FACTORS AFFECTING EGG MASS LOSS IN THE PHOENIX PETREL ON CHRISTMAS ISLAND

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Abstract.—Field measurements revealed that the mass loss of naturally incubated Phoenix Petrel (*Pterodroma alba*) eggs was only 76.8% of the expected value for a procellariiform egg. The low mass loss could not be attributed to a low egg temperature, characteristic of many procellariiform eggs; egg temperature (37.3 C) was higher than expected, while the body temperature of incubating adult birds was 38.2 C. The body temperature—egg temperature difference (0.9 C) was the lowest reported for any bird. Laboratory measurements on the egg shells indicated that the low mass loss of the eggs could not be accounted for by a thick eggshell; it appeared to be related to a low porosity of the eggshell.

FACTORES QUE AFECTAN LA PÉRDIDA DE PESO EN LOS HUEVOS DE INDIVIDUOS DE *PTERODROMA ALBA*, EN LA ISLA CHRISTMAS

Sinopsis.—Datos de campo revelaron que la pérdida de peso de huevos incubados natural-mente por individuos de *Pterodroma alba* resultó ser el 76.8% de los valores esperados para un huevo de procelariforme. La baja pérdida de peso no puede ser atribuida a la baja temperatura de los huevos, típica de este grupo de aves. La temperatura de incubación resultó ser más alta de lo esperado (37.3 C), mientras que la temperatura del ave que in-cubaba fué de 38.2 C. La diferencia entre la temperatura del ave incubando y la del huevo (0.9 C) ha resultado ser la más baja informada para ave alguna. Medidas del grosor de los huevos indican que la baja perdida de peso no puede atribuirse al grosor de estos. La misma parece estar relacionada a la baja porosidad de los cascarones.

The Phoenix Petrel (*Pterodroma alba*) is a tropical procellariiform sea-bird that nests on small islands in the central Pacific Ocean (Warham 1990). It lays a single white egg on the surface of the ground (Murphy et al. 1954). Only fragmentary information on the incubation biology of the egg is available in the literature. Murphy and Pennoyer (1952) pub-lished the dimensions of eight Phoenix Petrel eggs, and Schreiber and Ashmole (1970) reported the incubation period to be 53 d. The present report stems from the opportunity to obtain additional data on Phoenix Petrel eggs. The emphasis of the study was to measure the mass loss of naturally incubated eggs and to relate the mass loss to other characteris-tics of the egg.

METHODS

Observations were made on Motu Tabu and Motu Upua islets in the lagoon of Christmas Island (1°59′N, 157°26′W). The dimensions of 31 eggs were measured with dial micrometer calipers that could be read to 0.025 mm. The mass loss of 20 naturally incubated, unpipped eggs was measured by weighing the eggs at intervals of 19.5–48.1 h on an Ohaus field balance (model 1010-10) at the nest site. The temperature of ten

other incubated eggs was determined by quickly removing the egg from the nest and inserting a fast-response, needle-thermistor probe (Yellow Springs Instrument Company, "YSI", no. 524) into the egg. This procedure required approximately 20 s. All egg temperatures were taken from the center of the egg and they were measured by connecting the thermistor lead to a YSI Telethermometer (model no.43 TK). The mass of 20 adult Phoenix Petrels was measured with an Ohaus spring balance (model 8011) graduated in divisions of 2 g. The stomach temperatures of 20 adult birds were measured with a YSI thermistor probe (no. 401) connected to the YSI Telethermometer. All measurements of stomach temperature were made on birds that were incubating their eggs. A record was kept of the sequence of events during pipping of the eggs. Some measurements were made on eggshells transported to the University of Hawaii in Honolulu. Shell thickness was measured with micrometer calipers equipped with a ball attachment on the spindle to fit the curvature of the shell. The smallest micrometer graduations were 0.025 mm; all measurements were made on eggshells that had been dried in the laboratory at the University of Hawaii. The number of pores in the shells was counted by the method described by Tyler (1953) and Roudybush et al. (1980). The measure of variation used in this report is one standard deviation (SD).

<div align="center">RESULTS AND DISCUSSION</div>

The egg measurements are presented in Table 1, together with the predicted values for procellariiform eggs based either on the mass of the freshly laid egg, or on the fresh-egg mass and the incubation period (Rahn and Whittow 1988).

Egg dimensions, body mass, and incubation period.—The mean dimensions (length = 5.606 cm; width = 4.254 cm) of eight eggs collected by Murphy and Pennoyer (1952) at Christmas Island and in the Tonga group, are very similar to the mean values shown in Table 1. The mean dimensions of the eggs may be used to obtain an estimate of the mass of the freshly laid eggs (Hoyt 1979). The mean value for fresh-egg mass so obtained is 54.94 g. The mean body mass of 20 adult birds measured in the present study is 259.4 g ± 28.1 (SD). Hence, the estimated fresh-egg mass is 21.2% of the adult mass—higher than the mean value of 15.8% for Procellariiformes (Rahn and Whittow 1988). The estimated mass of the freshly laid egg (54.94 g) may be used to predict an expected incubation period for a procellariiform bird (Rahn and Whittow 1988). The predicted value is 52.2 d, close to the incubation period (53 d) measured by Schreiber and Ashmole (1970).

Egg mass loss.—The fresh-egg mass and the incubation period may be used to predict the daily mass loss of the egg (Rahn and Whittow 1988). The measured value in unpipped eggs (Table 1) was only 76.8% of the predicted value (160.62 mg/d) for a procellariiform egg weighing 54.94 g with an incubation period of 53 days. The mass loss of the avian egg during incubation is due entirely to the loss of water vapor (Rahn and

TABLE 1. Measured and predicted values for Phoenix Petrel eggs (mean values ± 1 SD).
         Number of measurements in parentheses. Predictions are from Rahn and Whittow
         (1988) unless indicated otherwise.

	Measured	Predicted	Measured/Predicted × 100	P[d]
Egg length (cm)	5.771 ± 0.198 (31)	—	—	—
Egg width (cm)	4.168 ± 0.114 (31)	—	—	—
Daily water loss from unpipped eggs (mg/d)	123.34 ± 23.97 (20)	160.62	76.8	<0.001
Egg temperature (C)	37.28 ± 0.65 (10)	35.1[a]	—	—
Shell thickness (mm)	0.18 ± 0.01 (142)	0.27[b]	96.3	—
Outer shell membrane thickness (mm)	0.06 ± 0.01 (56)	—	—	—
Inner shell membrane thickness (mm)	0.02 ± 0.01 (7)	—	—	—
Shell pore density (pores/cm²)	55.1 ± 4.5 (8)	110.8[c]	49.7	<0.001
Number of pores (pores/egg)	3778.8	4283.4	88.2	—

[a] Rahn (1991).
[b] Shell and shell membranes.
[c] Tullet and Board (1977).
[d] Statistical significance of differences between measured and predicted values.

Ar 1974). One of the determinants of the water loss from the egg is the
egg temperature, which defines the water-vapor pressure of the contents
of the egg (Rahn et al. 1977). The higher the water-vapor pressure of the
egg, the greater the rate of water loss.

  Egg and body temperature.—The mean egg temperature of ten Phoenix
Petrel eggs (37.3 C, Table 1) was higher than expected; the mean egg
temperature of eight species of Procellariiformes was 35.1 C, according
to Rahn (1971). Although environmental temperatures were not mea-
sured in this study, the climate of Christmas Island is equatorial (Gallagh-
er 1960), and it seems possible that the high egg temperature was related
to the hot conditions at the nesting site, as well as to the fact that the
Phoenix Petrel lays its egg on the surface of the ground. It is unlikely
that the relatively high egg temperature reflects a high body temperature
of the incubating adult bird because the measured deep-body tempera-
ture of 20 incubating adult Phoenix Petrels was 38.2 C ± 0.56. This is
slightly lower than the mean body temperature (38.78 C) of 31 species
of Procellariiformes (Warham 1971). Noteworthy is the small temperature
difference (0.9 C) between the incubating bird (38.2 C) and the egg (37.3
C)—the smallest bird-egg temperature difference reported for any bird
(Rahn 1991). This small difference may reflect the warm conditions at
the nest site, but it also suggests a tight coupling between the bird and
its egg, in the Phoenix Petrel. Support for the latter possibility comes

from Gallagher's (1960) statement ". . . the parent bird sits very close." The close coupling of egg and body temperature may help to prevent over-heating of the egg.

Eggshell thickness and porosity.—Two characteristics of the eggshell may have a profound effect on the mass loss of the egg. The thickness of the eggshell defines the length of the diffusion pathway along which water leaves the egg (Ar et al. 1974). The thicker the shell, the lower the water loss (and thus mass loss) of the egg. The measured thickness of the shell (plus the shell membranes) is 0.26 mm (Table 1); this is very close to the predicted value (0.27 mm) for a procellariiform egg weighing 54.94 g (Rahn and Whittow 1988).

Potentially more important than the thickness of the eggshell in limiting the water loss from the avian egg is the number of microscopic pores in the eggshell. Water vapor diffuses out of the egg through the pores; consequently, with fewer pores, there is reduced egg mass loss. The pore density of Phoenix Petrel eggs was only 49.7% of that of birds in general (Table 1; Tullet and Board 1977). The total number of pores in each egg may be calculated from the pore density if the total surface area of the eggshell is known. Shell surface areas were not measured in the present study but they may be calculated from the estimates of the mass of the freshly laid egg using the relationship reported by Paganelli et al. (1974). Multiplying this estimated mean surface area (68.58 cm^2) by the measured mean pore density (Table 1), yields a mean value (3778.8) for the total number of pores (Table 1). This value is considerably less than the predicted value (4283.4) for a procellariiform egg weighing 54.94 g with an incubation period of 53 d (Table 1). Thus, the proximate cause of the low rate of mass loss of the Phoenix Petrel egg appears to be a reduced porosity of the shell.

Sequence of events during pipping.—The initial event during pipping of the Phoenix Petrel egg is a star-fracture of the shell (external pipping). This is followed by the formation of a pip-hole in the shell and penetration of the aircell by the beak of the embryo (internal pipping). This sequence of events is similar to that in the congeneric Bonin Petrel (*Pterodroma hypoleuca*), another tropical petrel (Pettit et al. 1982). The initial star fracture of the shell, signalling the beginning of pipping, occurred 3.75 d before hatching. Hence, the duration of the pre-pipping period was 49.25 (53 − 3.75) d. In three Phoenix Petrel eggs, the mean duration of the pip-hole phase was 47.7 h. This is longer than the pip-hole phase in the Bonin Petrel.

CONCLUSIONS

It is interesting to speculate on the reasons for the low egg mass loss (in unpipped eggs) and low shell porosity in the Phoenix Petrel, even by procellariiform standards (Rahn and Whittow 1988). Both features are characteristic of seabirds with prolonged incubation (Whittow 1980, 1984). The incubation period of the Phoenix Petrel egg, however, is no longer than expected for a procellariiform egg of its size. The low egg

mass loss cannot be explained by the relatively high egg temperature: other things being equal, a high egg temperature implies a high water-vapor pressure inside the egg, and a high rate of water loss from the egg (Whittow 1984). A possible explanation may lie in the observations on pipping of the eggs. Egg mass loss is much greater from pipped than from unpipped eggs (Pettit and Whittow 1983), and it is greatest of all from eggs with a distinct pip hole. The pip-hole phase seems to be particularly long in the Phoenix Petrel egg and, although water loss from pipped eggs was not measured in the present study, it may be safely inferred that it is high during the pip-hole phase. It is conceivable that water loss from unpipped eggs is curtailed as a result of a low porosity, in order to compensate for a high mass loss from pipped eggs. Water loss from pipped eggs occurs largely through cracks and pip holes in the shell. The total water loss from eggs during incubation is closely regulated (Rahn and Ar 1974). Hence, unusually high mass loss from pipped eggs might have to be balanced by reduced mass loss in unpipped eggs. Some support for this contention comes from computation of the total mass loss of the egg before pipping. Multiplying the duration of the pre-pipping period (49.25 d) by the daily mass loss of the egg (Table 1) yields the total mass loss of the egg during the pre-pipping period (=6.074 g). This represents 11.0% of the mass of the freshly-laid egg (54.94 g) and it is lower than the corresponding figure for four other species of Procellariiformes (Whittow et al. 1982). Thus, as a working hypothesis, the total mass loss of the unpipped Phoenix Petrel egg is reduced to balance the relatively high mass loss of pipped eggs. Further field measurements of the mass loss of pipped Phoenix Petrel eggs will be needed to substantiate this.

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