974: The Avian egg: Surface area, volume, and density. *Condor 76,* 319—325.

Rahn, H., Paganelli, C.V. & Ar, A. 1975: Relation of avian egg weight to body weight. *Auk 92,* 750—765.

Rahn, H., Greene, D.G., Tøien, Ø., Krog, J. & Mehlum, F. 1984a: Estimated laying dates and eggshells conductance of the Fulmar and Brunnich's Murre in Spitsbergen. *Ornis Scand. 15,* 110—114.

Rahn, H., Ackerman, R.A. & Paganelli, C.V. 1984b: Eggs, yolk and embryonic growth rates. Pp. 89—112 in Whittow, G.C. & Rahn, H. (eds.): *Seabird Energetics.* Plenum Press, New York.

Rahn, H., Sotherland, P.R. & Paganelli, C.V. 1985: Interrelationships between egg mass and adult body mass and metabolism among passerine birds. *J. Orn. 126,* 263—271.

Schönwetter, M. 1960: *Handbuch der Oologie.* Meise, W. (ed.). Akademie Verlag, Berlin.

Tullett, S.G. & Board, R.G. 1977: Determinants of avian eggshell porosity. *J. Zool. London 183,* 203—211.

Warham, J. 1977: Wing loadings, wing shapes and flight capabilities of Procellariiformes. *New Zealand J. Zool. 4,* 73—83.

Watson, G.E. 1975: *Birds of the Antarctic and Sub-Antarctic.* Amer. Geophysic. Union, Washington, D.C.

Whittow, G.C. 1984: Physiological ecology of incubation in tropical seabirds. Pp. 47—72 in Schreiber, R. (ed.): *Tropical Seabird Biology. Studies in Avian Biology, No. 8. Cooper Ornith. Soc.*

Whittow, G.C., Simons, T.R. & Pettit, T.N. 1984: Water loss from the eggs of a tropical seabird *(Pterodroma phaeopygia)* at high altitude. *Comp. Biochem. Physiol. 78A,* 537—540.