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EGG WEIGHT LOSS AND NEST HUMIDITY DURING INCUBATION IN TWO ALASKAN GULLS

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Although weight loss of eggs during natural incubation has long been recognized, little is known about the mechanism by which water vapor is conveyed from the eggs to the atmosphere surrounding the nest. It has been suggested that this occurs in two steps: (1) molecular diffusion from the egg across the gas-filled pores of the shell to the microclimate of the nest, (2) convection from the microclimate of the nest to the ambient environment (Rahn et al. 1976, 1977). To evaluate these processes, one must not only measure the flux of water from the egg but also estimate or measure the vapor pressure of water in the egg, the nest and the ambient atmosphere. We attempted this in the Black-legged Kittiwake (*Rissa tridactyla*) and the Glaucous-winged Gull (*Larus glaucescens*) when they were nesting on Gull Island, Kachemak Bay near Homer, Alaska, during June 1974.

In this study we have determined the rate of water loss from the egg during natural incubation, the egg temperature, the water vapor conductance and physical dimensions of the egg, and calculated the water vapor pressure of the egg, the microclimate of the nest and the nest ventilation.

MATERIALS AND METHODS

Black-legged Kittiwakes and Glaucous-winged Gulls coexist at the island rookery but select different nesting sites. A gull nest consists of a moderate depression in the soil lined with dried grass. A clutch typically contains three eggs though two-egg clutches are fairly common. The scattered nests are concealed within waist-high vegetation covering the horizontal platform of the island. In contrast, Kittiwakes nest densely on narrow ledges of seacliffs. Nests are composed of seaweed securely plastered to the rock, and the substantial cup is lined with moss. Two eggs complete the normal clutch.

Nests and their individual eggs were marked and weighed on a battery-powered Sartorius balance with an accuracy of 0.01 g on five occasions over a period of nine days. Additional eggs were brought to a nearby field station where they were placed in thermostatted desiccators over silica gel and maintained at 25°C. Their weight loss was recorded once a day for a period of five days on an analytical balance (sensitivity ±0.1 mg). The mean water loss was then divided by the saturation pressure of water vapor at 25°C, 23.7 torr, since the vapor pressure in the desiccator is essentially zero, in order to establish the water vapor conductance as originally described and defined by Ar et al. (1974) in terms of $mg \cdot day^{-1} \cdot torr^{-1}$.

Later, the eggs were weighed on a specially designed balance both in air and while submersed so that their volume could be obtained. All weights had an accuracy of ±10 mg at 21°C. The buoyancy of the suspension for holding the egg under water was corrected for, and corrections for water and air densities at 21°C were used in the calculation of the volume. After being weighed, the egg was held under water and the gas in the air cell was displaced by injecting water from a hypodermic syringe. In this manner we obtained egg weight at time of laying (see Rahn et al. 1976), and calculated their initial density.

These eggshells were later emptied, dried, and sent to the home laboratory for additional measurements of their physical dimensions as described by Paganelli et al. (1974). From the water vapor conductance value and the measurement of shell thickness, which is equivalent to pore length, we calculated the total effective pore area of the shell as described by Ar et al. (1974). A revised constant for this calculation was given by Rahn et al. (1976).

The mean temperature of eggs in the nest was measured by placing calibrated thermistors next to the embryo within the incubated egg. A 150-ft cable from the nest to the read-out instrument permitted us to estimate the mean temperature of incubation with minimal disturbance to the adult on the nest. Egg temperatures were recorded every three minutes over a period of 34 to 45 min only after a plateau had been reached following the return of the adult. This afforded a reliable estimate of the mean temperature of incubation because incubating gulls regulate the egg temperature within a relatively narrow range.

Mean ambient temperature and dew point data were obtained from the National Weather Service Station at Homer, Alaska, approximately 5 mi from Gull Island. Dry bulb and dew point data were available every 3 h. These were averaged and their standard deviation obtained for the period when we measured weight loss in the field.

RESULTS

Various physical dimensions of the egg and its shell for both species, together with comparable values reported by Schönwetter (1963), are given in Table 1. The table also shows the values for the water vapor conductance, G_{H_2O}, and the total effective pore area calculated from the relationship $Ap = .477\ G_{H_2O} \cdot L$ where L is the pore length or shell thickness (Rahn et al. 1976).

Table 2 gives the weight losses of eggs over a period of nine days; the cumulative weight

TABLE 1. Physical dimensions of egg and shell of the Glaucous-winged Gull and Black-legged Kittiwake. Also included are the water vapor conductance and the calculated total effective pore area. In parentheses are the mean values reported by Schönwetter (1963) based respectively on 65 and 43 specimens.

		EGG						SHELL					
		Wt g	Vol cm³	Density g·cm⁻³	Area cm²	Length cm	Width cm	Wt g	Thickness mm	Vol cm³	Density g·cm⁻³	G mg/day·torr	Ap mm²
Glaucous-winged Gull	Mean	98.20	92.51	1.062	100.30	7.35	5.00	6.79	.351	3.52	1.92	22.56	3.61
	SE	1.93	1.82	.001	1.61	.08	.03	.16	.003	.07	.01	1.00	.17
	n	21	21	8	15	20	20	16	16	15	15	18	16
		(98)				(7.26)	(5.00)	(7.00)	(.35)				
Black-legged Kittiwake	Mean	51.54	49.03	1.051	65.58	5.66	4.15	3.10	.260	1.70	1.82	9.67	1.10
	SE	1.01	1.02	.001	.90	.04	.03	.09	.007	.05	.02	.78	.07
	n	11	11	9	11	11	11	10	10	10	10	11	10
		(53.5)				(5.84)	(4.13)	(3.00)	(.23)				

TABLE 2. Mean daily weight losses of Glaucous-winged Gull and Black-legged Kittiwake eggs.

	Gull (n = 27)		Kittiwake (n = 4)	
	m·day⁻¹	SE	m·day⁻¹	SE
June 8–10	535	27	267	30
June 10–12	604	28	365	65
June 12–15	615	26	330	37
June 15–17	475	19	320	46
Weighted mean	563	25	321	44

losses are shown in Figure 1. The mean dry bulb temperature, integrated over the nine-day period, was 10.5°C SD ± 3.5°C. The mean dew point temperature was 4.72°C SD ± 1.5, which is equivalent to a mean vapor pressure of 6.4 torr. The mean egg temperature for the gull was 36.0°C and for the kittiwake 37.4°C.

DISCUSSION

ESTIMATE OF THE TOTAL WATER LOSS DURING INCUBATION

As Groebbels (1932), Drent (1975), Rahn et al. (1976), and others have pointed out, the weight loss of eggs during incubation is not only equivalent to water loss but remarkably constant from day to day. The mean weight or water vapor loss for the gull egg is 0.563 g·day^{-1}; multiplying this by the incubation period of 27 days yields a total weight loss of 15.2 g or 15.5% of the initial egg weight. The kittiwake egg has a mean weight loss of .321 g·day^{-1},

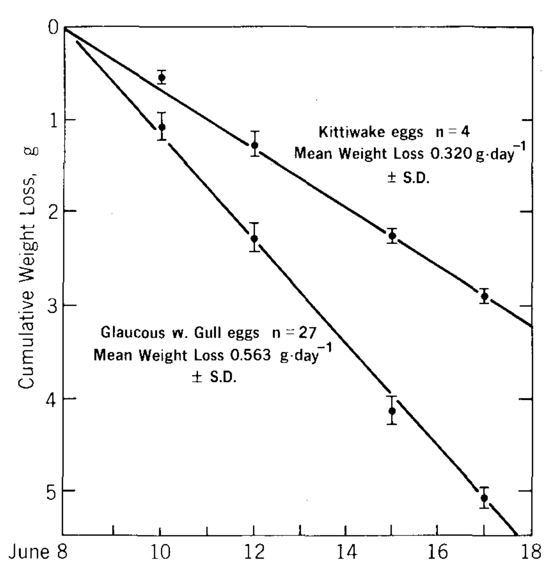

FIGURE 1. The cumulative weight loss of the eggs of the Glaucous-winged Gull and the Black-legged Kittiwake during natural incubation.

which, multiplied by its incubation period of 25 days, means that 8.0 g or 15.6% of its initial egg weight is lost. This loss does not include that which occurs after the first shell star fracture and pipping of the shell, but only that amount which is lost by molecular diffusion through the gas-filled pores of the eggshell. The total amount, expressed as the function of the initial egg weight, is close to 14% recently reported for seven species of terns whose nests ranged from the same area as our present two species to Enewetak Island in the Mid-Pacific (Rahn et al. 1976) and the value of 16% reported by Drent (1975) for birds in general.

WATER VAPOR TRANSPORT FROM THE EGG TO THE AMBIENT ATMOSPHERE

The source of vapor pressure resides inside the egg, and since the osmotic pressure of the albumen is not sufficient to depress the vapor pressure more than a fraction of a torr, one can estimate the saturation vapor pressure of the egg from its mean temperature. Thus the gull egg at 36.0°C has a water vapor pressure of 44.6 torr and the kittiwake egg at 37.4°C, 48.1 torr.

The next step is to calculate the water vapor pressure difference across the eggshell during incubation; Ar et al. (1974) and Rahn et al. (1976) pointed out that this can be expressed as follows:

$$(P_A - P_N) = \dot{m}_{H_2O}/G_{H_2O} \qquad (1)^*$$

where P_A = saturation water vapor pressure in egg, torr
P_N = water vapor pressure in the microclimate of the nest, torr
$\dot{m}_{H_2O}$ = water loss of egg in the nest, mg·day^{-1}
and G_{H_2O} = water vapor conductance of the egg, mg·day^{-1}·torr^{-1}.

When the appropriate values from Tables 1 and 2 are substituted into Eq. (1), we have for the gull egg $(P_A - P_N) = 563/22.56 = 24.6$ torr and for the kittiwake egg $(P_A - P_N) = 321/9.67 = 33.2$ torr.

WATER VAPOR PRESSURE IN THE NEST'S MICROCLIMATE

Since P_A can be estimated from the egg temperature and $(P_A - P_N)$ is derived as shown above, we subtract the latter value from P_A to obtain the vapor pressure of the nest. Thus $P_N = P_A - (P_A - P_N) = 44.6 - 24.6$ or 20 torr for the gull nest and $48.1 - 33.2$ or 15 torr for the kittiwake nest. Assuming that the typical nest air temperature is 34°C (Drent 1975), one can also express the absolute nest humidity in terms of relative humidity at that temperature. At 34°C the saturation vapor pressure is 39.9 torr. Thus the average relative humidity of the gull nest is (20/39.9) 100 or 50% and for the kittiwake nest (15/39.9) 100 or 38%.

WATER VAPOR PRESSURE IN THE AMBIENT ATMOSPHERE AND NEST VENTILATION

That the water lost from the egg must also be removed from the nest's microclimate was clearly stated by Chattock (1925) who suggested convection as the logical transport mechanism. Since the water loss from the egg must on the average equal the water loss from the nest, and if the absolute humidities of the nest and the ambient atmosphere are known, then the required nest ventilation can be calculated (Rahn et al. 1976, 1977) by the following relationship:

$$\dot{V}_N = \dot{m}_{H_2O}/[(P_N - P_I)\cdot\beta] \qquad (2)$$

where $\dot{V}_N$ = nest ventilation at 34°C (the assumed typical nest air temperature, Drent 1975), l·day^{-1}
$\dot{m}_{H_2O}$ = water loss from the nest = water loss from the egg, mg·day^{-1}
P_N = water vapor pressure in the nest, torr
P_I = ambient vapor pressure, torr
β = transport coefficient, mg·l^{-1}·torr^{-1} which at 34°C is equal to .941 (see Piiper et al. 1972)
and where $(P_N - P_I)\beta$ = concentration difference of water vapor between the nest and the ambient atmosphere, mg·l^{-1}.

The weather records gave us a mean value for P_I of 6.4 torr, and we can now substitute all values into Eq. (2) to estimate the nest ventilation. For the gull it is equal to 563 mg·day^{-1}/(20–6.4) .941 = 44 l·day^{-1} or 1.83 l·h^{-1}, a value similar to that estimated for the chicken egg by Chattock (1925) and the pheasant egg by Rahn et al. (1977). For the kittiwake we calculate 321/(15 – 6.4) .941 = 39.7 l·day^{-1} or 1.65 l·h^{-1}. How the nest is ventilated by these birds, where both parents incubate and the nest is rarely left unattended, is not known. However, to do so, the incubating parent need only stand up momentarily from time to time in order for the relatively drier ambient air to replace the moister air of the nest.

The two steps of water vapor transport from

* Due to typographic limitations, a lower case "m" with a dot, rather than a capital "M" with a dot, is used throughout this article.

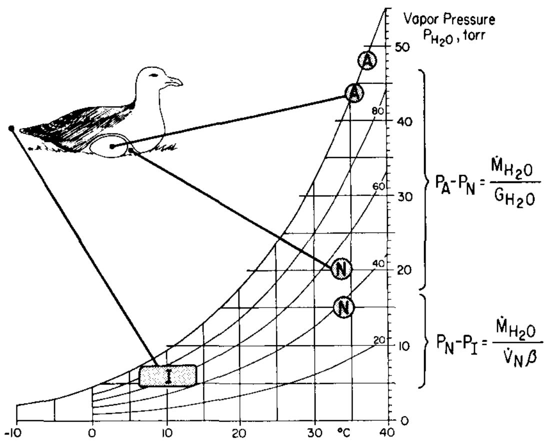

FIGURE 2. The water vapor pressure gradient from the egg to the ambient environment plotted on a vapor pressure-temperature grid with relative humidity isopleths. Circle A represents the temperature and vapor pressure of the Black-legged Kittiwake egg above and the Glaucous-winged Gull below. The vapor pressure of the nest microclimate is shown for each species by Circle N, while the mean ambient temperature and humidity are represented by Area I. The upper bracket, $P_A - P_N$, indicates the vapor pressure difference required for the egg to lose the observed water loss by molecular diffusion, the lower bracket, $P_N - P_I$, the difference achieved by ventilation of the nest.

the egg to the ambient atmosphere are summarized in Figure 2 which shows the background grid of the absolute humidity of the environment expressed as vapor pressure of water plotted against temperature with isopleths of relative humidity. The vapor pressures of the gull and kittiwake eggs are shown at their respective incubation temperatures. The vapor pressure in the egg (P_A) is labelled A in this diagram. The area labelled I represents the mean temperature and the vapor pressure of the ambient environment, which is the final sink for water vapor. In order for an egg to lose water by molecular diffusion through the fixed pore geometry of the shell, it becomes apparent from Eq. (1) that $P_A - P_N$, the water vapor difference across the eggshell, must be rather precisely maintained. P_A is fixed by the egg temperature and therefore P_N must somehow be regulated by nest ventilation if the requisite amount of water is to be lost.

The brackets in Figure 2 delineate the two mechanisms of water vapor transport. For the given water loss, $\dot{m}_{H_2O}$, the large gradient, $P_A - P_N$, is inversely proportional to the eggshell conductance for the molecular diffusion of water vapor. The smaller gradient, $P_N - P_I$, is inversely proportional to the convective transfer of water vapor. These two systems must be precisely meshed. The first depends upon the pore geometry of the eggshell, the second upon as yet inadequately described incubation patterns of the parent.

SUMMARY

We measured the weight or water loss, water vapor conductance and temperature of eggs of the Glaucous-winged Gull and the Black-legged Kittiwake during incubation, as well as the ambient humidity. From these data we calculated the nest humidity as well as the ventilation required to remove the water vapor from the nest.

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