SCHÜZ, E. (1971): Grundriß der Vogelzugkunde. Paul Parey. ● SCHÜZ, E. & W. MEISE (1968): Zum Begriff des Teilziehers. Vogelwarte 24: 213—217. ● WINKLER, R. (1974): Der Herbstdurchzug von Tannenmeise, Blaumeise und Kohlmeise (*Parus ater, caeruleus* und *major*) auf dem Col de Bretolet. Orn. Beob. 71: 135—152.

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Initial Mass of Avian Eggs: Comparison between Measured and Calculated Values

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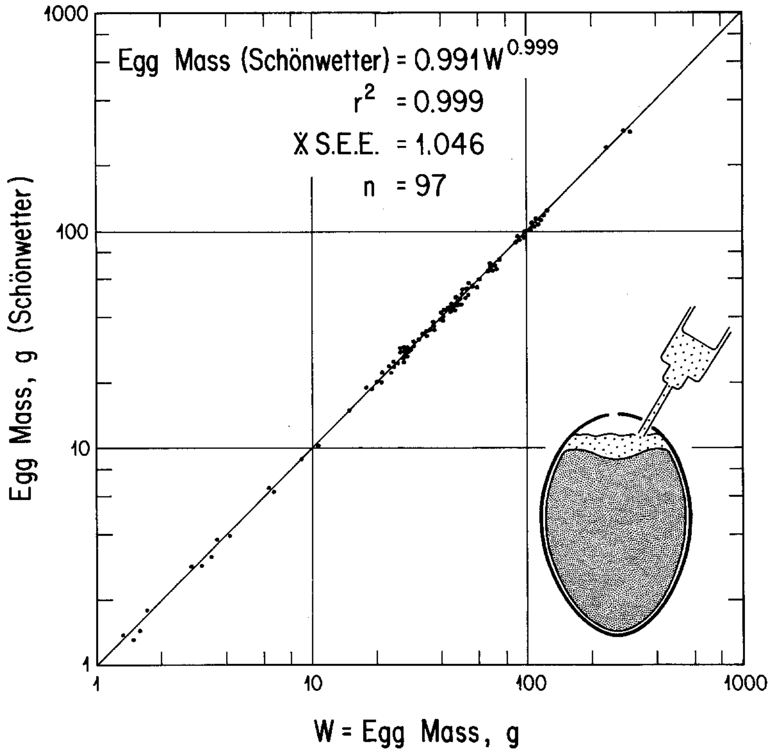
Determination of initial egg mass has always been elusive because from the moment an egg is laid it begins to lose water vapor. The vapor pressure of water within the egg's air space is essentially fully saturated at all temperatures, while the environment surrounding the egg has generally a lower vapor pressure, that is, relative humidities much less than 100 %. As soon as incubation increases egg temperature, the water vapor pressure difference between the egg and the microclimate of the nest is greatly increased, and during the course of incubation about 15 % of the egg's initial mass is lost by diffusion of water vapor across the pores of the eggshell. This water loss has now been established for 83 species of birds (AR & RAHN 1980). Additional water vapor is lost after the eggshell is pipped. Because the mass of an egg changes once it has been laid, it has been customary to report the length and width of bird eggs, providing a later option to calculate the initial egg mass or egg volume from these two dimensions. Over the years various formulas have been proposed for such calculations (HOYT 1979), at least two of which were proposed by SCHÖNWETTER many years ago (GROEBBELS 1932: 291). However, the particular equation used by SCHÖNWETTER (1960—84) for calculation of egg mass awaits publication in Volume IV.

Direct Measurement of Initial Egg Mass

Replacement of egg content with water: The difficulties associated with indirect approaches to calculating initial egg mass led GROEBBELS & MOEBERT (GROEBBELS 1932: 291) to propose a technique for weighing eggs after their empty shells had been refilled with water. They weighed and then emptied 54 fresh eggs of birds from 15 species, and immediately reweighed them after refilling them with water. On the average the refilled eggs weighed 2,8 % less than their fresh egg mass, and GROEBBELS & MOEBERT suggested that by adding 2,8 % to the mass of a water-filled egg a reliable value of the fresh egg mass could be obtained. In 1982 RAHN et al. determined indirectly the density of the egg content in 23 species of birds (representing 7 orders) and found a surprisingly uniform value of $1.031\ g \cdot cm^{-3}$, $\pm$ 0.003 S. D. These results corroborate those of GROEBBELS & MOEBERT and allow us to suggest that with this method one should increase the mass of water which filled the empty eggshell by 3.1 % to obtain the initial egg mass.

Replacement of air cell with water: Rather than replacing the whole egg content with water and adding a factor which represents the density of the original content, we chose to replace the air cell with water, which yields directly the initial egg mass at the time of laying. This approach is based upon the analysis of DRENT (1970) who showed that during egg development changes in egg mass can be entirely accounted for by loss of water. Changes in mass attributable to metabolism can be ruled out in the developing egg because the average respiratory quotient is very close to 0.72, where the mass of CO_2 given off equals the mass of O_2 taken up (AR & RAHN 1980).

To test the validity of this concept AR & RAHN (1980) compared the initial mass of chicken eggs (obtained within 15 minutes of laying) with the mass of the same egg after filling the air cell with water on day 18 of development. In 10 fertile and 10 infertile eggs the mean difference after



Regression of SCHÖNWETTER's calculated egg mass values plotted against egg mass values from the same species obtained by replacing the air cell with water.

18 days of incubation (and the loss of about 7 g) was 0.014 g for fertile eggs and 0.003 for the infertile eggs, changes which are inconsequential for our considerations.

We also tested the same method during natural incubation (GRANT et al. 1982), using eggs of the Laysan Albatross (*Diomedea immutabilis*) and the Black-footed Albatross (*D. nigripes*) on Midway Island in the Pacific. At the beginning of the laying season daily rounds of the nests were made to obtain initial mass of eggs within 24 hours of laying. After 30—64 days of incubation (and loss of 20—42 g) the air cells of the eggs were filled with water and the eggs reweighed. The mean difference between the initial egg mass and that after replacing the air cell with water, in 22 Laysan Albatross eggs, was 0.39 g (initial egg mass 282 g), and in 16 eggs of the Black-footed Albatross, 0.89 g (initial egg mass 302 g). We therefore suggest that this method provides a reliable measurement of initial egg mass at time of laying.

The technique for the displacement of gas in the air cell with water was actually developed more than ten years ago. We use a water-filled syringe with an 18-gage needle, which for most eggs is strong enough, to make two openings in the shell above the air cell (figure). The egg is submersed in a pan of water and by injecting water through one opening, the escape of gas bubbles from the other opening can be seen. Repeated flushings easily remove all gas, a fact that can be verified by candling the egg.

Initial Egg Mass: Calculated versus Measured Values

We are now in a position to compare initial egg mass determination by the air cell displacement method with values calculated by SCHÖNWETTER (1960—84). During the last ten years we made such measurements for a large number of species in Alaska, Mexico, Antarctica, Spitsbergen, Pacific Islands, Canada, USA, as well as yearly measurements of eggs of certain seabird species in a given colony in North Carolina. Altogether 97 mean values of initial egg mass in 68 species were compared with the mean values of SCHÖNWETTER. The average number of eggs for our mean values was 12 (a total of 1164 eggs). SCHÖNWETTER's mean values were based on an average of 112 eggs for each species (a total of 7616 eggs). The overall average ratio of SCHÖNWETTER's value for each correlation to our value is 1.01 ± 0.045 S. D.

The SCHÖNWETTER mean egg mass (68 species representing 9 orders) plotted against our mean measured values, W, for 97 pairs of values leads to the regression equation

SCHÖNWETTER's egg mass (g) $= 0.991\ W^{0.999}$, $r^2 = 0.999$, X SEE $= 1.046$, $n = 97$, where W = our egg mass determination (g).

Because the slope and the intercept values are essentially 1.0, SCHÖNWETTER's calculated values are in excellent agreement with empirical values obtained by refilling the air cell with water, suggesting that his values represent initial egg mass.

Summary

It had previously been demonstrated that by weighing an egg after replacing the air cell with water the initial egg mass at the time of laying is obtained during any stage of incubation. The average egg mass of SCHÖNWETTER (1960—84) compared with those obtained by weighing fresh eggs of the same species after replacement of the air cell with water gives an excellent agreement, as shown in the regression curve, with a slope of 1.0.

Zusammenfassung

Das Wägen eines Vogeleies, dessen Luftkammer mit Wasser gefüllt worden ist, gibt sein Frischgewicht zum Zeitpunkt des Legens wieder. So kann auch nachträglich auf einfache Weise das Frischgewicht eines Vogeleies bestimmt werden. Die durchschnittlichen Frischvollgewichte von SCHÖNWETTER (1960—84) stimmen auffallend gut mit unseren Wägungen überein, wie die berechnete Regressionsgerade (Steigung = 1.0) beweist. Letztere stützt sich einerseits auf 97 an 1164 Eiern ermittelten Durchschnittsgewichte von 68 Arten (9 Ordnungen) der verschiedensten Faunengebiete und anderseits auf 7616 SCHÖNWETTERS Berechnungen zugrundeliegende Eiern derselben Arten.

Literatur

AR, A., & H. RAHN (1980): Water in the avian egg: Overall budget of incubation. Amer. Zool. 20: 373—384. ● DRENT, R. H. (1970): Functional aspects of incubation in the Herring Gull. Behaviour, Suppl. 17: 1—132. ● GRANT, G. S., C. V. PAGANELLI, T. N. PETTIT, G. C. WHITTOW, & H. RAHN (1982): Determination of fresh egg mass during natural incubation. Condor 84: 121—122. ● GROEBBELS, F. (1932): Der Vogel, Vol. 2. Borntraeger, Berlin. Reprinted 1969. J. Cramer, Lehrte. ● HOYT, D. F. (1979): Practical methods of estimating volume and fresh egg weight of bird eggs. Auk 96: 73—77. ● RAHN, H., P. PARISI & C. V. PAGANELLI (1982): Estimating the initial density of bird eggs. Condor 84: 339—341. ● SCHÖNWETTER, M. (1960—84). Handbuch der Oologie. Band I—III. Ed. W. MEISE. Akademie Verlag, Berlin.

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