

# Water loss during incubation in red bishop (*Euplectes orix*) eggs

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The red bishop (*Euplectes orix*) is a small passerine, breeding in woven, enclosed nests. Incubated eggs lost water at a rate (16,6 mg day<sup>-1</sup>) similar to that predicted by the egg weight and incubation period (18,5 mg day<sup>-1</sup>). Deserted eggs lost water at a much lower rate (3,1 mg day<sup>-1</sup>). The daily variation in water loss was much greater than has been previously reported. Much of this variation is correlated with changes in atmospheric humidity but heavy rainfall, wetting the nest, may also be important. Incubated eggs showed less daily variation in weight loss (co-efficient of variation 41%) than deserted eggs (co-efficient of variation 165%). The estimated nest humidity of deserted eggs (12,6 torr) was close to the mean ambient humidity (13,4 torr). The microclimate of incubated eggs was calculated to have a higher humidity (16 torr) than ambient and this would require nest ventilation of 1,18 l h<sup>-1</sup> to maintain water loss from the eggs.

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Die rooivink (*Euplectes orix*) is 'n klein passerniforme voël wat in toe, geweefde nessies broei. Bebroeiende eiers het water verloor teen 'n tempo (16,6 mg dag<sup>-1</sup>) gelykstaande aan dié wat voorspel kan word op grond van die eier se gewig en broeiperiode (18,5 mg dag<sup>-1</sup>). Eiers wat verlaat is het water teen 'n baie laer tempo verloor, nl. 3,1 mg dag<sup>-1</sup>. Die daaglikse variasie in waterverlies was baie meer as wat voorheen gerapporteer is en heelwat van hierdie variasie is gekorreleer met lugvogtigheid alhoewel swaar reëns wat die nes natmaak ook van belang kan wees. Bebroeiende eiers het minder daaglikse variasie getoon in gewigsvermindering (koëffisiënt van variasie 41%) as verlate eiers (koëffisiënt van variasie 165%). Die beraamde nesvogtigheid van verlate eiers (12,6 torr) was naby aan die gemiddelde omgewingslugvogtigheid (13,4 torr). Die lugvogtigheid van die mikroklimate van bebroeiende eiers is volgens berekening hoër (16 torr) as dié van die omgewing en dit vereis nesventilasie van 1,18 l h<sup>-1</sup> om waterverlies vanaf die eiers te handhaaf.

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Avian eggs lose weight during incubation and this weight loss, almost entirely due to water loss, is generally considered to be at a constant rate (Drent 1970). However, Rahn & Ar (1974) have shown that the water loss of an egg ( $M_{H_2O}$ ) is dependent upon the water vapour conductance of the egg shell ( $G_{H_2O}$ ) and the water vapour difference ( $\Delta P_{H_2O}$ ) between the inside of the egg and the surrounding microclimate:

$$M_{H_2O} = G_{H_2O} \times \Delta P_{H_2O}$$

They suggest that  $\Delta P_{H_2O}$  will vary between species depending on the type of nest, incubation behaviour and general climatic conditions.

Most previous studies have been concerned with water loss from the eggs of ground nesting gulls and terns (Drent 1970; Rahn, Paganelli, Nisbet & Whitlow 1976; Morgan, Paganelli & Rahn 1978; Rahn & Dawson 1979) or other species laying in open nests (Lomholt 1976; Furness & Furness 1981).

For comparative purposes, we investigated the water loss from the eggs of a small passerine which constructs an enclosed nest. The red bishop (*Euplectes orix*) is a colonial nester and its domed, woven nests are placed high in reedbeds (mainly *Phragmites mauritianus*) probably to escape ground predators but also exposing the nests to sun and rain. It is also found in areas subject to heavy rainfall and therefore environmental factors could be expected to have a marked effect on the water loss of its eggs.

## Materials and Methods

Data were obtained (by D.F.P.) from a colony at the Groombridge marsh, Salisbury, Zimbabwe (17°46'S/31°04'E). On the day of laying, each egg was marked with pencil dots so that it could be subsequently identified. Protected and insulated in cotton wool, the eggs were briefly removed to the Dept of Zoology, University of Zimbabwe, where they were weighed to 0,1 mg on a Mettler (H10) balance before being returned to the nest. This weighing procedure was repeated at each daily visit and the eggs were out of the nest for a maximum of 50 min each day. Several nests were deserted within the first few days of incubation and their eggs could be distinguished by a much lower rate of weight loss (Figure 1) and eventually by the failure to hatch. In the other nests, incuba-

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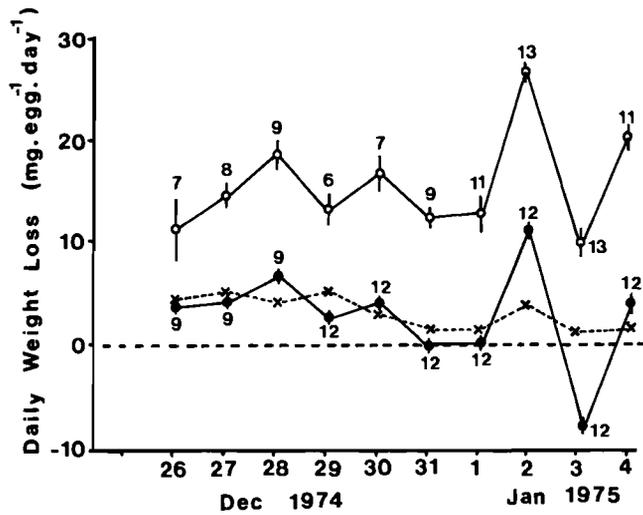
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**Figure 1** Mean daily weight loss of red bishop eggs. Separate values are shown for incubated eggs (o); deserted eggs (●); and a predicted weight loss for deserted eggs (x) calculated from the ambient climatic data. Vertical lines indicate one standard error on either side of the mean and numbers indicate the sample size.

tion did not seem to be significantly affected by the weighing procedure since young were successfully hatched following the usual incubation period.

It was not possible to record the temperature of the nest or eggs but ambient climatic data (mean daily temperature, humidity and rainfall) were obtained from nearby weather stations maintained by the Dept of Meteorological Services (Table 1).

**Table 1** Parameters of ambient climate and water loss from red bishop eggs

	Ambient climate		Initial egg mass	Egg water loss in nest	
	Absolute humidity torr	Air temperature °C	g	Unincubated $M_{H_2O}$ mg day <sup>-1</sup>	Incubated $M_{H_2O}$ mg day <sup>-1</sup>
$\bar{X}$	13,4	20,0	1,73	3,1	16,6
S.E.	0,7	1,6	0,03	0,5	0,7
C.V.	5	8	7	165	41
n	10 days	10 days	15 eggs	111 egg.days	98 egg.days

## Results

### Observed weight losses from eggs

A freshly laid red bishop egg weighed 1,73 g (Table 1) and, during the incubation period of 14 days (PFW pers. obs.), the mean weight loss from incubated eggs was 16,6 mg day<sup>-1</sup>, much higher than the mean weight loss of 3,1 mg day<sup>-1</sup> of deserted eggs (Table 1).

The daily variation in mean weight loss of both incubated and deserted eggs was considerable (Table 1). There were some differences in the mean weight loss between nests and, within a nest, there was much variation in the mean weight loss from one day to another (Figure 1). It seemed likely that much of the daily variation in the weight loss could be explained by changes in the water vapour gradient between the egg and its microclimate.

This was investigated by predicting the daily weight losses of the deserted eggs.

### Estimated weight loss from eggs

The deserted eggs were assumed to be at ambient temperature and to have a water vapour pressure of saturation at that temperature, neglecting the very small reduction in water vapour tension caused by the egg solutes (Ar, Paganelli, Reeves, Green & Rahn 1974). The partial pressure of atmospheric water vapour was calculated from the daily mean % relative humidity and temperature (Burns & MacDonald 1975). Thus the water vapour difference ( $\Delta P_{H_2O}$ ) between the inside of the egg and the surrounding microclimate could be calculated by subtraction. The water vapour conductance ( $G_{H_2O}$ ) of the egg shell was estimated from the equation of Ar & Rahn (1978):

$$G_{H_2O} = 5,13 W/I = 5,13 (1,73/14) = 0,63 \text{ mg day}^{-1} \text{ torr}^{-1}$$

(where  $W$  = egg mass [g] and  $I$  = incubation time [days]). Estimated weight losses ( $M_{H_2O}$ ) for the deserted eggs ( $\bar{D}$ ) were calculated using Rahn & Ar's (1974) formula (see above) and were corrected to ambient barometric pressure (636 – 640 mmHg) (Figure 1).

There was a significant correlation between the observed daily water loss for deserted eggs ( $D$ ) and the predicted water loss ( $\bar{D}$ ) (correlation co-efficient,  $r = +0,63$ ,  $0,05 > P > 0,02$ ). However, there was a high unexplained residual variation ( $\bar{D} - D$ ). This was not closely correlated with rainfall (correlation co-efficient,  $r = +0,43$ ,  $P > 0,10$ ), but showed a significant negative auto-correlation ( $[\bar{D} - D]_t$  vs  $[\bar{D} - D]_{t-1}$ : correlation coefficient,  $r = -0,70$ ,  $0,05 > P > 0,02$ ), i.e. there was a fairly regular succession of 'more than expected – less than expected' values (Figure 1) and the cumulative totals of this residual variation remained low. A possible reason for this residual variation was that the climatic data were recorded between 06h00 – 08h00 each day and the eggs were weighed between 13h00 – 14h00. Thus there was an unavoidable time lag between the two measurements which could lead to slight day to day variation.

On two occasions there were more marked differences between observed and predicted weight losses. There was a large drop in the rate of water loss of 3 January 1975 (Figure 1) and the deserted eggs actually gained weight. This was associated with particularly heavy rainfall (28,7 mm) and it seems certain that the deserted nests became thoroughly soaked, resulting in water (in the liquid phase) being absorbed by the egg shells. This may also have been an important factor for some of the other 'less than expected' weight losses but was impossible to quantify from these data. On 2 January 1975, the water loss was considerably 'more than expected'. This followed two days of 'less than expected' water loss and, associated with high winds and relatively low rainfall, it may represent drying of the egg shells.

Temperatures of the incubated eggs were not available and therefore expected daily water losses cannot be calculated from them. However, the pattern of observed weight losses was very similar to that of the deserted eggs (Figure 1) (correlation coefficient,  $r = +0,82$ ,  $P < 0,01$ ) and one can assume that they were both being affected by

similar environmental factors. In comparison with the deserted eggs, the incubated eggs would have been maintained by the female at an elevated and comparatively constant temperature. This would account for their greater water loss and lower co-efficient of variation (Table 1).

### Nest humidity

It was possible to calculate the nest humidity for the deserted eggs using the calculated value for water vapour conductance [ $0,63 \text{ mg (day torr)}^{-1}$ ] and assuming that the deserted eggs were at ambient temperature ( $20^\circ\text{C}$ ). The water vapour difference ( $\Delta P_{\text{H}_2\text{O}}$ ) between the unincubated egg and the nest microclimate was:

$$\begin{aligned}\Delta P_{\text{H}_2\text{O}} &= M_{\text{H}_2\text{O}}/G_{\text{H}_2\text{O}} \\ &= 3,1 / 0,63 = 4,9 \text{ torr.}\end{aligned}$$

Assuming that the vapour pressure of an unincubated egg was  $17,5$  torr (saturated water vapour pressure at  $20^\circ\text{C}$ ), the microclimate of the unincubated egg was ( $17,5 - 4,9$ ) =  $12,6$  torr. This calculated value was very similar to that of the ambient air ( $13,4$  torr, Table 1).

The calculation of nest humidity for the incubated eggs is made more difficult because their temperatures were not available. However, Drent (1975) has shown that the incubation temperature for nine small passerines was in the range  $34,0 - 35,4^\circ\text{C}$  and the mean,  $35,0^\circ\text{C}$ , has been used here. The water vapour difference between the incubated egg and nest microclimate was:

$$\begin{aligned}\Delta P_{\text{H}_2\text{O}} &= M_{\text{H}_2\text{O}}/G_{\text{H}_2\text{O}} \\ &= 16,6 / 0,63 = 26,3 \text{ torr.}\end{aligned}$$

Assuming that the vapour pressure of an incubated egg was  $42,2$  torr (saturated water vapour pressure at  $35^\circ\text{C}$ ), the microclimate of the incubated egg was ( $42,2 - 26,3$ ) =  $15,9$  torr. This is higher than the humidity of the ambient air.

### Nest ventilation

Since the incubated eggs are continually losing water at a relatively constant rate, ventilation of the nest is essential to prevent an excessive accumulation of water vapour (and carbon dioxide) around the eggs. Rahn, Ackerman & Paganelli (1977) have provided an equation to calculate the nest ventilation required to remove the egg water loss from the nest:

$$V\beta = M_{\text{H}_2\text{O}}/(P_{\text{N}} - P_1)_{\text{H}_2\text{O}}$$

where  $M_{\text{H}_2\text{O}}$  = water loss of egg during incubation;  $P_{\text{N}} - P_1$  = vapour pressure difference between the nest and the ambient atmosphere (torr.);  $V$  = nest ventilation at  $34^\circ\text{C}$  ( $\text{l day}^{-1}$ );  $\beta$  = transport co-efficient equal to  $0,941 \text{ mg l}^{-1} \text{ torr}^{-1}$  at  $34^\circ\text{C}$ . Substituting values for the red bishop nest,

$$\begin{aligned}V &= 16,6 / (2,5 \times 0,941) \\ &= 7,06 \text{ l day}^{-1} \text{ egg}^{-1}\end{aligned}$$

Thus a clutch of four eggs would require nest ventilation of  $28,23 \text{ l day}^{-1}$ , or  $1,18 \text{ l h}^{-1}$ . This is a considerable

quantity when one realizes that the mean volume of the nest is  $0,52 \text{ l}$ , or  $0,25 \text{ l}$  for the portion beneath the entrance hole (Woodall 1971).

### Discussion

The observed daily weight loss of incubated red bishop eggs ( $16,6 \text{ mg}$ ) can be compared with estimated values. Ar & Rahn (1980) found that the daily water loss of some 85 species was best described by the equation:

$$M_{\text{H}_2\text{O}} = 150 [\text{egg wt (g)/incubation time (days)}]$$

Substituting the observed values,

$$M_{\text{H}_2\text{O}} = 150 (1,73/14) = 18,5 \text{ mg day}^{-1}$$

This is slightly higher, but quite close to the observed weight loss ( $16,6 \text{ mg}$ ) indicating that red bishop eggs have a similar weight loss during incubation to that found in many other species.

Rahn *et al.* (1976) found that seven species of terns, varying considerably in size, all lost approximately 14% of their fresh egg weight before hatching and they suggested that this might be essential to allow the embryo to fill its lungs and air-sacs prior to pipping the egg shell and hatching. The red bishop egg also loses a similar amount of water prior to hatching (13,4%) but the daily weight loss is quite variable.

Many reports in the literature remark on the constant rate of water loss during incubation (Drent 1970; Rahn *et al.* 1976; Morgan, *et al.* 1978). In the herring gull *Larus argentatus*, Drent (1970) presents data showing a co-efficient of variation of 11% for the daily mean weight loss during most of the incubation period (calculated from Drent's (1970) Figure 32). In contrast, this study showed considerable daily variation in the mean daily weight loss (co-efficient of variation; incubated eggs = 41%, unincubated eggs 165%). Much of this variation in weight loss can be explained by changes in atmospheric humidity producing changes in the water vapour pressure gradient across the egg shell. Heavy rainfall which can soak the nest and wet the eggs may also be important, although this produced much less effect on incubated than on deserted eggs (Figure 1).

Most eggs were laid at the beginning of the study period and were due to hatch one or two days after it terminated. Drent (1970) found no indication that the stage of embryonic development affects the rate of water loss (apart from when the egg shell is cracked prior to hatching) and this is supported by the close correlation of water loss from deserted and incubated eggs in this study.

The calculated nest humidity of the incubated eggs (16 torr) is lower than the range of 18–26 torr recorded by Rahn, *et al.* (1977). This figure must be treated with some caution since it was calculated using data on egg temperatures obtained from the literature (Drent 1975) but, since the weight loss of the eggs was measured accurately, either the egg temperatures and/or the nest humidity of the red bishop in this study were lower than normal.

It was surprising to find that the humidity in the enclosed red bishop nest was not greater than that of a gull's open nest. This must be the result of ventilation by

the incubating female. The required rate of ventilation seems considerable, but may be achieved merely by the female leaving the nest periodically. Rahn & Dawson (1979) calculated that gulls' eggs would require ventilation of  $3,4 \text{ l (h egg)}^{-1}$  but that this could be achieved by the incubating bird standing up regularly.

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