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Relationship of Weight Loss to Ambient Humidity of Birds Eggs during Incubation

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Summary. Eggs of birds nesting in wet and dry habitats, have been artificially incubated at controlled humidity while weight loss of the eggs and shell water vapour conductance have been determined. Eggs of species from wet habitats loose weight at a higher rate than those from drier habitats at a given relative humidity.

It is suggested that the conductance of the egg shell to water vapour is adapted to the conditions of humidity in the environment such that weight loss varies little (and less than predictable) in relation to the relative humidity at the nesting sites.

The relative humidity surrounding eggs during natural incubation was found to be in the range of 30–50% in 4 different species. Humidity in the nest during natural incubation was found to be higher than what would result if ambient air was heated to incubation temperature indicating that the sitting bird conserves humidity around the eggs.

Introduction

The avian egg shell constitutes a barrier to evaporation and thus enables birds to reproduce in a terrestrial environment. While the egg shell protects the embryo against excessive water loss, it must, at the same time, be sufficiently permeable to allow respiratory gas exchange. The influence of the relative humidity on hatchability has been extensively studied during artificial incubation of chicken eggs. It has been demonstrated that reduced evaporation during incubation at very high humidity causes a decline in hatchability (Romanoff, 1930; Robertson, 1961; Lundy, 1969), allegedly because the air space within the egg must have a certain size to permit the initiation of lung ventilation and the movements necessary to break through the shell during hatching.

Two factors are important in controlling the evaporative water loss from eggs during incubation: the conductance of the shell to water vapour and the relative humidity surrounding the eggs.

The conductance of the shell to water vapour is defined according to Ar *et al.* (1974) as

$$G_{H_2O} = \frac{\dot{M}_{H_2O}}{\Delta P_{H_2O}}. \qquad (1)$$

G_{H_2O} = water vapour conductance (mg·day^{-1}·torr^{-1}).
$\dot{M}_{H_2O}$ = rate of water loss (mg·day^{-1}).
ΔP_{H_2O} = difference in vapour pressure across the shell (torr).

Rahn and Ar (1974) have demonstrated the existence of an inverse relationship between the length of the period of incubation and the conductance of the shell to water vapour when eggs of similar size are considered. Ar *et al.* (1974) have presented the following equation describing the relationship between egg weight and water vapour conductance of the shell:

$$G_{H_2O} = 0.432\ W^{0.780} \qquad (2)$$

W = initial egg weight in gram.

They point out that such a relationship is a generalization describing the behaviour of the "ideal" egg. Rahn and Ar (1974) found the "ideal" egg to loose 18% of its initial weight during incubation corresponding to a gradient in water vapour pressure across the shell of 35 torr.

Different species of birds place their nests in habitats fluctuating widely with respect to humidity and the question arises,whether such species of birds have evolved water vapour conductances of the shell in response to the varying conditions of humidity at the nesting sites.

Little is known of the humidity under the naturally incubating bird (Robertson, 1961), probably because of technical difficulties in measuring relative humidity in small confined spaces.

The present paper reports on a comparison of the weight loss from eggs of species inhabiting relatively dry and very moist habitats, respectively, when these eggs were artificially incubated at known and controlled relative humidity. Weight changes due to the respiratory gas exchange of the egg are negligible except at the very end of the period of incubation (Lundy, 1969). Hence weight loss can be considered equal to water loss. The relative humidity of the air surrounding the eggs during natural incubation in some bird species was also measured.

Material and Methods

Humidity measurements during natural incubation were done in the nests of the great tit (*Parus major*), the eider duck (*Somateria mollissima*), the domestic chicken (*Gallus domesticus*), and the domestic pigeon (*Columba livia*). For measurement of evaporative weight loss at controlled conditions, eggs were collected from the great crested greebe (*Prodiceps cristatus*), the coot (*Fulica atra*), the common gull (*Larus canus*), and the black headed gull (*Larus ridibundus*). A single egg of the sandwich tern (*Sterna sandwichensis*) found outside a nesting colony was also included in these measurements.

A "Sinascope" electronic hygrometer was used for the humidity measurements. This instrument is battery operated and the probe is sufficiently small (1 by 4 cm) to allow placement in a nest just underneath the eggs. Included in the probe is a thermosensor which permits temperature readings from exactly the same site where the humidity is measured. Calibration is checked by exposing the probe to water vapour in equilibrium with moist crystals of certain salts giving reproducible and accurate values of relative humidity.

Artificial incubation was done in a small still air incubator at 38 °C. The humidity in the incubator was monitored by the same hygrometer.

Results

Table 1 gives data on the total evaporative weight loss throughout the entire period of incubation expressed as a percentage of the initial weight of the eggs. The durations of the incubation periods are also listed (Witherby, 1943) as is the relative humidity in the incubator during the different experiments. Because in most cases the eggs were incubated for only part of the incubation period, the total weight loss was obtained by extrapolation. This is justified because the rate of weight loss is practically constant throughout the period of incubation (Boone and Barmore, 1965; Lundy, 1969; Rahn and Ar, 1974). The results presently obtained on eggs of the blackheaded gull showed constant weight loss and thus confirmed the findings of earlier investigators (Fig. 1). A substantial difference in weight loss exists, however, among the different species. Thus the greebe lost weight most rapidly followed by the coot. The difference between the greebe and the coot is significant when tested by *t*-test ($0.005 < P < 0.01$). The coot lost weight somewhat faster than the blackheaded gull and the common gull, but the differences are hardly statistically significant ($0.05 < P < 0.1$ resp. $0.2 < P < 0.25$). In both species of gull there is a significant

Table 1. Initial weight of eggs and total weight loss (in per cent of initial weight) throughout the period of incubation. Mean values ± standard deviation

Species	No. of eggs	Egg weight (g)	Duration of incubation (days)	Incubator humidity (%)	Total weight loss (%)
Greebe					
(*Podiceps cristatus*)	5	41.1 ± 3.0	28	65	23.2 ± 2.6
Coot					
(*Fulica atra*)	5	40.1 ± 4.2	23	65	14.7 ± 5.0
Blackheaded gull					
(*Larus ridibundus*)	10	38.1 ± 2.8	23	25	19.9 ± 7.4
	10	37.3 ± 3.3	23	65	11.2 ± 2.8
Common gull					
(*Larus canus*)	5	58.3 ± 3.5	24	25	20.3 ± 4.1
	5	53.8 ± 4.7	24	65	11.6 ± 1.5
Tern					
(*Sterna sandwichensis*)	1	38.1	21	25	14.2

Table 2. Water vapour conductance of egg shells. Predicted values are calculated from initial egg weight using the equation $G=0.432 \cdot W^{0.780}$. Observed values are calculated from the weight loss data of Table 1. Relative humidity in the incubator and the corresponding difference in water vapour pressure (ΔP_{H_2O}) between the eggs and the surrounding air

Species	Incubator humidity (%)	ΔP_{H_2O} (torr)	Water vapour conductance ($mg \cdot day^{-1} \cdot torr^{-1}$)	
			predicted from weight	observed
Greebe (*Podiceps cristatus*)	65	17.4	7.84	19.48
Coot (*Fulica atra*)	65	17.4	7.69	14.37
Blackheaded gull (*Larus ridibundus*)	25	37.3	7.39	8.49
	65	17.4	7.27	10.40
Common gull (*Larus canus*)	25	37.3	10.30	13.11
	65	17.4	9.67	14.82
Tern (*Sterna sandwichensis*)	25	37.3	7.39	6.91

increase in weight loss when going from 65% to 25% relative humidity ($P<0.005$ in both species). The weight loss of the tern egg was considerably less than the mean value for the two species of gull.

Values of water vapour conductance (G_{H_2O}) calculated from Equations (1) on the basis of the mean weight loss data together with values calculated from Eq. (2) using the mean initial egg weight are listed in Table 2. Table 2 also includes incubator humidity and the corresponding value of ΔP_{H_2O}.

With the exception of the common gull the species studied have nearly the same egg weight and therefore the estimate of G_{H_2O} based on egg weight is about the same. The estimates of G_{H_2O} based on actual weight losses during incubation at known humidity yielded different values. The greebe showed the highest value followed by the coot. The blackheaded gull occupied an intermediate position while the tern showed the lowest value.

The range of humidities measured in the nests of four different species is presented in Table 3. Since the humidity probe was situated below the eggs, the recorded temperature was lower than the true incubation temperature which can only be measured by inserting a temperature sensor into an egg. The air surrounding the humidity probe is, however, in free communication with the airspace between the eggs and will reflect the absolute humidity between the eggs. Provided the surface temperature of the eggs is known, the actual relative humidity can be estimated by means of the Mollier diagram. For the sake

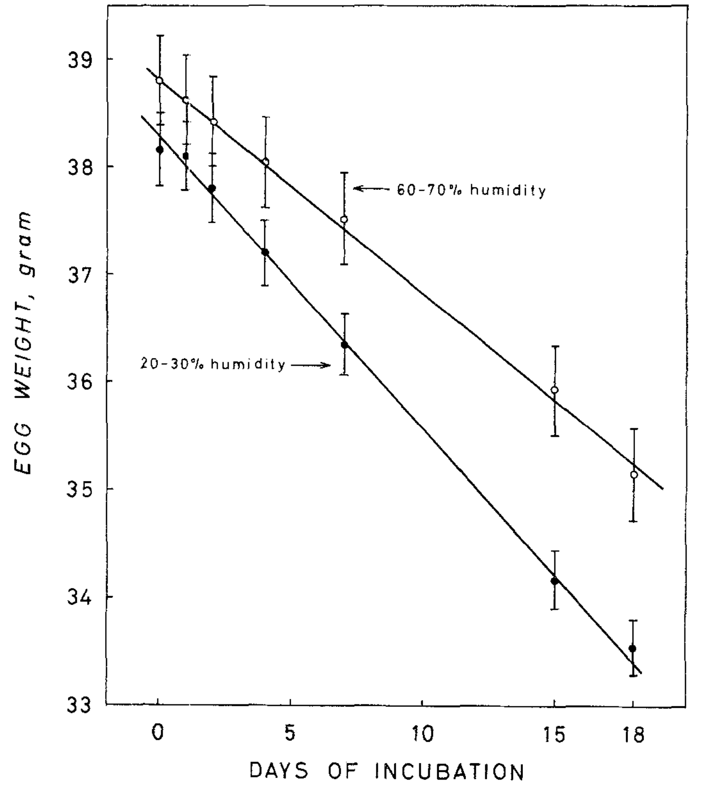

Fig. 1. Weight of eggs of blackheaded gull throughout incubation at 25% (lower curve) and 65% (upper curve) relative humidity in the incubator. Each point is the average of 5 eggs. Bars are ± one standard deviation from mean. Line is fitted by method of least squares.

Table 3. Relative humidity surrounding eggs during natural incubation

Species	Range of relative humidity (%)	Temperature (°C)	Rel. humidity corrected to 37 °C (%)	Period of observation (h)
Great tit (*Parus major*)	37–47	34–37	32–47	4
Eider duck (*Somateria mollissima*)	72–81	27–29	42–50	12
Pigeon (*Columba livia*)	46–52	33–34	38–45	24
Chicken (*Gallus domesticus*)	42–45	31–32	30–35	19

of comparison, all relative humidities have been corrected to 37 °C. These corrections may not be strictly correct since the actual incubation temperature is known to vary somewhat among different species (Huggins, 1941).

Discussion

The eggs of the great crested greebe lost weight at a higher rate than the other species studied at similar humidity. This bird builds a floating nest and the nesting material is permanently soaked with water. Furthermore, the bird covers the eggs when leaving the nest.

The coot is breeding in the same type of habitat but the nest is a substantial construction built from dry reed stems. Consequently the nest cup is dry and somewhat elevated above the water or mud surface. Correspondingly the water vapour conductance and the weight loss is less than for the greebe.

The two species of gull showed very similar weight losses. This may appear as a contradiction to the idea that the water vapour conductance of the shell is adapted to the prevailing conditions of humidity, since the eggs of the black-headed gull were collected in a boggy fresh water locality whereas the common gull eggs were taken at a sandy islet at the sea shore, which would seem quite arid. It should be kept in mind, however, that the blackheaded gull is a very versatile species capable of colonizing different types of habitat as for instance the one inhabited by the common gull. The danish population of common gull, on the other hand, is restricted to the sea shore and does not penetrate into fresh water swamps and lakes.

The single egg of the sandwich tern lost considerably less weight than the gull eggs. This is in accord with the fact that this bird places the eggs on beaches directly in the hot dry sand without any nesting material.

Fig. 2 compares the values of water vapour conductance of egg shells studied presently with the data of Ar *et al.* (1974). The values for the greebe and the coot are clearly higher than the values previously reported. The two species of gull are within the range but still somewhat on the high side whereas the tern is close to the average.

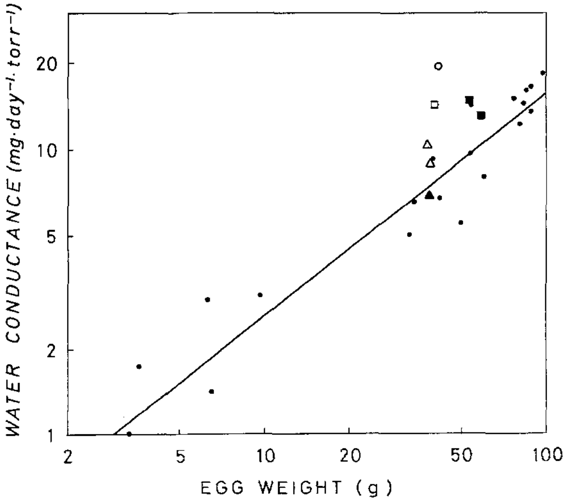

Fig. 2. Water vapour conductance of egg shells obtained presently and by Ar *et al.* (1974), plotted against initial egg weight. ● Data from Ar *et al.* (1974). The largest and smallest eggs of Ar *et al.* (1974) are omitted. The line is the regression line for all the data of Ar *et al.* (1974), $G = 0.432 \cdot W^{0.780}$ ○ Greebe; □ Coot; △ Blackheaded gull; ■ Common gull; ▲ Sandwich tern

The values of water vapour conductance recorded presently are thus generally somewhat higher than those of Ar *et al.* (1974). These investigators performed their determinations of water vapour conductance by subjecting the eggs to zero humidity in a dessicator, whereas in the present study the eggs were subjected to more natural conditions of humidity.

The relative humidity in the nest when corrected to 37 °C, is seen to vary between 30 and 50% in the four different species (Table 3). The recommended humidity for artificial incubation of chicken eggs is 40–70% (Barott, 1937; Robertson, 1961; Lundy, 1971). According to local game keepers and duck breeders, wild as well as domestic duck eggs require a higher humidity than chicken eggs. Koch and Steinke (1944) also recorded rather low relative humidities (30–37%) in the nests of domestic goose, turkey and chicken. In contrast to this, Rahn and Ar (1974) estimated a gradient in water vapour tension of 35 torr between the two sides of the egg shell and hence a relative humidity around the eggs of approximately 25%.

The great tit nests in a nest box. The eider duck has a rich supply of down in the nest, whereas the pigeon does not collect much nesting material. In spite of this, the humidities are within the same range.

Since cold air holds little water vapour, low ambient temperature will tend to cause a low relative humidity when such cold air is warmed up to the incubation temperature. One may ask, therefore, to what extent the sitting bird is able to retain a high level of humidity surrounding the eggs.

The temperature and relative humidity in the pigeon house were 18 °C and 65%. Using the Mollier diagram, this air would have a relative humidity of about 26% if heated to 34 °C. However, the readings in the nest at the same time were 34 °C and 52%, which shows how the sitting bird retains humidity around the eggs. In the case of the eider duck ambient conditions were 13 °C and 70% which corresponds to 28.5 °C and 28% relative humidity. The reading in the nest was 28.5 °C and 74% relative humidity at the same time.

The data presented support the idea that shell porosity is adapted to the habitat in such a way that birds from damp habitats show a higher conductance of the shell to water vapour than do species from dry habitats. This will assist in assuring that the eggs are subjected to about the same weight loss during incubation in spite of the different nesting conditions.

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