WATER LOSS AND PIPPING SEQUENCE IN THE EGGS OF THE RED-TAILED TROPICBIRD (*PHAETHON RUBRICAUDA*)

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ABSTRACT.—Measured values for the water loss from unpipped eggs, the water-vapor conductance and functional pore area of the shell, and the number of pores in the shell were all lower than predictions based on fresh-egg mass. Predictive equations incorporating incubation period yielded closer approximations to measured values. The total water loss from the egg represented 12.9% of the mass of the freshly laid egg. The initial event in the pipping process was star-fracture of the shell, which occurred 3.5 days before hatching. It was followed by internal pipping and the formation of a pip-hole. The duration of the interval between star-fracture of the shell and hatching represented 8.0% of the total incubation period but accounted for 17.1% of the total water loss from the egg. *Received 5 July 1984, accepted 12 April 1985.*

THE Red-tailed Tropicbird (*Phaethon rubricauda*) is a tropical seabird that lays its single egg in a depression in the ground. The mean incubation period of the egg is 43.8 days (Fleet 1974), 47% longer than the value predicted on the basis of the mass of two freshly laid eggs (Ar and Rahn 1978). Prolonged incubation in seabirds is associated with a low rate of water loss from the unpipped eggs and a low water-vapor conductance of the shell (Whittow 1980, 1984). Data are not available for the water loss from Red-tailed Tropicbird eggs. The water-vapor conductance of the shells of two eggs was measured by Ar and Rahn (1978); the values appear to be low. The present note stems from the opportunity to measure the water loss from eggs of the Red-tailed Tropicbird, and to obtain additional information on the water-vapor conductance and other factors affecting water loss from the eggs. Special attention was paid to the water loss from pipped eggs, which in other species has been shown to amount to a significant fraction of the total water loss from the egg (Pettit and Whittow 1983).

METHODS

Studies were conducted in the Northwestern Hawaiian Islands on Tern Island, French Frigate Shoals (23°52′N, 166°17′W); Sand Island, Midway Atoll (28°13′N, 177°23′W); and Green Island, Kure Atoll (28°24′N, 178°18′W).

Water loss from unpipped eggs was determined by weighing the eggs at intervals of 49.2–115.5 h on an Ohaus 1010-10 balance. Some eggs were weighed on more than two occasions, resulting in a total of 44 determinations of water loss on 29 eggs. A careful study was made of the sequence of events during pipping in some of the eggs, and the mass loss of the pipped eggs also was recorded.

The temperatures of 6 eggs were measured with a Yellow Springs Instrument Company (YSI) needle-thermistor probe (model 524) inserted into the egg until its tip lay approximately in the center of the egg. The egg was removed rapidly from under the bird, and a temperature reading was obtained within 20 s. The thermistor probe was connected to a YSI Telethermometer (model 43TK). In an additional 10 eggs, the highest egg temperature was sought by moving the thermistor needle vertically and laterally from the center of the egg. In each instance, only one measurement of egg temperature was made on each egg.

The water-vapor conductance of the shell (G_{H_2O}) was measured in 12 eggs by the procedure described by Ar et al. (1974). The fresh-egg mass of 11 eggs was determined by filling the aircell with distilled water (Grant et al. 1982a). The volumes of 11 eggs were measured by weighing the eggs in air and while submerged in water (Morgan et al. 1978). Shell thickness was measured, on eggshells that had been dried, by means of a Starrett (model no. 230) micrometer calipers fitted with a ball attachment on the spindle to accommodate the curved surface of the eggshell. The shell mass of 6 eggs that had been dried in a desiccator was determined and the number of pores in the shell was counted by the method described by Rou-

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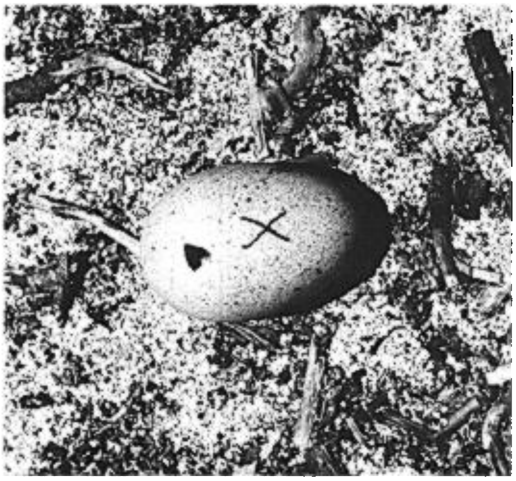

Fig. 1. Marked Red-tailed Tropicbird egg showing pip-hole. The egg was removed from the nest site for photography.

dybush et al. (1980). To arrive at the number of pores/egg, 120 fields, each 1.25 mm^2 in area, were counted in each egg and the number of pores/cm^2 multiplied by the surface area of the egg calculated from the fresh-egg mass (Tullett and Board 1977).

The dimensions of all eggs were measured by means of a dial calipers.

RESULTS

Pipping sequence.—The initial event in the pipping process was a series of star-fractures in the shell toward the blunt pole of the egg. This occurred 74 and 93 h before hatching in 2 eggs. In 3 other eggs the duration of the interval between the first star-fracture and hatching was determined to be in excess of 49, 70, and 70 h, although the total duration of the interval was not measured. The second event during pipping was penetration of the aircell by the embryo's beak, detected by the presence of "cheeping" (internal pipping) sounds from the egg. In 1 egg, internal pipping occurred 48 h before the chick hatched. A distinct pip-hole in the shell, through which the chick's beak could be seen, was observed in only 2 out of 6 eggs examined during the few days prior to hatching (Fig. 1). The pip-hole was evident 18.9 and 19.6 h prior to hatching in the two eggs.

TABLE 1. Egg dimensions for the Red-tailed Tropicbird. *n* = number of measurements.

	$\bar{x}$	SD	*n*
Fresh-egg mass (g)	71.56	6.36	11
Volume (ml)	66.29	5.81	11
Length (mm)	63.5	2.6	41
Width (mm)	44.5	1.4	41

TABLE 2. Mean water loss (mg/day) from the eggs of the Red-tailed Tropicbird. *n* = number of measurements.

	$\bar{x}$	SD	*n*
Unpipped	189.40	55.82	44
Unpipped/star-fractured[a]	319.69	126.55	9
Star-fractured	424.97	100.81	8
Star-fractured/pip-hole[b]	540.75	94.64	2

[a] Unpipped at the time of the first weighing and star-fractured when the second weighing was made.

[b] Star-fractured at the time of the first weighing; with a pip-hole when weighed on the second occasion.

Egg dimensions.—The fresh-egg mass together with data for the volume of the eggs and their linear dimensions are presented in Table 1.

Egg temperature.—The mean central temperature of 6 eggs was 36.0°C ± 1.0 SD. In 10 other eggs in which the highest egg temperature was recorded, the mean temperature was 36.7°C ± 0.4 SD.

Water loss from the eggs.—The mean daily water loss ($\dot{M}_{H_2O}$) from unpipped eggs was 189.4 mg/day (Table 2). The water loss from star-fractured eggs was greater, and the highest rate of water loss was from eggs with a pip-hole (Table 2).

Eggshell characteristics.—The properties of the eggshell that have a bearing on the water loss from the egg are presented in Table 3. The thickness of the inner shell membrane was 0.01 mm ± 0.01 SD ($n = 24$) and that of the outer membrane, 0.08 mm ± 0.03 SD ($n = 19$). The

TABLE 3. The measured water-vapor conductance (G_{H_2O}), thickness (L), mass (M_{sh}), and pore density (P_D) of the eggshells of the Red-tailed Tropicbird. *n* = number of measurements.

	$\bar{x}$	SD	*n*
G_{H_2O} (mg/day torr)	8.98	1.22	12
L[a] (mm)	0.31	0.02	78
M_{sh} (g)	5.6740	0.4395	6
P_D (pores/cm^2)	57.7	2.4	6[b]

[a] Excluding shell membrane.

[b] $n = 6$ eggs.

thickness of the shell plus that of the two shell membranes was 0.38 mm ± 0.02 SD ($n = 55$).

DISCUSSION

Fleet (1974) reported that "The hatching process, from pipping until the hatchling emerges, requires only a few hours." It seems imperative, in the light of the results of the present study, to make an important qualification of Fleet's statement. It has been shown here that the initial event in the pipping process (star-fracture of the shell) takes place 3-4 days before hatching. The discrepancy between the present observations and those made by Fleet probably arises from a different usage of the term "pipping." If, as seems likely from Fleet's report, pipping was identified by the presence of a pip-hole, then it is clear from both Fleet's paper and the present one that a pip-hole is formed less than 24 h before hatching. Nevertheless, the events that precede the formation of a pip-hole (star fracture/internal pipping) have a very important effect on gas exchange between the egg and its environment (Pettit and Whittow 1983, Whittow 1984), and their time relations should be documented in a complete description of the pipping process. In fact, the sequence of events during pipping in the Red-tailed Tropicbird, described in the present report, resembles that in the White-tailed Tropicbird (*Phaethon lepturus*; Stonehouse 1962), although the time intervals appear to be somewhat different in the two species.

Comparison (on the basis of fresh-egg mass) of measured values with values predicted for birds in general (Table 4) revealed that the daily rate of water loss from unpipped eggs was lower than predicted, primarily because the water-vapor conductance of the eggshell was low. The water-vapor conductance was low not because of a thick shell or small pore radius, but because there were fewer pores in the shell. The number of pores was even lower than predicted for seabirds. The mean central egg temperature, which determines the water-vapor pressure of the egg contents, was 1°C higher than that recorded in the Red-tailed Tropicbird by Howell and Bartholomew (1962) but close to the mean value for birds in general (Table 4). The water-vapor pressure of the nest microclimate was somewhat higher than predicted values (Table 4).

TABLE 4. Comparison of measured or calculated values with predicted values for the daily water loss from unpipped eggs ($\dot{M}_{H_2O}$), water-vapor conductance of the shell (G_{H_2O}), shell thickness (L), total functional pore area (A_p), total number of pores in the eggshell (N), pore area (P_a), pore radius (P_r), egg temperature (T_{egg}), and the water-vapor pressure of the nest microclimate ($P_{H_2O,nest}$).

	Measured	Predicted	(Measured/predicted) × 100
$\dot{M}_{H_2O}$ (mg/day)	189.4	331.4[a]	57.1
G_{H_2O} (mg/day torr)	8.98	12.42[b]	72.3
L (mm)	0.38	0.36[c]	105.6
A_p (mm^2)	1.63	2.01[b]	81.1
N (pores/egg)	4,074	8,958[d]	45.5
		5,632[e]	72.3
P_a (μm^2)	400.1	168.1[f]	238.0
		210.1[e]	190.4
P_r (μm)	11.3	8.2[e]	137.8
T_{egg} (°C)	36.0	35.6[a]	101.1
$P_{H_2O,nest}$ (torr)	23.5	19.0[b]	123.7
		20.8[g]	113.0

[a] Ar and Rahn 1980.
[b] Ar and Rahn 1978.
[c] Ar et al. 1974.
[d] Hoyt et al. 1979.
[e] Whittow 1984.
[f] Tullett and Board 1977.
[g] Walsberg 1980.

The incubation period of the Red-tailed Tropicbird (43.8 days, Fleet 1974) is 146.5% of the expected value for an egg weighing 71.56 g (Ar and Rahn 1978). Prolonged incubation is a common feature of tropical seabirds and, in previous analyses (Whittow 1980, 1984), many of the characteristics of tropical seabirds' eggs were related to their long incubation periods. Comparison of measured values with those derived from predictive equations, incorporating incubation period as well as the mass of the freshly laid egg, help to indicate the extent to which prolonged incubation contributes to deviations from predictions based solely on fresh-egg mass. Predictions incorporating the incubation period as well as the fresh-egg mass were closer to the measured values than were predictions based on egg mass alone (Table 5). Nevertheless, discrepancies still remained, particularly for the daily water loss from unpipped eggs. Changes in both the egg temperature and the water loss from the eggs, as incubation proceeds, may contribute to these discrepancies. Such changes are not known to occur in Red-tailed Tropicbirds, but they have

TABLE 5. Measured values, predicted values based on fresh-egg mass, and predicted values incorporating incubation period for the daily water loss from the egg ($\dot{M}_{H_2O}$), water-vapor conductance of the shell (G_{H_2O}), functional pore area (A_p), and number of pores in the shell (N) in the Red-tailed Tropicbird. M = fresh-egg mass (g), I = incubation period (days), L = shell thickness (mm).

		Predicted	
	Measured	Value based on fresh-egg mass	Value incorporating incubation period
$\dot{M}_{H_2O}$ (mg/day)	189.4	$\dot{M}_{H_2O} = 13.243\ M^{0.754} = 331.4$ (Ar and Rahn 1980)	$\dot{M}_{H_2O} = 151\ (M/I) = 246.7$ (Rahn and Ar 1980)
G_{H_2O} (mg/day torr)	8.98	$G_{H_2O} = 0.384\ M^{0.814} = 12.42$ (Ar and Rahn 1978)	$G_{H_2O} = 2.32\ (M^{0.976}/I^{0.730}) = 9.49$ (Hoyt 1980)
A_p (mm^2)	1.63	$A_p = 9.72 \cdot 10^{-3}\ M^{1.249} = 2.01$ (Ar and Rahn 1978)	$A_p = 2.2\ (ML/I) = 1.36$ (Ar and Rahn 1978)
N (pores/egg)	4,074	$N = 278\ M^{0.704} = 5{,}632$ (Whittow 1984)	$N = 3{,}390\ (M^{0.96}/I) = 4{,}669$ (Rahn and Ar 1980)

been reported in other species (Grant et al. 1982b, Carey 1983). However, the nature of our measurements was such that these changes would average out. Furthermore, the predictive equations that are available do not take into account sequential changes during incubation.

The data for the duration of the interval between the initial event in the pipping process (star-fracture of the shell) and hatching, together with the water loss from pipped eggs, permit an estimate to be made of the total water loss from the egg over the entire incubation period. Thus, star-fracture of the shell occurred 83.5 h (3.5 days) prior to hatching, so that the prepipping period was 40.3 days (43.8 − 3.5). The water loss from unpipped eggs was 189.4 mg/day; consequently, the total water loss during the prepipping period was 7,632.8 mg (40.3 × 189.4). The interval between the initial star-fracture of the shell and the formation of a pip-hole was 64.2 h and the water loss from star-fractured eggs was 424.97 mg/day, yielding a total water loss from star-fractured eggs of 1,136.8 mg. A pip-hole was formed 19.3 h prior to hatching and the water loss from eggs with a pip-hole was 540.75 mg/day, resulting in a total water loss from the eggs during the pip-hole phase of 434.9 mg. Thus, the total water loss from the egg over its entire incubation period was 9,204.5 mg (7,632.8 + 434.9 + 1,136.8). This represents 12.9% of the mass of the freshly laid egg. This is below the average value of 15% presented by Ar and Rahn (1980) for birds in general, in spite of the fact that, in the Red-tailed Tropicbird, the additional water loss from pipped eggs was taken into account. However, the present value (12.9%) is within one standard deviation (2.5) of Ar and Rahn's (1980) mean value (15.0%). The cumulative water loss from the eggs from the initial star-fracture of the shell to hatching (1,571.7 mg) amounts to 17.1% of the total water loss from the egg over the entire incubation period. Thus, the pipping period (star-fracture to hatching) represents 8.0% of the total incubation period and accounts for a considerably greater percentage of the total water loss. Unfortunately, similar data for other members of the Pelecaniformes are not available for comparative purposes. In members of other orders that have similar pipping sequences, the water loss from pipped eggs is a disproportionately large fraction of the total water loss from the egg (Pettit and Whittow 1983, Whittow et al. 1985).

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