Water vapour conductance of wildfowl eggs and incubator humidity

N.A. FRENCH and R.G. BOARD

Introduction

Fertile eggs lose water progressively throughout incubation, the rate of loss being a function of the water vapour concentration in the atmosphere around the eggs, the eggshell porosity, the temperature and the length of incubation. Optimum hatchability of domestic hen eggs occurs when about 12% of the initial weight of an egg is lost before pipping, and 4% between pipping and hatching (Lundy 1969; Robertson 1961a, b). Weight loss is due entirely to the diffusion of water vapour from the egg contents through the pores in the eggshell (Romanoff & Romanoff 1949). Field observations have confirmed a 12% weight loss as being widespread (Drent 1975), though a few exceptions have been noted. This level of loss of fresh egg weight is common to all sizes of egg, and the actual rate appears to be adapted to incubation period (Rahn & Ar 1974; Ar & Rahn 1978). Thus the eggs of birds with prolonged incubation, e.g. Shearwaters with *c.* 52 days (Whittow 1980) and Kiwis with 71 days (Calder 1978), still lose only 12% weight. Indeed, adaptation of the eggshell porosity results in a constant egg weight loss across the broad spectrum of egg size and variation in incubation period (Rahn & Ar 1974). Exceptionally, there is no appreciable water loss from the eggs of the Brush Turkey *Alectura lathami* (Seymour & Rahn 1978) and the Mallee Fowl *Leipoa ocellata* (Seymour & Ackerman 1980) incubated in nest mounds with saturated atmospheres.

The humidity settings required for artificial incubators used in the poultry industry have been established empirically over many years (Lundy 1969). A trial and error approach is possible when large numbers of eggs are available, but it should not be considered by aviculturists who often have few eggs and a need for a high hatchability, especially with birds whose existence in the wild is threatened. In the absence of pertinent information, they have generally adopted the humidities which had been selected for domesticated species on the unwarranted assumption that such values are suitable for the eggs of wild birds also.

Recent advances in our understanding of the mechanism of water loss from incubating eggs means that it is now possible to predict the humidity setting for an incubator that will ensure a 12% weight loss in the egg(s) of a given species (Tullett 1981). There are two possible approaches to establishing the humidity setting required. In one case, the humidity in the natural nest cup of the species in question can be determined with an egg hygrometer – an eggshell filled with silica gel (Rahn *et al.* 1977), or with electronic sensors (Howey *et al.* 1977). These techniques will also indicate whether or not there are changes in nest humidity during incubation. In the other case measurements of the porosity of the eggshell are used (Tullett 1981). This present communication, which involved the second approach, determines the incubator humidity settings for 34 species of Anatidae.

Mechanism of water loss – the theory

Rahn and his colleagues (Rahn & Paganelli 1981) have shown that water is lost from eggs by diffusion of vapour through pores in the eggshell (Figure 1), the loss being governed by Fick's law of diffusion (Wangensteen & Rahn 1970/71). It can be shown (Ar *et al.* 1974) that:

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

$\dot{M}_{H_2O}$ is the rate of water loss per day (mg/day); G_{H_2O} is the water vapour conductance of the eggshell (mg/day/torr), – i.e. a measure of the porosity of the eggshell to water vapour – which is determined by the number and the geometry of the pores in the eggshell and the

Wildfowl 34 (1983): 144–152

diffusivity of water vapour; ΔP_{H_2O} (torr) is the difference between the water vapour partial pressure inside ($P_{H_2O_{egg}}$) and outside ($P_{H_2O_{nest}}$) the egg, where the former has been shown to be saturated at incubation temperatures. In this paper partial pressure is measured in torr, the unit in general use in egg respiration physiology. Millibars is the unit in the Systeme Internationale convention. These units are related thus:

$$0.75 \text{ torr} = 1 \text{ millibar}$$

As it is a direct measure of water vapour concentration, water vapour partial pressure is used in preference to the more commonly used term, relative humidity. These two are related thus:

$$\text{R.H.\%} = \frac{P}{P\,(\text{sat.})} \times 100 \qquad (2)$$

where P = measured partial pressure (torr); P (sat.) = saturated partial pressure at incubator temperature (torr), these values can be obtained from standard tables (Unwin 1980).

Oxygen and carbon dioxide diffusion across the eggshell can be described in the same manner as for water vapour. Equation (1) can be generalized to describe any gas diffusing across a shell:

$$\dot{M}_y = G_y \cdot \Delta P_y \qquad (3)$$

where $\dot{M}_y$ = rate of flux of gas_y (ml/day); G_y = the conductance of the shell to gas_y (ml/day/torr); ΔP_y = the difference in partial pressure of gas_y across the shell (torr). There is a linear relationship between G_{H_2O}, G_{O_2} (oxygen conductance), and G_{CO_2} (carbon dioxide conductance), and it is possible to calculate the last two from the first (Hoyt *et al.* 1979).

If the G_{H_2O} of an eggshell is known, the correct incubator humidity setting to achieve a 12% fresh egg weight loss during incubation can be calculated from equation (1). The aggregate 12% weight loss can be used to establish the daily weight loss requirement, viz:

$$\dot{M}_{H_2O} = \frac{W \times 0.12 \times 1000}{(I-2)} \qquad (4)$$

where W = fresh egg weight (grams); (I–2) = incubation period minus 2 days for the hatching period (days); the equation is multiplied by 1000 to convert grams into milligrams. Incubator partial pressure can be calculated rearranging equation (1), viz:

$$P_{H_2O_{nest}} = P_{H_2O_{egg}} - (\dot{M}_{H_2O}/G_{H_2O})$$

$P_{H_2O_{egg}}$ is obtained by consulting standard tables of saturated water vapour partial pressure at incubation temperature.

G_{H_2O} can be determined by storing an egg in an environment where P_{H_2O} is known and daily weight loss ($\dot{M}_{H_2O}$) is measured. With an egg in a desiccator, having a $P_{H_2O_{nest}}$ = zero, then $\Delta P_{H_2O} = P_{H_2O_{egg}}$, and $G_{H_2O} = \dot{M}_{H_2O}/P_{H_2O_{egg}}$ (Ar *et al.* 1974).

Materials and methods

Three hundred and fifty infertile eggs from 76 species of Anatidae and 1 species of Phoenicopteridae were obtained from the Wildfowl Trust, Slimbridge, England, in the 1980 and 1981 breeding seasons. The eggs had shown no embryo development during incubation for six days under bantam hens.

In the 1980 breeding season, the water vapour conductance of all eggs were determined as in Hoyt *et al.* (1979). They were stored in desiccators containing silica gel at 25°C, and weighed daily for up to seven days. The silica gel was replenished regularly.

To overcome the potential problem of the back pressure of water vapour in the desiccator (where its partial pressure no longer equals zero; Dr. A. H. J. Visschedijk pers. com.), the Hoyt *et al.* (1979) technique gas modified for the 1981 breeding season. The air in the desiccators was circulated by an aquarium pump to ensure rapid uptake of water vapour by the silica gel.

The water vapour conductance was calculated by dividing the average daily weight loss for each egg by the saturation water vapour partial pressure in the egg at 25°C (23.7 torr). The result was corrected for barometric pressure (Ar *et al.* 1974), obtained from the Gloucester Meteorological Office, Gloucester, approximately 15 miles from Slimbridge.

Results and discussion

The water vapour conductances (G_{H_2O}) obtained in this study, as well as those quoted in the literature, for Anatidae eggs are summarised in Table 1. Fresh egg weights and incubation periods were obtained from the literature or records at the Wildfowl Trust.

The calculated incubator humidity required for 34 species from 9 tribes of Anatidae are shown in Table 2. These had at least 8 measurements of water vapour conductance. With an incubator

Table 1. The water vapour conductances (GH_2O), fresh egg weight (W) and incubation period (I) for Anatidae eggs. Figures in brackets are coefficients of variation.

Species	No.	GH_2O (mg/day/torr)	W (gm)	I (day)
Anatidae				
Dendrocygnini				
Dendrocygna				
guttata Spotted Whistling Duck	3	11.8 (23.8)	50	30
bicolor Fulvous Whistling Duck	20	14.3 (17.6)	51	26
	7 (a)	17.1 (9.5)	54	25
arborea Cuban Whistling Duck	6	18.5 (23.1)	54	30
	9 (a)	11.6 (12.1)	60	30
arcuata Wandering Whistling Duck	4 (b)	6.1	36	30
viduata White-faced Whistling Duck	9	8.3 (6.7)	36	27
autumnalis Red-billed Whistling Duck	10	11.6 (16.0)	43	27
Thalassornis				
l. leuconotus African White-backed Duck	1	21.8	84	26
Anserini				
Cygnus				
melanocoryphus Black-necked Swan	5	41.9 (16.4)	247	36
columbianus bewickii Bewick's Swan	4	38.8 (6.5)	260	29
Anser				
cygnoides Swan Goose	7 (a)	26.7 (17.6)	146	28
fabalis Bean Goose	9 (a)	24.9 (30.3)	152	27
f. rossicus Russian Bean Goose	2	33.7 (1.2)	146	28
f. brachyrhynchus Pink-footed Goose	3 (a)	23.4 (37.0)	139	27
albifrons frontalis Pacific Whitefront	6	23.3 (24.3)	133	26
a. gambelli Tule Goose	1	22.3	133	26
a. flavirostris Greenland Whitefront	1	15.4	117	26
erythropus Lesser Whitefront	3	25.1 (16.1)	100	25
	7 (a)	20.6 (23.1)	123	25
canagicus Emperor Goose	6	23.1 (19.3)	120	24
	7 (a)	27.4 (20.3)	136	24
anser Greylag Goose	3 (a)	33.2 (11.2)	163	27
	3 (c)	35.1	195	28
anser Embden Goose	11 (c)	27.7	170	28
indicus Bar-headed Goose	2 (a)	8.4 (7.9)	110	28
	? (d)	25.6	110	28
caerulescens atlanticus Greater Snow Goose	5	25.1 (5.8)	127	23
rossi Ross's Goose	3	18.6 (9.1)	92	22
Branta				
canadensis parvipes Lesser Canada Goose	5	36.3 (6.8)	91	24
canadensis leucopareia Aleutian Canada Goose	5	23.6 (16.1)	93	27
	3 (a)	21.4 (15.1)	117	28
canadensis minima Cackling Canada Goose	3 (a)	18.0 (8.7)	100	28
sandvicensis Hawaiian Goose	2	33.7 (12.2)	131	29
	3 (a)	33.4 (21.0)	154	30
leucopsis Barnacle Goose	15	19.8 (26.3)	107	24
	7 (a)	19.6 (23.3)	107	24
ruficollis Red-breasted Goose	1	5.8	90	24
	5 (a)	12.9 (20.9)	68	25

Table 1 continued.

Species	No.	GH2O (mg/day/torr)	W (gm)	I (day)
Tadornini				
Tadorna				
tadorna Common Shelduck	4	10.8 (52.2)	78	30
	4 (a)	15.3 (10.1)	80	28
variegata Paradise Shelduck	2	9.7 (56.2)	91	30
	6 (a)	14.1 (12.4)	90	30
ferruginea Ruddy Shelduck	2	11.7 (7.1)	83	28
	2 (a)	16.6 (39.5)	79	29
Cyanochen				
melanoptera Abyssinian Blue-winged Goose	5	16.2 (28.4)	85	32
	2 (a)	14.7 (6.0)	83	30
Neochen				
jubatus Orinoco Goose	8	10.7 (7.0)	63	30
Chloephaga				
poliocephala Ashy-headed Goose	5	6.5 (22.4)	89	30
	1 (a)	13.9	79	30
picta picta Lesser Magellan Goose	2	19.6 (25.8)	122	30
p. leucoptera Greater Magellan Goose	1 (a)	23.8	106	30
rubidiceps Ruddy-headed Goose	3 (a)	11.7 (35.1)	84	30
Anatini				
Marmaronetta				
angustirostris Marbled Teal	1	9.4	31	25
Anas				
v. versicolor Northern Versicolor Teal	8	6.1 (12.6)	34	25
	3 (a)	4.5 (28.6)	29	24
v. puna Puna Teal	6	7.9 (10.8)	42	24
	5 (a)	7.2 (34.6)	42	24
erythrorhyncha Red-billed Pintail	2	11.8 (1.9)	39	26
	5 (a)	7.5 (6.3)	38	24
a. acuta Northern Pintail	1	3.6	45	23
bahamensis Bahama Pintail	1 (a)	8.5	35	25
crecca carolinensis American Green-winged Teal	2	2.6 (24.0)	?	21
falcata Falcated Teal	5 (a)	7.2 (17.6)	41	24
flavirostris Chilean Teal	7 (a)	6.0 (6.5)	29	26
capensis Cape Teal	1 (a)	9.2	31	21
gibberifrons gracilis Australian Grey Teal	9	6.9 (36.5)	35	24
	8 (a)	8.5 (27.2)	33	24
castanea Chestnut Teal	4	11.6 (10.6)	40	28
aucklandica chlorotis New Zealand Brown Teal	7	16.7 (7.2)	62	28
p. platyrhynchos Mallard	4	11.3 (55.9)	54	28
	11 (c)	14.5	54	28
p. diasi Mexican Duck	1	10.7	58	27
	9 (a)	12.2 (14.4)	46	27
p. fulvigula Florida Duck	3 (a)	16.7 (12.9)	56	25
p. wyvilliana Hawaiian Duck	3 (a)	9.5 (29.7)	50	27
luzonica Philippine Duck	3	13.8 (15.4)	51	25
p. poecilorhyncha Indian Spotbill	1	9.3	57	28
p. zonorhyncha Chinese Spotbill	1	13.0	?	?
melleri Meller's Duck	2	16.2 (19.4)	?	?
s. sparsa African Black Duck	2	10.0 (0.4)	72	28
penelope Wigeon	4	5.5 (24.2)	44	24
	2 (a)	6.1 (29.5)	37	24
americana American Wigeon	2	7.2 (3.5)	43	24
sibilatrix Chiloe Wigeon	1	7.9	53	26
discors Blue-winged Teal	1 (a)	4.6	25	23
r. rhynchotis Australian Shoveler	1	4.9	43	26
platalea Red Shoveler	1 (a)	7.8	35	25
smithi Cape Shoveler	1 (a)	7.3	36	26

Table 1 continued.

Species	No.	GH2O (mg/day/torr)	W (gm)	I (day)
Merganettini				
Merganetta				
a. armata Chilean Torrent Duck	3	10.4 (8.9)	?	?
Somateriini				
Somateria				
m. mollissima European Eider	8	21.4 (28.0)	110	26
	1 (a)	19.8	110	26
m. v-nigra Pacific Eider	5 (c)	21.4	100	25
spectabilis King Eider	1	21.5	73	23
fischeri Spectacled Eider	5	18.4 (26.0)	73	24
Aythyini				
Netta				
rufina Red-crested Pochard	1	7.7	56	27
	7 (a)	10.7 (16.5)	54	27
peposaca Rosybill	2 (a)	15.8 (14.9)	54	28
Aythya				
valisineria Canvasback	2	15.9 (2.8)	68	24
nyroca Ferruginous Duck	1	8.4	43	26
baeri Baer's Pochard	2	4.7 (47.2)	43	27
americana Redhead	1 (a)	13.9	65	24
novae-seelandiae New Zealand Scaup	4	14.2 (49.9)	63	28
	4 (a)	10.5 (15.6)	64	26
fuligula Tufted Duck	8	9.1 (18.7)	56	24
affinis Lesser Scaup	8	8.0 (41.4)	51	24
marila mariloides Pacific Greater Scaup	1	13.7	67	24
Cairinini				
Calonetta				
leucophrys Ringed Teal	20	5.6 (35.4)	32	27
	10 (a)	6.1 (28.7)	32	23
Chenonetta				
jubata Australian Wood Duck	1	7.1	54	28
Aix				
galericulata Mandarin	8	4.4 (40.0)	41	29
	4 (a)	8.0 (15.5)	43	29
	2 (b)	3.7	27	29
sponsa North American Wood Duck	1	3.9	44	30
	5 (c)	8.4	43	30
	10 (b)	5.7	44	30
	10 (b)	6.0	43	30
Sarkidiornis				
m. melanotos Comb Duck	10	8.3 (9.6)	66	30
Cairina				
moschata Muscovy Duck	9	11.9 (18.1)	74	35
	4 (c)	12.3	80	35
scutulata White-winged Wood Duck	12	19.9 (28.2)	72	34
	1 (a)	22.8	99	30
Mergini				
Bucephala				
islandica Barrow's Goldeneye	9	8.6 (24.5)	70	32
	6 (a)	11.4 (8.9)	67	32
c. clangula Goldeneye	8	10.6 (28.0)	57	30
	6 (a)	10.6 (10.2)	64	30
Mergus				
albellus Smew	14	9.1 (16.6)	42	28
cucullatus Hooded Merganser	5	7.4 (51.4)	60	32
	5 (a)	8.3 (28.8)	55	33
	5 (b)	6.5	50	31

Table 1 continued.

Species	No.	GH2O (mg/day/torr)	W (gm)	I (day)
s. serrator Red-breasted Merganser	6	5.7 (14.0)	72	32
	10 (b)	6.1	66	29
m. merganser Goosander	4 (a)	14.9 (13.8)	69	32
Oxyurini				
Oxyura				
leucocephala White-headed Duck	3	19.3 (26.0)	96	25
	5 (a)	20.9 (18.1)	92	22
jamaicensis North American Ruddy Duck	11	20.1 (36.5)	73	24
	9 (a)	20.3 (9.4)	74	21
vittata Argentine Ruddy Duck	3 (a)	22.7 (13.4)	87	21
maccoa African Maccoa Duck	3	24.2 (8.1)	96	26
Biziura				
lobata Musk Duck	1	21.8	128	?
Heteronetta				
atricapilla Black-headed Duck	2	18.7 (22.1)	60	21
Phoenicopteridae				
Phoenicoparrus				
andinus Andean Flamingo	1	21.2	c. 29	c.29

? = Data unavailable.

Data from this study and also: a = Hoyt *et al.* (1979), b = K. R. Morgan, unpublished data quoted in Hoyt *et al.* (1979); c = Ar & Rahn (1978); d = Snyder *et al.* (1982).

temperature of 37°C, 12% fresh egg weight would then be lost during the incubation period up until pipping. The nest humidity of only a few Anatidae has been measured (Table 3). It is noteworthy, however, that these reported values are similar to those predicted in Table 2.

It is evident from Table 2 that the estimated relative humidity for an artificial incubator set at 37°C covers a broad spectrum, viz 22–70% R.H. With most of the Anatidae eggs, 20–50% R.H. would assure the required 12% loss in egg weight during incubation. The eggs of the Whistling Ducks (Dendrocygnini) and the White-winged Wood Duck *Cairina scutulata,* however, appear to require incubator humidities of around 60% and 70% R.H. respectively. The Red-breasted Merganser *Mergus s. serrator,* on the other hand, cannot lose 12% of its fresh egg weight even with an incubator humidity of 0% R.H.

Most of these suggested settings are much less than the 70% R.H. commonly used in artificial incubation. Moreover, our results suggest that several incubators set at different humidities will be required to incubate successfully the range of Anatidae eggs. There would appear to be a need for an improvement in incubator design, because the incubators used in aviculture do not permit easy maintenance of a defined humidity.

It should also be noted that eggs that require low incubator humidities also require higher ventilation rates, particularly just prior to pipping. Such eggs have a low G_{H_2O}, and therefore a low G_{O_2} and G_{CO_2}. To ensure sufficient oxygen flow into the egg to meet the embryo's metabolic demand, and rapid removal from the egg of carbon dioxide to prevent asphyxiation, P_{O_2} and P_{CO_2} must be increased (equation 3). This can be achieved by increasing incubator ventilation. Porosity may be so low in certain eggs that the embryo's requirements at the late stage of incubation will not be met even with increased ventilation.

The coefficients of variation for G_{H_2O} within a species can be large (Table 1). Therefore in instances where it is vital to maximise a hatch – as in the case of the eggs of rare wildfowl – it would be preferable to determine the

Table 2. Estimated artificial incubator humidities for 34 species of Anatidae.

Species	No.	G_{H_2O} (mg/day/torr)	M_{H_2O} (mg/day)	Incubator humidity P (torr)	RH%
Cairina scutulata	13	20.1	280	33.1	70.3
Dendrocygna arborea	15	14.3	240	30.3	64.4
Dendrocygna bicolor	27	15.0	266	29.3	62.2
Dendrocygna autumnalis	10	11.6	214	28.6	60.8
Anas p. platyrhynchos	15	13.7	259	28.2	59.9
Oxyura j. jamaicensis	20	20.2	407	26.9	57.1
Dendrocygna viduata	9	8.4	180	25.6	54.4
Mergus albellus	14	9.1	202	24.9	52.9
Cairina moschata	13	11.8	278	23.5	49.9
Aythya novae-seelandiae	8	12.4	296	23.2	49.3
Bucephala clangula	14	10.6	253	23.2	49.3
Anas platyrhynchos diazi	10	12.0	290	22.9	48.7
Anser erythropus	10	21.9	545	22.2	47.2
Anas gibberifrons gracilis	17	7.7	195	21.7	46.1
Oxyura leucocephala	8	20.3	524	21.3	45.3
Neochen jubatus	8	10.7	280	20.9	44.4
Anser canagicus	13	25.4	670	20.7	44.0
Anser fabalis	11	26.5	701	20.6	43.8
Tadorna tadorna	8	13.1	347	20.6	43.8
Somateria m. mollissima	9	21.2	562	20.6	43.8
Netta rufina	8	10.3	280	19.9	42.3
Calonetta leucophrys	30	5.8	160	19.5	41.4
Anser anser (domestic)	11	27.7	816	17.6	37.4
Bucephala islandica	15	9.7	290	17.2	36.5
Branta leucopsis	22	19.7	597	16.8	35.7
Tadorna variegata	8	13.0	404	16.0	34.0
Aix sponsa	26	6.3	196	16.0	34.0
Anas versicolor puna	11	7.6	239	15.6	33.1
Anas v. versicolor	11	5.7	181	15.3	32.5
Mergus cucullatus	15	7.4	244	14.1	30.0
Aythya fuligula	8	9.1	320	11.9	25.3
Sarkidiornis m. melanotos	10	8.3	293	11.8	25.1
Aix galericulata	14	5.3	189	11.4	24.2
Aythya affinis	8	8.0	291	10.7	22.7

M_{H_2O} required for the egg to lose 12% of its fresh egg weight (equation 4).

Table 3. Measured humidity of Anatidae nests.

Species	No.	Ref.	Method	Nest humidity (torr)
Cygnus atratus	3	1	A	22.4
c. cygnus	1	1	A	32.9
Anser caerulescens	1	3	B	24.2
anser	1	3	B	22.3
Branta leucopsis	3	1	A	18.2
Alopochen aegyptiacus	1	3	B	19.2
Anas p. platyrhynchos	1	2	B	26.7
	1	3	B	17.4
Somateria m. mollissima	1	2	B	23.6
Aythya novae-seelandiae	1	2	B	15.3
Oxyura leucocephala	2	2	B	21.5
vittata	1	2	B	26.0

Methods: A = electronic measurement; B = egg hygrometry.
References: 1 = Howey (1982); 2 = French (unpublished observations); 3 = Rahn *et al.* (1977).

required humidity for each egg, rather than taking the values cited in this paper. Tullett (1981) for this purpose used eggs with a known G_{H_2O}) to establish the G_{H_2O} of other eggs. The G_{H_2O} of the 'calibrated' egg — this can be any egg - can be determined by the methods described above. The 'calibrated' egg is then simply incubated with the other of unknown G_{H_2O} and weight loss of both recorded daily. The unknown G_{H_2O} can be calculated, viz:

$$\frac{\dot{M}_{H_2O}\ \text{(calibrated egg)}}{G_{H_2O}\ \text{(calibrated egg)}} = \frac{\dot{M}_{H_2O}\ \text{(unknown egg)}}{G_{H_2O}\ \text{(unknown egg)}}$$

The daily weighings need to be repeated until a constant G_{H_2O} is calculated, normally after 2-3 days. The only expensive equipment required is a balance, accurate to 0.01 grams for small eggs ($<$50 grams). With less accurate balances, it may be sufficient to weigh the whole clutch and determine the mean daily egg-weight loss. This would be a reasonably accurate method as G_{H_2O} varies less within a clutch than between clutches (Sotherland *et al.* 1979).

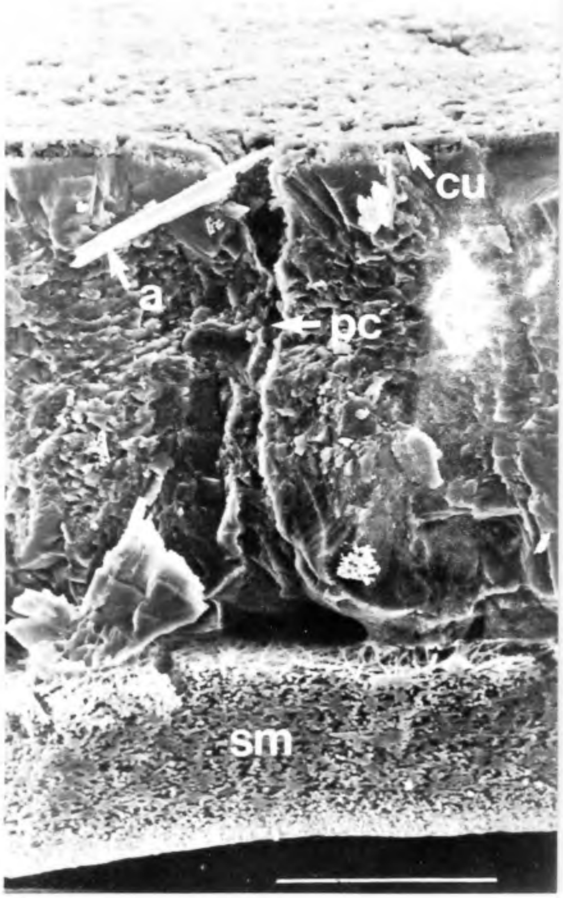
The eggs of the Red-breasted Merganser deserve especial mention. In this study as well as that of K. R. Morgan (unpublished observations), their G_{H_2O} was very low (Table 1), and even zero R.H. would not give the required 12% loss. Red-breasted Merganser eggs used in this study were unincubated and there is some evidence that the G_{H_2O} of unincubated Anatidae eggs is lower than incubated ones (Prof. H. Rahn, pers. com.). It is not known where the eggs used by K. R. Morgan were obtained nor whether or not they were incubated. Passerine eggshells have been shown to increase their G_{H_2O} at the onset of incubation (Carey 1979), but the evidence for this change in G_{H_2O} in Anatidae eggs is tentative, and needs further study. If shown to be true, it will dictate that G_{H_2O} should be determined after the onset of incubation.

Several practices in aviculture may well need to be reconsidered. The aim ought to be to ensure that captive breeding birds are not subjected to selection pressures such that there is a marked change in the G_{H_2O} of the eggshell. This would cause a progressive reduction in hatchability. Also adjusting incubator conditions to favour those eggs with abnormal shell formation would result in unsatisfactory eggs or young for re-establishment of the species in the wild. Measurement of the G_{H_2O} of eggs collected in the wild ought to be determined before progeny are introduced into bird collections, and the incubator conditions adjusted to maintain this value, involving routine checks of G_{H_2O}.

Acknowledgements

It is a pleasure to thank Sir Peter Scott, Professor G. V. T. Matthews and M. Ounsted of the Wildfowl Trust, Slimbridge, for the use of the Trust's facilities, and T. Richardson and the ground staff for the eggs. Professor G. V. T. Matthews and M. Ounsted also made many helpful comments about this paper for which we are grateful. We would also like to thank the Science and Education Research Council for

Figure 1. Radial fracture of a Pink-eared Duck *Malacorhynchus membranaceus* eggshell showing respiratory pore; pc = pore canal, cu = cuiticle, sm = shell membrane, a = artifact, bar = 100µm. Electron micrograph taken on the JOEL 35C SEM.



funding this work and N. Sparks for the micrograph.

Summary

The humidity setting for an artificial incubator for the eggs of most avian species can be assessed by measuring the water vapour conductance (GH_2O) of the eggshell. This study reports the GH_2O from 350 eggs of 76 species of Anatidae and 1 species of Phoenicopteridae. These data, combined with GH_2O of Anatidae eggs reported in the literature, were used to estimate the required incubator humidity setting for 34 Anatidae species. Techniques for measuring eggshell GH_2O in a hatchery are proposed, and the implications of GH_2O for avicultural practice are discussed.

References

Ar, A., Paganelli, C. V., Reeves, R. B., Greene, D. G. & Rahn, H. 1974. The avian egg: water vapour conductance, shell thickness and functional pore area. *Condor* 76: 153-8.

Ar, A. & Rahn, H. 1978. Interdependence of gas conductance, incubation length and weight of the avian egg. Pp 227-236 in Piiper, J. (ed.). *Respiratory function in birds, adult and embryonic.* New York: Springer-Verlag.

Calder, W. A. III 1978. The kiwi: a case of compensating divergences from allometric predictions. Pp 239-242 in Piiper, J. (ed.). *Respiratory function in birds, adult and embryonic.* New York: Springer-Verlag.

Carey, C. 1979. Increase in conductance to water vapour during incubation in eggs of two avian species. *J. of Exp. Zool.* 209: 181-6.

Drent, R. H. 1975. Incubation. Pp 333-420 in: Farner, D. S. & King, J. R. (eds.). *Avian Biology.* Vol. 5. New York: Academic Press.

Howey, P. W. 1982. A radio telemetric study of the avian nest microclimate. Ph.D. Thesis. University of Bath.

Howey, P. W., Board, R. G. & Kear, J. 1977. A pulse-position-modulated multichannel radio telemetry system for the study of the avian nest microclimate. *Biotelemetry* 4: 169-80.

Hoyt, D. F., Board, R. G., Rahn, H. & Paganelli, C. V. 1979. The eggs of the Anatidae: Conductance, pore structure and metabolism. *Physiol. Zool.* 52: 438-50.

Lundy, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hen's egg. Pp 143-176 in: Carter, T. C. & Freeman, B. M. (eds.). *The fertility and hatchability of the hen's egg.* Edinburgh: Oliver & Boyd.

Rahn, H., Ackerman, R. A. & Paganelli, C. V. 1977. Humidity in the avian nest and egg water loss during incubation. *Physiol. Zool.* 50: 269-83.

Rahn, H. & Ar, A. 1974. The avian egg: incubation time and water loss. *Condor* 76: 147-52.

Rahn, H. & Paganelli, C. V. 1981. *Gas exchange in the avian egg.* Buffalo: State University of New York.

Robertson, I. S. 1961a. Studies on the effects of humidity on the hatchability of the hen's egg. I. The determination of optimum humidity. *J. of Agric. Sci., Cambs.* 57: 185-4.

Robertson, I. S. 1961b. Studies on the effects of humidity on the hatchability of the hen's egg. II. A comparison of hatchability, weight loss and embryonic growth in eggs incubated at 40 and 70% R. H. *J. of Agric. Sci., Cambs.* 57: 195-8.

Romanoff, A. L. & Romanoff, A. J. 1949. *The avian egg.* New York: John Wiley & Sons.

Seymour, R. S. & Ackerman, R. A. 1980. Adaptions to underground nesting in birds and reptiles. *Amer. Zool.* 20: 437-47.

Seymour, R. S. & Rahn, H. 1978. Gas conductance in the eggshell of the mound-building brush turkey. Pp 243-246 in Piiper, J. (ed.). *Respiratory function in birds, adult and embryonic.* New York: Springer-Verlag.

Snyder, G. K., Black, C. P. & Birchard, G. F. 1982. Development and metabolism during hypoxia in embryos of high altitude *Anser indicus* versus sea level *Branta canadensis* geese. *Physiol. Zool.* 55: 113-23.

Sotherland, P. R., Packard, G. C. & Taigen, T. L. 1979. Permiability of magpie and blackbird eggshells to water vapour: variation among and within nests of a single population. *Auk* 96: 192-5.

Tullett, S. G. 1981. Theoretical and practical aspects of eggshell porosity. *Turkey* 29: 24-28.

Unwin, D. M. 1980. *Microclimate measurement for ecologists.* London: Academic Press.

Wangensteen, O. D. & Rahn, H. 1970/71. Respiratory gas exchange by the avian embryo. *Respir. Physiol.* 11: 31-45.

Whittow, G. C. 1980. Physiological and ecological correlates of prolonged incubation in sea birds. *Amer. Zool.* 20: 427-436.

N. A. French and **R. G. Board**, School of Biological Sciences, University of Bath, Bath, BA2 7AY.