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WATER LOSS FROM PIPPED WEDGE-TAILED SHEARWATER EGGS

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ABSTRACT.—The sequence of events during the prolonged pipping process in the Wedge-tailed Shearwater (*Puffinus pacificus*) was chronicled. The initial event, a series of star-fractures in the shell, occurred five to six days before the chick hatched. The daily rate of water loss from pipped eggs was considerably greater than that from unpipped eggs; the highest water loss (858.4 mg/day) occurred in eggs with a distinct pip-hole. It was estimated that approximately 16% of the water loss from eggs with a pip-hole could be attributed to embryonic pulmonary ventilation. Comparison with three other species of procellariiform sea birds with a seven-fold range of egg mass, revealed that the total water loss from the egg over the entire incubation period varied from 16.1 to 18.6% of the fresh egg mass. The main difference between the four species lay in the way in which the water loss was divided between the pre-pipping period and the period between the initiation of pipping and hatching.

The initial event in the pipping process of the eggs of many species of birds is the penetration, by the embryo's beak, of the air cell at the blunt pole of the egg, an event that has been termed "internal pipping" (Ar et al. 1980). Internal pipping allows the embryo to rebreathe the air in the aircell but it has little effect on the water loss from the egg, because the integrity of the egg shell, which presents the main barrier to the diffusion of water vapor out of the egg (Paganelli 1980), is intact. Following internal pipping, a series of star-fractures is made in the shell, by the embryo, and, subsequently, a distinct hole—the "pip-hole"— is made in the shell. Both of these events are likely to result in an increased rate of water loss from the egg (Whittow 1980), because the water loss is then no longer limited by the number and size of the minute pores in the shell, through which gases diffuse.

In the eggs of the Wedge-tailed Shearwater (*Puffinus pacificus*) the sequence of events during pipping differs markedly from that just described. In this species, the initial event in the pipping process is a series of star-fractures in the shell (Ackerman et al. 1980), an event that we have called "external pipping" (Grant et al. 1982a). In addition, the duration of the pipping process—from the initial star-fractures in the shell, to the hatching of the chick—is relatively long (Ackerman et al. 1980, Whittow 1980). It seemed likely, therefore, that a substantial fraction of the total water loss from the egg of the Wedge-tailed Shearwater might occur during the pipped phase of incubation. We conducted a study to document the sequence of events during pipping and to measure directly the water loss during the pip-to-hatch period. An ancillary objective was to estimate the contribution of embryonic pulmonary ventilation to the water loss during this period.

PROCEDURES AND METHODS

Observations in the field were made on Manana Island, a small island off the main island of Oahu, Hawaii. Eggs of known age were carefully examined on alternate days in late July and August 1979, in order to chronicle the events during pipping in naturally-incubated eggs. Internally-pipped eggs were identified by "peeping" and/or breathing sounds made by the chick, aided by auscultation with a bell stethoscope. The mass loss of externally-pipped eggs was also measured on Manana; the eggs were weighed to 0.01 g at intervals of 46.9–72.6 h on an Ohaus balance (model 1010-10).

Other shearwater eggs were collected and incubated in the laboratory at 36°C (relative humidity 40%). The eggs were four to five weeks old when first placed in the incubator; the eggs were turned twice daily before external pipping. The artificially incubated eggs were weighed periodically to measure the pre-pipping daily water loss (Ackerman et al. 1980). After the initial star-fracture of the shell had occurred, the eggs were weighed daily.

The respiratory water loss ($\dot{m}_{H_2O}$, g/h) from the embryo after internal pipping was calculated from the following equation:

$$\dot{m}_{H_2O} = \dot{V}_E (e_{ex} - \emptyset\, e_{in})$$

$\dot{V}_E$ = mean pulmonary ventilation (l/h) reported for the shearwater's embryo (Pettit and Whittow 1982)

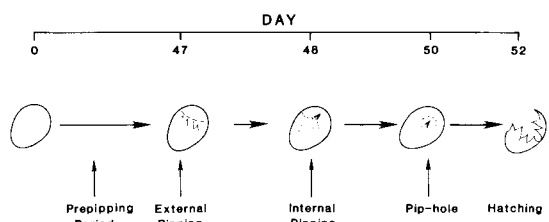e_{ex} = water vapor content of expired air (g/l) derived from

FIGURE 1. Sequence of events during the pipping process in the egg of Wedge-tailed Sherawater.

TABLE 1. Duration of the phases of pipping, and water loss before and after pipping, in naturally and artificially incubated eggs of the Wedge-tailed Shearwater. The variation is the standard deviation; the numbers in parentheses are the number of observations.

		Manana Is.	Laboratory
Time intervals (days)	External pipping–hatch	5.6 ± 1.2 (27)	4.5 ± 0.8 (20)
	External pipping–pip-hole	3.3 ± 1.2 (27)	2.3 ± 0.5 (20)
	Pip-hole–hatch	2.2 ± 0.8 (20)	2.4 ± 0.6 (24)
	Internal pipping–hatch	4.2 ± 0.9 (11)	4.0 ± 1.0 (6)
	Internal pipping–pip-hole	2.1 ± 0.4 (8)	1.5 ± 0.6 (6)
Water loss (mg/day)	Pre-pipping	154.6 ± 33.5* (60)	170 ± 22 (38)
	Externally pipped eggs	490.6 ± 128.4 (19)	544.6 ± 118.1 (19)
	Eggs with pip-hole	—	858.4 ± 121.5 (15)

* Whittow et al. 1982.

the measured temperature of expired air at the nares (assumed to be saturated with water vapor)

$\emptyset$ = relative humidity of the air in the incubator/100

e_{in} = water vapor content of incubator air (inspired air) at 36°C, relative humidity 40% (g/l).

RESULTS

The sequence of pipping in the eggs of the Wedge-tailed Shearwater is shown in Figure 1. Forty-seven days after the egg was laid, the first of a series of star-fractures (external pipping) was made in the shell. One day later, the embryo penetrated the air cell with its beak, an event known as "internal pipping." Two days later, a distinct hole (pip-hole) was made in the shell, and two days after that, the embryo hatched. The exact duration of each phase of pipping, together with the water loss from the egg, prior to and during pipping, are presented in Table 1.

The water loss from unpipped eggs was significantly greater in the incubator than on Manana Island ($t = 2.75$; $0.01 > P > 0.002$). This was to be expected as the egg temperature was slightly higher (1°C) and the water-vapor pressure lower (1.77 torr) in the incubator than under natural conditions. However, in both the naturally incubated eggs ($t = 18.61$; $P < 0.001$) and in the artificially incubated eggs ($t = 18.83$; $P < 0.001$), the water loss was

significantly higher in eggs that were star-fractured than in those that were not pipped. In addition, the water loss from eggs with pip-holes was significantly greater ($t = 7.60$; $P < 0.001$) than that from star-fractured eggs. Eggs with pip-holes were not weighed under field conditions because the fragments of shell resulting from enlargement of the pip-hole could not be retrieved for weighing. The time periods for the different phases of pipping tended to be shorter, but not significantly so, in the laboratory than in naturally incubated eggs.

DISCUSSION

Using the data obtained in the laboratory (right-hand column in Table 1), it may be calculated that the total water loss from the egg during the entire incubation period was 11.388 g. Of this amount, 3.313 g (29.1%) was lost during the interval between external pipping and hatching. A similar calculation performed on the data obtained on Manana (left-hand column, Table 1), assuming that the water loss from eggs with pip-holes was the same as that observed in the laboratory, yielded a figure of 32.8% for the contribution of the external-pip-to-hatch interval. In Table 2 data for the water loss during the interval between external pipping and hatching are presented for four species of Procellariiformes. The duration of the interval between

TABLE 2. Water loss from pipped eggs of four species of Procellariiformes.

	Fresh egg mass (g)	External pipping–hatching interval as % of total incubation	Water loss during the interval between external pipping–hatching		Total water loss during incubation as % of fresh egg mass	Reference
			As % of total water loss	As % of fresh egg mass		
Bonin Petrel (Pterodroma hypoleuca)	39.20	12.1	34.9	6.5	18.6	Grant et al. 1982a
Wedge-tailed Shearwater (Puffinus pacificus)	60.04	9.2	29.0	5.0	17.2	Ackerman et al. 1980; Whittow et al. 1982
Laysan Albatross (Diomedea immutabilis)	284.8	4.9	8.8	1.4	16.0	Grant et al. 1982b
Black-footed Albatross (Diomedea nigripes)	304.9	5.6	11.1	1.8	16.1	Grant et al. 1982b

external pipping and hatching is a greater percentage of the total incubation period for the smaller eggs. The total water loss during this interval is also a greater percentage of the total water loss over the entire incubation period, in the smaller eggs. These results are a corollary to a previous report that the duration of the pre-pipping phase of incubation, and the water loss during this phase, tend to be relatively less in the smaller procellariiform eggs than in the larger ones (Whittow et al. 1982). Table 2 also reveals that the total water loss over the entire incubation period tends to be relatively greater in the smaller eggs. It is, in fact, likely that the water loss from the Bonin Petrel eggs has been somewhat underestimated because Grant et al. (1982a) did not obtain data for water loss from eggs with a pip-hole. Nevertheless, this consideration should not alter the main conclusion to be drawn from Table 2 viz. that, over a range of egg size of almost eight-fold, the main variation in water loss from the eggs consists of a change in the division of water loss between the pre-pipping period on the one hand, and the period between external pipping (star-fracture of the shell) and hatching, on the other.

Ar and Rahn (1980) reported that the mean paranatal water loss in a variety of species was "about one quarter of the total calculated water loss." They used Visschedijk's (1962) definition of the paranatal period: "between internal pipping . . . and hatching." Ar and Rahn (1980) assumed that "Within this period, external pipping designates the beginning of the hatching process." Unfortunately, this is not the case in the Wedge-tailed Shearwater, or in many other species in which external pipping precedes internal pipping. In addition, Ar and Rahn (1980) calculated paranatal water loss in such a way as to exclude the water loss by simple diffusion during this period. The *total* water loss during the paranatal period must therefore have been greater than the paranatal water loss as defined by Ar and Rahn (1980).

It is clear from Table 1 that external pipping results in an increased water loss from the egg and that the production of a pip-hole results in a further increase in water loss. Using a value of 7.09 ml/min for the respiratory minute volume of embryos in eggs with pip-holes (Pettit and Whittow 1982; Table 2), a water content of inspired air of 0.017 g/l (air temp. = 36°C; relative humidity = 40%) and a water content of expired air of 0.030 g/l (measured expired air temp. = 30°C; saturated with water vapor), it was calculated that the respiratory water loss, under laboratory conditions, was 0.133 g/day. The total water loss from eggs with pip-holes was 0.858 g/day (Table 1). Therefore the respiratory water loss represented 15.5% of the total water loss. A maximal value for respiratory water loss, assuming expired air to be at 36°C and saturated with water vapor, was calculated to be 29.7% of the total water loss from eggs with pip-holes. Therefore, even at this late stage of development, most of the water loss from the egg was by way of extrapulmonary pathways.

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VARIATION IN THE EGG MARKINGS OF THE BROWN-HEADED COWBIRD

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Previous studies of the parasitic Brown-headed Cowbird (*Molothrus ater*) have assumed that eggs from individual female cowbirds are consistent in their shape and pigmentation markings (Friedmann 1929, Walkinshaw 1949, McGeen and McGeen 1968, Elliott 1977). However, it has not been possible to attribute specific eggs to specific females in the wild because of difficulties in observing actual egg-laying (cf. Hann 1941). I collected four pairs of eggs known to have been laid by four different female cowbirds. I determined whether eggs from individual females are consistent in their appearance by testing the ability of human subjects to identify the four pairs from a random arrangement of the eight eggs.

During the breeding season (April–June) of 1981 I captured cowbirds in grain-baited traps on the grounds of the Rockefeller University Field Research Center in Millbrook, New York. The birds were color-banded, and fe-