

REGULATION OF WATER LOSS FROM BONIN PETREL (*PTERODROMA HYPOLEUCA*) EGGS

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ABSTRACT.—Burrow-nesting Bonin Petrels (*Pterodroma hypoleuca*) lay a single egg that represents 22% of their body mass; the mean incubation period is 48.7 days, almost twice as long as the value predicted on the basis of egg mass. In spite of the prolonged incubation, the total water loss from the egg represents only 13.7% of the fresh egg mass. This small amount of total water loss is achieved by reducing the daily water loss from the egg to 110 mg/day, which is accomplished by a decrease in both the water-vapor conductance of the shell ($5.2 \text{ mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$) and the egg temperature (33.8°C). The reduction in the water-vapor conductance is achieved by reducing the number of pores in the shell. The water-vapor pressure of the microenvironment of the incubated egg (18.1 torr) is similar to that of many other species. Received 23 February 1981, accepted 1 September 1981.

PROLONGED incubation in seabirds is associated with an array of adaptive physiological differences, including reduced daily water loss from the egg, decreased water-vapor conductance of the shell, and decreased, calculated total functional pore area (Whittow 1980). These differences appear to be related to a restriction of the amount of water that may be lost over the entire incubation period. Long incubation times are ubiquitous in procellariiform birds, and incubation times are relatively longer in relation to egg mass in the smaller members of the order (Ackerman et al. 1980, Whittow 1980, Rahn unpubl. data). It is reasonable to expect, therefore, that the adaptive differences observed in the Wedge-tailed Shearwater (*Puffinus pacificus*, Paganelli et al. 1980, Ackerman et al. unpubl. data) would be more pronounced in the smaller petrels. The present paper was prompted by the opportunity to test this expectation in the Bonin Petrel (*Pterodroma hypoleuca*), an abundant Pacific seabird that has been little studied. A small number of preliminary observations reported by Whittow (1980) suggest that the daily water loss from the eggs of the Bonin Petrel is considerably less than expected.

The incubation period, the rate of water loss from the egg during natural incubation, egg

and burrow temperatures, nest and ambient vapor pressures, water-vapor conductance, and the physical dimensions of the egg, egg-shell, and its pores were determined. The humidity and thermal environment of the nest and egg were also studied.

MATERIALS AND METHODS

The birds were studied on Sand Island, Midway Atoll ($28^\circ 13' \text{N}$, $177^\circ 23' \text{W}$) in the Northwestern Hawaiian Islands during the breeding season of the petrels, January–March, 1980 and 1981.

Bonin Petrels excavate burrows 0.6–3 m long, and they lay a single white egg in a well-lined nest (Fig. 1). The nest is in an enlarged nest chamber at the end of the burrow. We dug shafts 15–20 cm in diameter to the nest chamber, 0.3–1.3 m vertically below the surface. The shafts were covered with plywood, and the shaft cover was lifted daily until the egg was laid in each nest.

Eggs were weighed on the day of laying and periodically throughout incubation; a torsion balance (Model DWL5) was used, and the eggs were weighed to $\pm 0.01 \text{ g}$. Additional eggs were placed over silica gel in desiccators in the laboratory. The mass loss of these eggs was recorded daily for 5 days. A recording hygrothermograph placed adjacent to the desiccators facilitated the monitoring of the desiccator temperatures. The mean daily water loss divided by the saturation pressure of water vapor at the mean temperature recorded gave the water-vapor conductance, as described by Ar et al. (1974), in terms of $\text{mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$. Water-vapor conductance values were corrected to 25°C (Paganelli et al. 1978). Volume, density, and fresh egg mass for these same eggs

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Fig. 1. Bonin Petrel in nest chamber. Note the large amount of nest lining material. The bird is temporarily off the egg due to photographer's presence.

were determined as described by Rahn et al. (1976) and Morgan et al. (1978). Additional measurements of the physical dimensions were obtained as described by Paganelli et al. (1974). Pore numbers were determined by the method of Roudybush et al. (1980). The total functional pore area, A_p , and the mean radius of individual pores were calculated from the relationship proposed by Rahn et al. (1976).

Ambient water-vapor pressure in burrows near the incubating petrels was measured with silica gel-filled eggshell hygrometers (Rahn et al. 1977). Calibrated chicken (*Gallus gallus*) eggshell hygrometers were placed under the birds, in substitution for their eggs, so that nest water-vapor pressure could be monitored. Chicken-eggshell hygrometers were approximately the same size, shape, and color as Bonin Petrel eggs and were readily incubated by the petrels. Ambient water-vapor pressures 2 m above ground were obtained from the U.S. Navy Meteorological Station less than 1 km from our study site.

TABLE 1. Physical dimensions of the Bonin Petrel egg and shell ($n = 12$).

	Egg		Shell	
	\bar{x}	SE	\bar{x}	SE
Mass (g)	39.5	0.5	1.97	0.04
Volume (cm ³)	37.3	0.5	0.991	0.026
Density (g/cm ³)	1.060	0.001	1.99	0.02
Thickness (mm)			0.181	0.004
Area (cm ²)	55.1	0.5		
Length (mm)	50.5	0.4		
Width (mm)	37.9	0.2		

The temperature of incubated eggs was measured by inserting a thermocouple into the center of the egg within 15–30 s of removal from the nest. An artificial polystyrene egg, with a thermocouple attached to its upper surface, was pegged in a fixed position in the nest. The birds readily incubated these eggs, which provided information on the attentiveness of the bird to its egg. The temperatures were recorded continuously on calibrated linear chart recorders. Air temperatures in the burrows were recorded continuously over several days with thermocouples placed about 10 cm from the incubating petrel.

RESULTS

Physical dimensions of the eggs.—Fresh egg mass determined at the time of laying for 85 petrel eggs was $39.16 \text{ g} \pm 0.3 \text{ SE}$. The physical dimensions of 12 freshly laid eggs appear in Table 1.

Bonin Petrels without a palpable egg weighed $182 \text{ g} \pm 4 \text{ SE}$ ($n = 27$). Female petrels with a palpable, calcified egg in the shell gland weighed $192 \text{ g} \pm 5 \text{ SE}$ ($n = 6$) after subtracting the mean egg mass of 39 g. Thus, the egg amounted to approximately 22% ($39 \text{ g}/182 \text{ g}$) of her body mass. The proportion of the body cavity filled with a calcified egg is illustrated in Fig. 2.

Incubation period.—The incubation period averaged $48.7 \text{ days} \pm 0.4 \text{ SE}$ in 19 nests (range:



Fig. 2. X-ray of female Bonin Petrel with egg in the oviduct.

43–51 days); egg neglect rarely occurs in this species (Grant et al. in press). Incubation in excess of the normal range occurred in two nests where we substituted infertile chicken eggs for petrel eggs. Incubation continued through day 60 in both nests until we terminated the experiment on 24 March.

Water loss from the eggs.—Eggs from 35 nests were weighed at approximately 2-week intervals after laying, for 33 days. The rate of mass loss, \dot{M}_{H_2O} , increased during incubation, from a value of 94 mg/day \pm 3 SE during the first third of incubation to 124 mg/day \pm 4 SE during the final third. The overall mean over the entire incubation period was 110 mg/day \pm 3 SE. Water loss from the eggs increased further between star-fracturing of the shell (external pipping) and hatching. The average daily mass loss of 41 externally pipped (star-fractured without penetrating the air cell) eggs was 341 mg/day \pm 19 SE, and the average daily water loss of 38 internally pipped (beak inside air cell) and star-fractured eggs was 453 mg/day \pm 29 SE. The duration of the stage in which there was a distinct pip hole in the shell was less than 1 day, and the rate of water loss for one egg was 1,160 mg/day during this interval. A

pip hole was seen in only 9 out of 31 eggs examined specifically for the presence of a pip hole, however, and in these instances the pip hole was very small (Pettit et al. in press).

Water-vapor conductance and functional pore area.—In Table 2 are shown the values for water-vapor conductance, G_{H_2O} , and the total effective pore area, A_p . The mean number of pores per egg (N) was 4,159. Dividing A_p by N gives the mean functional area of each pore, P_A , and its radius.

Nest humidity and temperature.—The water-vapor pressure in the microenvironment of the incubated egg (nest vapor pressure) averaged 18.1 torr \pm 0.3 SE in 26 petrel nests. The water-vapor pressure in the burrow adjacent to an incubating bird averaged 14.9 torr \pm 0.3 SE in 10 burrows; the vapor pressure in 13 abandoned burrows averaged 14.0 torr \pm 0.4 SE. Vapor pressure on the surface of the ground averaged 10.7 torr \pm 0.6 SE ($n = 17$) during the period when burrow vapor pressures were recorded. Mean burrow temperature recorded between 31 January and 3 March was 17.0°C \pm 0.3 SE ($n =$ three burrows for a total of 268.5 h). Saturated vapor pressure at this temperature is 14.5 torr, which is similar to that (14.0) actually measured by hygrometry in the burrows. That the burrows are saturated with water vapor is also evident in data for the \dot{M}_{H_2O} of four deserted eggs. Three eggs exhibited no measurable change in mass over 11 days, while one egg averaged a daily mass loss of 16 mg/day over 5 days. The latter egg may have been warmed by petrels briefly during this time interval.

Egg temperature and brood patch area.—The mean incubated egg temperature of 5 eggs was 33.8°C \pm 0.2 SE. The brood patch areas measured in two birds were 8.96 and 8.52 cm².

DISCUSSION

Drent (1970) showed that the daily mass loss of eggs during natural incubation was proportional to the egg mass raised to the 0.74 power, and he provided evidence that the mass loss was essentially due to the loss of water vapor. Rahn and Ar (1974) suggested that the total mass loss during incubation, expressed as a fraction of the initial egg mass, was constant among species, and a recent review of 81 species showed an average value of 15.2% (Ar and Rahn 1980). Drent (1975), however, questioned whether this relationship would apply

TABLE 2. Water-vapor conductance (G_{H_2O}) and pore geometry of 12 Bonin Petrel eggs: L = shell thickness or pore length; Ap = functional pore area; N = number of pores; P_A = area of an average pore, and Radius = radius of an average pore.

	G_{H_2O} ($\text{mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$)	Pores				
		L (mm)	Ap (mm^2)	N	P_A (μm^2)	Radius (μ)
\bar{x}	5.2	0.181	0.420	4,159	103.1	5.7
SE	0.2	0.004	0.023	190	6.8	0.2

to members of the order Procellariiformes, which have unusually long incubation periods and which nest mainly in burrows.

Our mean value for the water loss of the Bonin Petrel egg was 110 mg/day. On the basis of egg mass alone, one would predict from the equation of Drent (1970; $\dot{M}_{H_2O} = 0.015W^{0.74}$) a daily water loss twice that observed, namely 226 mg/day. The predicted incubation period (I), based on the relationship $I = 12.03W^{0.217}$ (Rahn and Ar 1974), however, is 26.7 days, or nearly half of that actually measured in the Bonin Petrel. Multiplying the daily water loss by the incubation period of 48.7 days yields a total mass loss of 5.4 g or 13.7% of the initial egg mass. The calculated fractional mass loss does not include the increment in water loss between external pipping (star-fracturing) and hatching. Water loss during the external pipping to hatching interval amounts to 1.9 g in excess of the mean of 110 mg/day calculated for this portion of the incubation period. Thus, total water loss up to the point of hatching represents 1.9 g + 5.4 g/39.16 g or 18.6% of fresh egg mass. It is apparent that the longer the interval between external pipping and hatching, the greater will be the divergence of the total water loss from 15.2% calculated in the conventional manner (Rahn and Ar 1974).

The question then remains, by what means is the low daily rate of water loss prior to pipping accomplished? There are several means by which the rate of water loss can be reduced. Thus, the rate of daily water loss of eggs is dependent upon the following relationship (Rahn and Ar 1974):

$$\dot{M}_{H_2O} = \Delta P_{H_2O} \cdot G_{H_2O}, \quad (1)$$

where ΔP_{H_2O} = water vapor pressure difference between the contents of the egg and its microclimate, in torr, and G_{H_2O} = water-vapor conductance of the shell and outer shell-membrane, in $\text{mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$. The measured

water-vapor conductance averaged 5.2 $\text{mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$ (Table 2). The predicted G_{H_2O} for a 39.16-g egg ($G_{H_2O} = 0.384W^{0.814}$; Ar and Rahn 1978) was 7.6 $\text{mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$, or 46% greater than that actually measured. A similar reduction in water-vapor conductance has been reported for the 13-g eggs of the burrow-nesting Fork-tailed Storm-Petrel (*Oceanodroma furcata*, Vleck and Kenagy 1980). Thus, a reduction in the water-vapor conductance of the shell is partly responsible for the reduced daily water loss from the egg of the Bonin Petrel.

The decreased water-vapor conductance of Bonin Petrel eggs may be attributed to a 49% decrease in the total functional pore area below the predicted value calculated from the relationship $Ap = 9.2 \cdot 10^{-5} \cdot W^{1.236}$ (Ar et al. 1974). Equations predicting the number of pores do not adequately describe the number of pores ($N = 4,159$) counted in Bonin Petrel egg shells (Table 2). The relationship incorporating both egg mass (W) and incubation (I) length ($N = 3,520 W/I$, Rahn and Ar 1980) predicts 2,848 pores, while the relationship based on egg mass alone ($N = 1,449W^{0.420}$, Tullett and Board 1977) predicts 6,762 pores. What can be concluded is that in the Bonin Petrel, as in other seabirds with prolonged incubation, the total functional pore area is reduced mainly by a reduction in the number of pores (Whittow 1980).

The average difference in water-vapor pressure (ΔP_{H_2O}) for most species is 30 torr (Ar and Rahn 1978), while that for the Bonin Petrel, calculated from equation 1 above, is lower (21.2 torr) by 29%. The vapor pressure gradient is a function of vapor pressure within the egg (P_A) and that in the nest micro-climate (P_N):

$$\Delta P_{H_2O} = P_A - P_N. \quad (2)$$

Measured egg temperature was 33.8°C, which is equivalent to a saturated vapor pressure of 39.4 torr within the egg. The measured nest

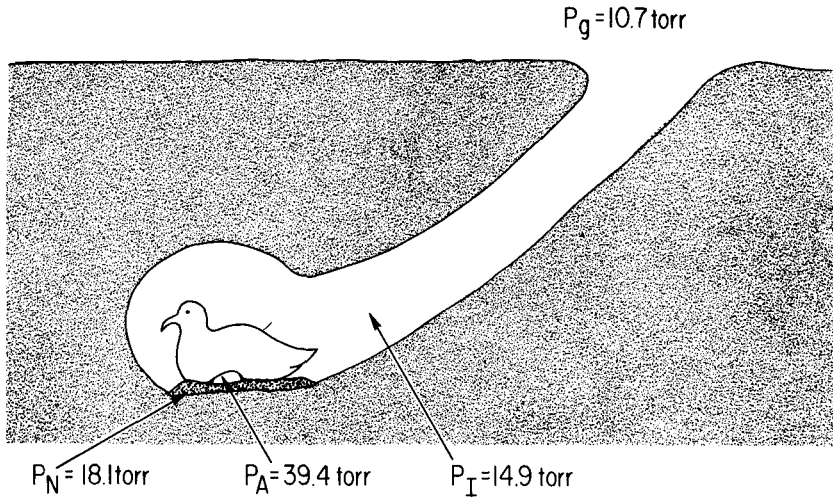


Fig. 3. Water-vapor pressure in the Bonin Petrel egg (P_A), around the incubated egg (P_N), in the burrow (P_I), and at the surface of the ground (P_g).

vapor pressure averaged 18.1 torr. Thus, the measured vapor-pressure gradient ($39.4 - 18.1 = 21.3$ torr) is similar to the calculated value (21.2 torr). Therefore, a reduced water-vapor pressure gradient between the egg and its environment also contributes to the low daily water loss from the egg.

As the vapor pressure of the egg microclimate is similar to that of most other birds (Rahn et al. 1977), the reduced value for ΔP_{H_2O} is the consequence of a low water-vapor pressure of the egg contents. The low water-vapor pressure inside the egg is, in turn, related to the low central egg temperature (33.8°C)—well below the average egg temperature for birds in general (36.2 ; Drent 1975) but close to that (32.5°C) reported in Leach's Storm-Petrel (*Oceanodroma leucorhoa*) by Ricklefs and Rahn (1979). Bonin Petrel egg temperatures were recorded in eggs less than 2 weeks old; therefore, metabolic heat production by the embryo was minimal.

The water-vapor pressure of the microenvironment of the petrel's incubated egg ($P_N = 18.1$ torr) is very close to that of many other birds (19 torr; Rahn et al. 1977). Therefore, the burrow environment has not resulted in a change in the water-vapor pressure of the nest. In fact, the difference in water-vapor pressure between the petrel's nest microenvironment (P_N ; 18.1 torr) and the air in the burrow (P_I ; 14.9 torr) is similar to that of the surface-nesting Heermann's Gull (*Larus heermanni*, Rahn and Dawson 1979). Figure 3 illustrates the sit-

uation for the Bonin Petrel, measured between January and early March 1980. In mid-March, however, both ambient and burrow temperatures increased significantly; the mean burrow temperature during this period was $20.8^\circ\text{C} \pm 0.2$ SE ($n = 11$). If the burrows remained saturated at these temperatures, the burrow water-vapor pressure would equal or exceed the nest vapor pressure measured earlier in the year. For water vapor to be lost from the nest under these conditions, nest vapor pressure would have to increase and remain above that in the burrows. Such an increase during days of high ambient vapor pressure has been observed in the surface-nesting albatrosses (Grant et al. unpubl. data).

Briefly summarized, egg temperature and thus vapor pressure within the egg are lower than average. As nest vapor pressure is similar to that of other birds, the vapor pressure gradient is below average. The incubation period is nearly twice as long as predicted, based on egg mass. Daily water loss and water-vapor conductance are nearly half of that predicted, based on egg mass. Reduction in conductance and daily water loss are functions of reductions in egg temperature, number of pores, and functional pore area.

Brood patch and central egg temperature recordings at five nests suggested that the incubating Bonin Petrel uncovered its egg twice each night on the average. The eggs were not uncovered during the day. The first central egg temperature decrease generally occurred be-

tween 2000 and 0120 (mean time was about 2200) and the second decrease occurred between 2230 and 0400 (mean time was about 0230). Intimate brood patch-egg contact was broken for varying lengths of time during these two temperature decreases, but it was sufficient to cause a mean central egg temperature decline of $1.6^{\circ}\text{C} \pm 0.3 \text{ SE}$ ($n = 11$) during the first off-egg period, followed by several hours of higher steady temperatures, and a $2.8^{\circ}\text{C} \pm 0.5 \text{ SE}$ ($n = 10$) decrease during the second off-egg period. The length of incubation shifts in this species averages 6.8 days (Grant et al. unpubl. data). The function of this incubation behavior is not known, but it may be associated with defecation (adults do not appear to defecate in the burrows during the incubation period), or other maintenance behaviors, and may secondarily ventilate the nest, removing water vapor (Rahn et al. 1976) and increasing the oxygen partial pressure in the vicinity of the egg (Pettit et al. in press).

Our measurements of the body mass of Bonin Petrels agree closely with those of Fisher (1961). Procellariiformes lay relatively large eggs in proportion to their body mass (Rahn et al. 1975). Smaller members of the order lay relatively larger eggs. For example, the egg mass/female body mass percentages for several species are: Wilson's Storm-Petrel (*Oceanites oceanicus*), 26% (Roberts 1940); Fork-tailed Storm-Petrel, 21% (Boersma et al. 1980); Bonin Petrel, 22% (this study); and Black-footed Albatross (*Diomedea nigripes*), 10% (Fisher 1969). As the smaller Procellariiformes have relatively more yolk in their eggs (Pettit et al. in press), the comparatively large egg reflects a greater investment in metabolic substrate to meet the greater energy requirements of incubation in petrels (Pettit et al. in press).

In summary, the incubation time of the Bonin Petrel is *relatively* longer than that of larger Procellariiformes. Thus, the measured/predicted incubation times are 1.82 in the Bonin Petrel (present data) and 1.79 and 1.6, respectively, in the larger shearwater and albatross (Whittow 1980). Associated with the relatively long incubation in the petrel are lower rates of daily water loss, lower water-vapor conductance of the shell, and lower egg temperatures.

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The sixth annual meeting of the **Colonial Waterbird Group** will be held 4–7 November 1982 in Washington, D.C. A symposium on the feeding biology of waterbirds is planned. Papers given at the meeting are eligible, after refereeing, for publication in *Colonial Waterbirds*. Anyone wishing to contribute to either the symposium (deadline **1 September**) or general session (deadline **15 September**) should contact **Dr. Michael Erwin, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708**. Information concerning registration can also be obtained from Dr. Erwin.