

# THE AVIAN EGG: INCUBATION TIME AND WATER LOSS

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The large difference in incubation time among bird eggs, ranging from a minimum of 11 days to nearly 90, has aroused man's interest since antiquity. In her critical review of the history of our knowledge of incubation periods, Margaret M. Nice (1954) wrote, "The people who have been concerned with incubation periods fall into three groups: the guessers, the copyists, the investigators." Guessers came first and these have been busily quoted since Aristotle for more than 20 centuries. It was not until Evans (1891) and Heinroth (1922) made their own observations that reliable data began to accumulate. In spite of the inaccuracies since Aristotle's time, and the many exceptions which are now well recognized, there is an obvious general correlation between egg weight and incubation period. These have been presented by Heinroth (1922), Needham (1931), and Worth (1940) in graphic form and were reinvestigated in this presentation on the basis of newer information in the literature. It is of interest to note in retrospect that all these correlations are essentially similar, that the standard error of estimates is large, and that there are many exceptions. This merely illustrates that the many factors which determine the incubation period are not understood.

For these reasons we analyzed other correlates of egg size such as the gas conductance of the egg shell and particularly the water loss properties of eggs, problems which Heinroth had already mentioned some 50 years ago in his classical treatise on incubation time. On the basis of water vapor conductivity measurements of the egg shell previously presented (Ar et al. 1974), the daily weight losses of eggs during natural incubation reported by Drent (1970), and the reported incubation periods, one is now able to derive new relationships which apply to eggs in general. These indicate that incubation time for a given egg weight is inversely proportional to the water vapor conductance of the egg shell. Furthermore, during natural incubation all eggs, regardless of size, lose approximately 18% of their initial weight and the mean water

vapor pressure difference between the egg and the microclimate of the nest is 35 torr.

## RESULTS

### OBSERVED INCUBATION TIME AND EGG WEIGHT

Heinroth (1922) plotted observed values of incubation time against egg weight on linear coordinates, while Needham (1931) and Worth (1940) used log coordinates. The latter approach is mathematically more manageable and was used in our evaluation. These data were recalculated in order to compare their results, based in large part upon different literature data, with our analysis. Our correlation is based upon 475 species of birds. Incubation periods were obtained from various sources (Groebbels 1932; Reilly 1968; Murphy 1936; issues of the *Auk*, 1940-72). Corresponding egg weights were obtained from Groebbels (1969) and Schönwetter (1960-71). These data were plotted on log coordinates and are shown in figure 1. A least square function for log incubation time on log egg weight yielded a weight power function and is shown below for our data and authors mentioned above.

	$r$	$P$	SE	$n$
Our data				
$I = 12.03 W^{0.217}$	0.86	$\ll 0.001$	$\pm 0.0922$	475
Heinroth (1922)				
$I = 12.09 W^{0.205}$	0.84	$\ll 0.001$	$\pm 0.0866$	194
Needham (1931)				
$I = 10 W^{0.240}$				
Worth (1940)				
$I = 12 W^{0.230}$				104

where  $I$  = days;  $W$  = egg weight (g);  $r$  = correlation coefficient;  $P$  = probability coefficient; SE = standard error of estimate of the log form of the equation; and  $n$  = number of observations.

The proportionality constants and exponents are remarkably similar among the various authors. We have been able to supply a correlation coefficient for Heinroth's original analysis which is in no way improved by in-

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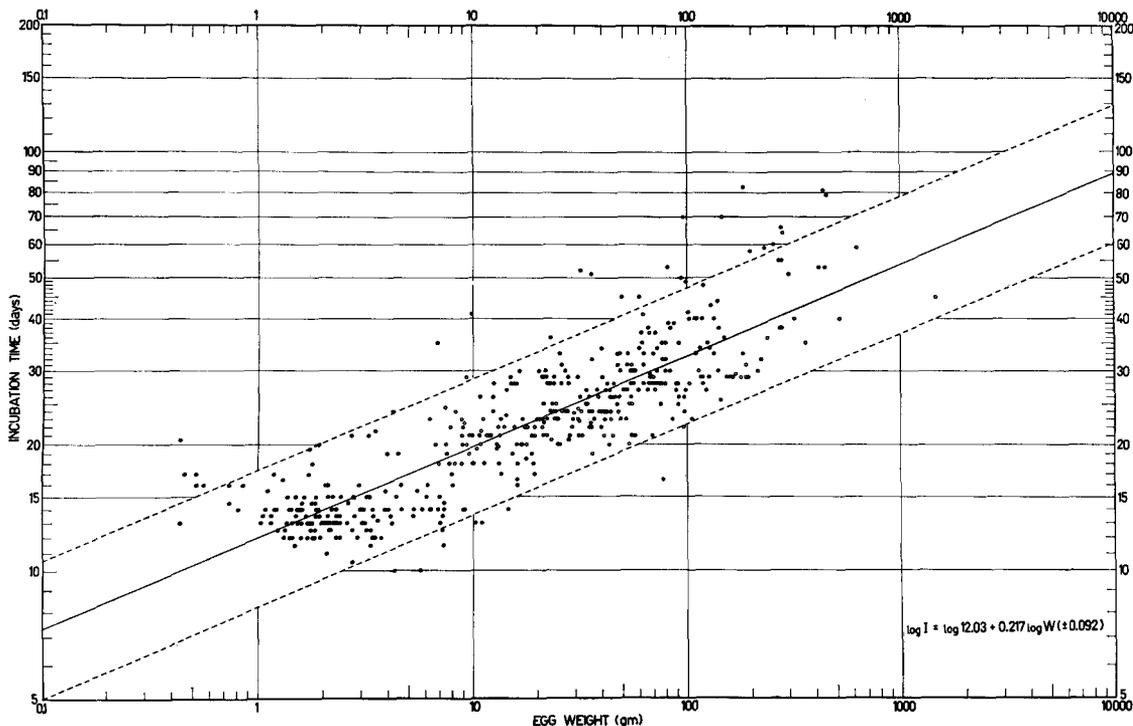


FIGURE 1. Incubation time (days) plotted against egg weight (g),  $n = 475$ . Solid line is the regression curve, dotted line encloses the 95% confidence limits. Scale, log-log.

creasing the number of observations we have added. Since the standard error of estimate is quite large, it would, therefore, suggest that little if any refinement will be gained in the future by the addition of further observations. Our individual data points, regression line, and 95% confidence limits are shown in figure 1.

We have tried to distinguish between altricial and precocial birds, but the slight mean difference is not statistically significant and better data are needed to establish such a fact. In figure 2 we have replotted the slopes of figure 1 on a semilog plot where the incubation time is presented on a linear coordinate. In Schönwetter's data, we find the smallest eggs to be for two species of the family Trochilidae, namely, 0.2–0.3 g. The largest eggs reported are those for 23 eggs of the extinct *Aepyornis*, which average about 9 kg, the largest being 12.6 kg. The longest incubation period we would predict for the *Aepyornis* species is a mean value of 89 days and one standard error of estimate between 72 and 110 days. It is of interest to note that Needham and Worth predicted a 90 and 85 day incubation period, respectively, for *Aepyornis*. Thus between the largest and smallest avian egg we have a 45,000-fold weight difference associated with a (89/11) or eightfold difference in incubation time.

#### INCUBATION TIME AND WATER LOSS OF THE EGG

It has long been appreciated that during artificial and natural incubation an egg loses weight. Not only is the weight loss under natural conditions rather constant from day to day (Groebbels 1932), but it can be ascribed almost exclusively to the loss of water vapor since the embryo has a typical respiratory quotient near 0.72 where the exchanging mass of  $O_2$  and  $CO_2$  molecules are equal (for review see Drent 1973). Furthermore, this water loss occurs by diffusion of water vapor across the egg shell and thus the total amount transferred is determined by the pore geometry of the shell which defines the water vapor conductance and the existing water vapor gradient between the inside of the shell and the microclimate surrounding the egg (Wangensteen and Rahn 1970–71; Paganelli et al. 1971).

These two relationships can be defined by the following equations:

$$FW = \dot{M}_{H_2O} \cdot I \quad (2)$$

and

$$\dot{M}_{H_2O} = G_{H_2O} \cdot \Delta P_{H_2O} \quad (3)$$

where  $W$  = initial weight of the egg (g)

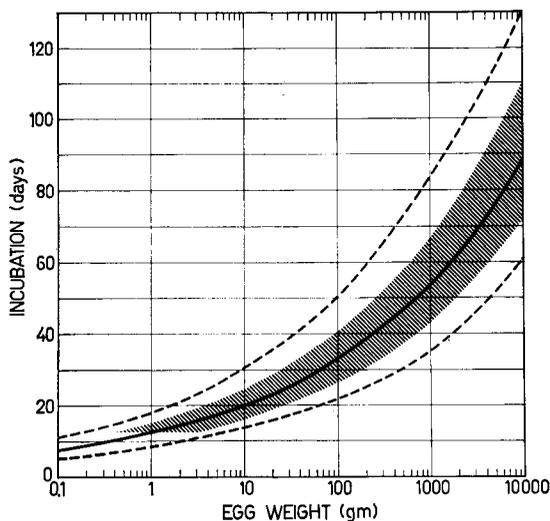


FIGURE 2. Regression lines of figure 1 plotted on semilog coordinates. Incubation time (days) on linear scale. Egg weight (g) on log scale. Shaded area encloses  $\pm 1$  SE or approximately 65% confidence limit; the dotted lines enclose the 95% confidence limits. Since these deviations were transferred from the log-log relationship, the deviations above the mean are larger than those below the mean value. Shaded area has been cut off below 11 days, the lowest recognized incubation time (Nice 1954).

$F$  = fraction of the initial weight which is lost during the period of incubation

$\dot{M}_{H_2O}$  = the weight loss = water loss ( $g \cdot \text{day}^{-1}$  or  $mg \cdot \text{day}^{-1}$  in Eq. (3))

$I$  = incubation time (days)

$G_{H_2O}$  = water vapor conductance of the egg ( $mg \text{ H}_2\text{O} \cdot \text{day}^{-1} \cdot \text{torr}^{-1} \text{ H}_2\text{O}$ )

$\Delta P_{H_2O}$  = water vapor pressure difference between the inside of the egg shell and the surrounding microclimate (torr).

Equation (2) defines the total water loss during incubation as the product of the daily water loss in the nest and the days of incubation. It assumes that the daily water loss is constant throughout incubation. Groebbels (1932) showed that this held true for the major part of the incubation for many species and Drent (1970) demonstrated it in a large series of Herring Gull (*Larus argentatus*) eggs. On the other hand, Drent (1970) has also shown that the optimal egg temperature is not reached during the first few days of incubation, so that one would expect at that time a somewhat smaller water loss, while after pipping, the eggs undergo a larger water loss. On balance, over the whole period, we have therefore assumed that an average constant

water loss throughout the period of incubation is a valid approximation.

Equation (3) describes the water vapor flux across the egg shell. The amount of water which is lost depends upon the pore geometry of the shell and the diffusion constant of water vapor in air on the one hand and the water vapor pressure difference which is set up between the inside of the shell and the microclimate of the nest surrounding the egg on the other hand. The former is expressed as the conductance,  $G_{H_2O}$ , which has been determined for 29 species (Ar et al. 1974).

It is of interest now to consider three relationships which have recently been established, namely, the incubation time, the daily water loss in the nest, and the water vapor conductance, all as a function of egg weight. When these are introduced into Eqs. (2) and (3), one can derive general relationships which apply to eggs of all sizes regardless of incubation time.

#### THE EGG WATER LOSS CONSTANT

Drent (1970) made a survey of reported weight losses of eggs during natural incubation. When these values for 46 species were plotted against egg weight, he obtained the following relationship:

$$\dot{M}_{H_2O} = 0.015 W^{0.74} \quad (4)$$

where all values are expressed in grams. Substituting Eq. (4) and (1) into Eq. (2) we have:

$$F = \frac{0.015 W^{0.74} \cdot 12 W^{0.22}}{W^{1.00}} = 0.18 \quad (5)$$

Assuming that the sum of the exponents, 0.96, is not significantly different from 1.00, this relationship tells us that all typical eggs regardless of incubation time will lose 18% of their initial weight during incubation. This is of course an average value which will vary from species to species. It is of interest to note that mean fractional weight loss for 17 species reported by Groebbels (1932) was  $0.16 \pm \text{SD } 0.04$ .

#### THE MEAN WATER VAPOR GRADIENT

In figure 3 (top line) we have plotted the individual water loss values in the nest against initial egg weight for the 46 species reported by Drent (1970), from which he obtained the relationship of Eq. (4). Below that we have plotted the water vapor conductances for 29 species reported by Ar et al. (1974), where

$$G_{H_2O} = 0.43 W^{0.78} \quad (6)$$

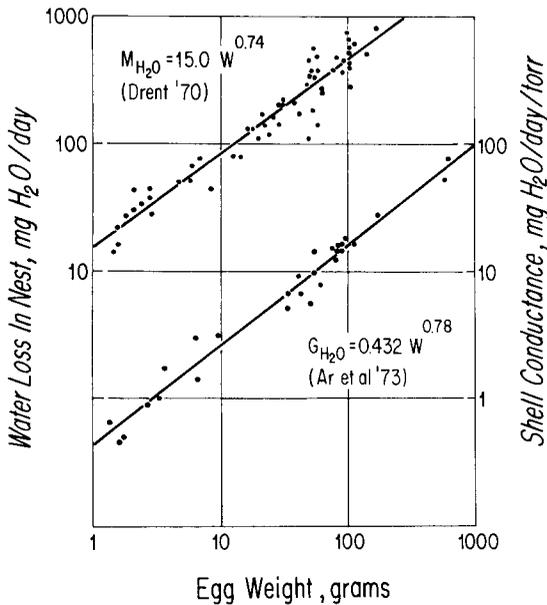


FIGURE 3. Relationship of daily water loss of eggs in the nest (Drent 1970) and the water vapor conductance of eggs (Ar et al. 1974) as a function of egg weight.

Substituting Eqs. (5) and (6) into the general water vapor flux Eq. (3), we can solve for the mean water vapor pressure difference,  $\Delta P_{H_2O}$ . Thus:

$$\Delta P_{H_2O} = \frac{\dot{M}_{H_2O}}{G_{H_2O}} = \frac{15 W^{0.74}}{0.43 W^{0.78}} = 35 \text{ torr } H_2O \quad (7)$$

if one assumes an insignificant difference between the two exponents 0.74 and 0.78.

This relationship tells us that the mean water vapor pressure difference between the inside of the egg shell and the surrounding microclimate is 35 torr. This value is expected to vary around this mean among species depending upon the type of nest, the incubation behavior, and general climatic condition. In desert nesters, one might expect a rather large water vapor gradient; in hole nesters, a relatively small gradient; and among the mound builders, which cover their eggs with decaying material, no gradient at all and therefore no water loss. In the latter case, one would also

predict that no air space develops in the egg during incubation.

For a few species the daily water loss and the water vapor conductance are known. For example,  $\dot{M}_{H_2O}$  is  $450 \text{ mg} \cdot \text{day}^{-1}$  in the Herring Gull (Drent 1970) and  $G_{H_2O} = 16 \text{ mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$  (Ar et al. 1974). Thus the mean water vapor pressure difference in this species is  $450/16$  or 28 torr. One can estimate the water vapor tension inside the egg shell to be 48 torr since the typical egg temperature for this species is  $37.5^\circ\text{C}$ . Thus the effective vapor tension in the microclimate surrounding the egg is  $(48 - 28)$  or 20 torr and the effective humidity is  $20/48$  or 42%.

#### RELATIONSHIP BETWEEN INCUBATION TIME AND WATER VAPOR CONDUCTANCE OF THE EGG

The two generalizations, namely, the fractional water loss constant and the mean water vapor gradient, can now be used to obtain a direct relationship between incubation time and water vapor conductance. By substituting Eq. (3) into Eq. (2) and introducing the value for  $F = 0.18$  and the value of  $\Delta P_{H_2O} = 35$  and solving for  $I$ , we obtain:

$$I = \frac{0.18 \cdot 10^3 \cdot W}{35 G_{H_2O}} = 5.2 \frac{W}{G_{H_2O}} \quad (8)$$

where  $10^3$  is introduced so that  $G_{H_2O}$  can be expressed in its conventional dimension of milligrams.

This equation indicates that for a given egg weight,  $W$ , the incubation period is inversely proportional to the water vapor conductance,  $G_{H_2O}$ , and implies a small pore area/shell thickness ratio in eggs with relatively long incubations and a large ratio for eggs with relatively short incubations. Four examples are taken from the values reported by Ar et al. (1974) which are shown in table 1. Eggs of the chicken and the puffin as well as the Rhea and Emu are similar in weight but not incubation time. The egg weight, conductance values, and the reported incubation periods for each species are shown as well as the predicted incubation based on Eq. (8). The agreement between reported and predicted incubation

TABLE 1. Reported and predicted incubation period for eggs having similar weight.

	W	$G_{H_2O}$	I reported	I predicted
<i>Gallus gallus</i> (Domestic Chicken)	54	14.4	21	19.5
<i>Fratercula arctica</i> (Common Puffin)	60	8.0	38	39.0
<i>Rhea americana</i> (Rhea)	609	78.0	40	40.5
<i>Dromiceius novae-hollandiae</i> (Emu)	578	52.0	58	58.0

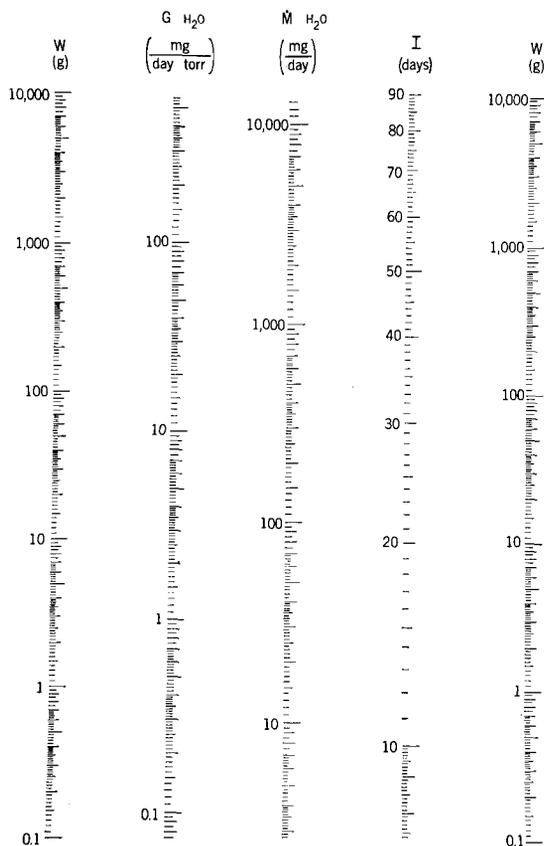


FIGURE 4. Alignment chart of water vapor conductance of the egg shell,  $G_{H_2O}$  ( $\text{mg H}_2\text{O} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$ ); the daily water loss of eggs in the nest,  $\dot{M}_{H_2O}$  ( $\text{mg H}_2\text{O} \cdot \text{day}^{-1}$ ) (Drent 1970); and of incubation time,  $I$  (days) as functions of fresh egg weight (g).

time is surprisingly good. It also illustrates how the tenfold difference in egg weight between the Rhea and puffin egg is associated with a tenfold difference in conductance and thus leads to similar incubation time for both species.

A similar relationship can be derived for incubation time which is inversely proportional to the daily water loss in the nest, namely,

$$I = 0.18 \frac{W}{\dot{M}_{H_2O}} \quad (9)$$

by substituting  $F = 0.18$  into Eq. (2). This relationship, however, is expected to exhibit greater variability since the daily water loss is not only a function of the water vapor conductivity,  $G_{H_2O}$ , but also of the water vapor gradient,  $\Delta P_{H_2O}$ . The latter will vary from species to species and is determined by the nest material, type of nest structure, and the incubation behavior of the parent. Figure 4 is an

alignment chart showing water vapor conductance of the eggshell, daily water loss of eggs in the nest, and incubation time as functions of egg weight.

#### EFFECT OF ALTITUDE ON EGG WATER LOSS

According to kinetic theory, the diffusivity of a gas varies inversely with the absolute pressure. Thus, for a given pore geometry and a given water vapor pressure gradient across the egg shell, one would predict that the water loss is inversely proportional to the barometric pressure. This was demonstrated by Paganelli et al. (1971) by exposing eggs at constant temperature in a desiccator to increasing and decreasing barometric pressure. Between 0.13 and 1 atm, the water loss rose linearly with  $1/P_B$ , the barometric pressure.

At least 15 species are known to nest at altitudes above 4600 m (15,000 ft) (O. P. Pearson and L. W. Swan, pers. comm.). Since several nesting species approach and one species exceeds altitudes where the total pressure is 0.5 atm (18,000 ft), it is of interest to inquire how the eggs cope with the problem of water loss. The highest nesting record is given at 6500 m (21,500 ft) for the Alpine Chough (*Phyrrhonorax graculus*) (Noel 1927). At this altitude the barometric pressure is 328 torr, and thus the binary diffusion coefficient for water in air,  $D_{H_2O\text{-air}}$ , which at 1 atm is  $0.218 \text{ cm}^2 \cdot \text{sec}^{-1}$ , is increased by  $(760/328)$  or 2.3-fold. With the typical pore geometry and water vapor gradient found at sea level, such an egg would theoretically lose 2.3 times more water at this altitude than at sea level.

Several adaptations would help to maintain a normal water balance of an egg at altitude. One would be to reduce the water vapor gradient between the egg and its microclimate by establishing nests in cavities and covering the eggs to provide a more humid atmosphere. Another approach would be to increase the relative water content of the egg so that in spite of increased dehydration a normal water content would be maintained at the end of incubation. Such an adaptation would be reflected in a higher albumen-yolk ratio. It is of interest to note that a recent analysis of the porosity of White Leghorn eggs from a colony established for 15 years at the White Mountain Laboratory of the University of California at 12,500 feet ( $P_B = 480$  torr) revealed a different trend (Wangensteen et al. 1974). These eggs had reduced their total pore area by about 60% which just offset the increased diffusion coefficient of water vapor at this altitude. Thus under natural conditions of incubation, their water loss would have been normal.

Whether a reduction in pore area of the egg shell commensurate with an increase of the diffusion coefficient is a general adaptation to high altitude remains to be investigated.

#### SUMMARY

Incubation time is proportional to egg weight raised to the 0.22 power for 475 species of birds whose incubation periods and egg weights were taken from the literature. Recent observations have shown that the water vapor conductance of an egg (Ar et al. 1974) and its rate of weight or water loss in the nest (Drent 1970) are proportional to egg weight raised to the 0.78 and 0.74 power, respectively. Since these three independently established equations all have egg weight as a common factor, they can be rearranged to arrive at the following relationships which apply generally to all incubating eggs: (a) during incubation the typical egg loses 18% of its initial weight; (b) the mean vapor pressure difference between the egg and nest microclimate during incubation is 35 torr; and (c) for any given egg weight, the incubation time is inversely proportional (1) to the water vapor conductance of the egg, which in turn is set by the pore area and thickness of the shell, and (2) to the rate of water loss in the nest.

The water loss of eggs incubated at altitudes presents a special problem, since the diffusivity of water vapor is inversely proportional to the absolute pressure. As there are many species which nest at altitudes, some as high as 18,000 ft (0.5 atm), the possible adaptations to prevent an increased rate of water loss are discussed.

#### LITERATURE CITED

- AR, A., C. V. PAGANELLI, R. B. REEVES, D. G. GREENE, AND H. RAHN. 1974. The avian egg: water vapor conductance, shell thickness, and functional pore area. *Condor* 76:153-158.
- DRENT, R. H. 1970. Functional aspects of incubation in the Herring Gull. *Behaviour*, Suppl. 17:1-132.
- DRENT, R. H. 1973. The natural history of incubation, p. 262-311. *In* Breeding biology of birds. Nat. Acad. Sci., Washington, D.C.
- EVANS, W. 1891. On the periods occupied by birds in the incubation of their eggs. *Ibis* 3:52-93.
- GROEBBELS, F. 1932. *Der Vogel*, Vol. I, II. Borntraeger, Berlin. Reprinted 1969. J. Cramer, Lehre.
- HEINROTH, O. 1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. *J. Ornithol.* 70:172-285.
- MURPHY, R. C. 1936. *Oceanic birds of South America*, Vol. I, II. Macmillan Co., New York.
- NEEDHAM, J. 1931. *Chemical embryology*, Vol. I. Cambridge Univ. Press.
- NICE, M. M. 1954. Incubation periods throughout the ages. *Centaurus* 3:311-359.
- NOEL, J. 1927. *The story of Everest*. Little, Brown & Co., New York, p. 193.
- PAGANELLI, C. V., A. AR, AND E. H. LANPHER. 1971. The influence of pressure and gas composition on water vapor diffusion. *Proc. Int. Union Physiol. Sci.* 9:436.
- REILLY, E. M., JR. 1968. *The Audubon illustrated handbook of American birds*. McGraw-Hill, New York.
- SCHÖNWETTER, M. 1960-71. *Handbuch der Oologie*, Lief. 1-19, W. Meise [ed.]. Akademie-Verlag, Berlin.
- WANGENSTEEN, O. D., AND H. RAHN. 1970-71. Respiratory gas exchange by the avian embryo. *Respir. Physiol.* 11:31-45.
- WANGENSTEEN, O. D., H. RAHN, R. R. BURTON, AND A. H. SMITH. 1974. Respiratory gas exchange of high altitude adapted chick embryos. *Respir. Physiol.* (in press).
- WORTH, C. B. 1940. Egg volumes and incubation periods. *Auk* 57:44-60.

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