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EGG WATER LOSS, SHELL WATER-VAPOR CONDUCTANCE, AND THE INCUBATION PERIOD OF THE GRAY-BACKED TERN (*STERNA LUNATA*)

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ABSTRACT.—The incubation period (30.3 days) of the Gray-backed Tern (*Sterna lunata*) is longer than would be expected from the mass of the freshly-laid egg. Measured values for the water loss from unpipped eggs, the water-vapor conductance and the functional pore area of the shell, and the number of pores in the shell are all lower than predictions based solely on fresh-egg mass, but are more closely approximated by equations incorporating incubation period as well as the egg's mass. The total water loss from the egg represents 14.7% of its mass when freshly laid. The interval between the first star-fracture of the shell and the hatching of the chick is 13.5% of the total incubation period, but accounts for 30.8% of the egg's total water loss.

Pettit et al. (1981) reported that the daily rate of water loss from the *unpipped* eggs of the White Tern (*Gygis alba*) was only 51% of the expected value, based on the mass of the freshly-laid egg. This discrepancy was attributed largely to low values for the water-vapor conductance and functional pore area of the shell (Rahn et al. 1976, Whittow 1980), features that, in turn, may be related to the long incubation period of this species (Whittow 1984). In addition, 42% of the total water loss from the egg over the entire incubation period (35.5 days) occurred in *pipped* eggs, during the 5-day interval between the initial star fracture of the shell and the hatching of the chick. In another tropical tern, the Sooty Tern (*Sterna fuscata*), the daily water loss from unpipped eggs and the incubation period were much closer to values predicted on the basis of the mass of the freshly-laid egg (Rahn et al. 1976; Whittow, in press) than in the White Tern. The cumulative water loss from the *pipped* eggs, however, was a very similar percentage of the total water loss from the egg in the two species. This suggested that the regulation of water loss from the egg before pipping was related to the duration of the incubation period, but that water loss during pipping was not. In order to elucidate these relationships further, we obtained information about water loss from the eggs of a congeneric species, the Gray-backed Tern (*S. lunata*). The Gray-backed Tern breeds on small islands in the Central Pacific Ocean (King 1967). Little is known about its breeding biology or incubation physiology, and neither the incubation period of the egg nor the sequence of events during pipping has been reported.

METHODS

Studies were conducted in June of 1979 and 1980 on Tern Island, French Frigate Shoals (23°52′N, 166°17′W), and in April and May 1981 on Eastern Island, Midway Atoll (28°13′N, 177°23′W) in the northwestern Hawaiian Islands. Eggs were also collected from Laysan Island (25°46′N, 171°44′W) in the northwestern Hawaiian Islands, in the spring of 1981.

Naturally incubated eggs were weighed at intervals of 21.7–188.4 h in order to determine the daily water loss (Drent 1973, Rahn and Ar 1974) using an Ohaus field balance (model 10-10). Central egg temperature was measured within 30 s of flushing the bird by rapidly inserting a thermocouple probe, connected to a Kane May Limited Digital Dependatherm, into its center. The thermocouple probe was calibrated against a mercury thermometer in a water bath. The mass of the freshly-laid egg was measured by filling the air cell with distilled water before weighing it (Grant et al. 1982) and egg volumes were measured by weighing the eggs in air and while submerged in water (Morgan et al. 1978). The water-vapor conductance of the shell was determined by the method described by Ar et al. (1974). The shell mass and the thickness of the shell and shell membranes were measured on shells that had been dried in a desiccator for at least one week. Shell mass was determined with a Mettler balance to the nearest 0.0001 g; the thickness of the shell and shell membranes was measured with a Starrett micrometer caliper (model no. 230) fitted with a ball attachment

FIGURE 1. Typical nest site of the Gray-backed Tern on Tern Island, French Frigate Shoals, northwestern Hawaiian Islands.

on the spindle to accommodate the curved surface of the egg shell. Four measurements of shell thickness were made at the equator of the egg and four at each end. The inner shell-membrane thickness could be measured only where the membrane had separated from the outer-shell membrane to form the air cell at the blunt end of the egg. The number of pores in the shell was counted by the method described by Roudybush et al. (1980). The dimensions of the eggs were measured by means of a dial caliper. A record was kept of the time of the initial star-fracture of the shell and of the appearance of a definite pip-hole. Internal pipping (penetration of the air cell by the embryo's beak) was estimated to occur when the chick could be heard "cheeping" inside the egg. Values in this paper were means ±1 SD.

RESULTS

Gray-backed Terns laid their single egg directly on the ground; nest materials were not used (Fig. 1). The egg was usually laid among pieces of coral and, in the absence of the parent bird, it was difficult to detect. Some birds nested near or among low herbaceous plants (*Chenopodium oahuensis*), but in most instances, the nest site was entirely open. The mean incubation period of 34 eggs was 30.3 ± 1.2 days. The first star-fracture of the shell was noted 4.1 ± 1.0 days before hatching in a sample of nine eggs. In a larger group of 32 eggs, for which the pipping events were timed less accurately, the mean interval between star-fracture and hatching was 4.3 ± 0.9 days. Internal pipping occurred in six eggs 51.8 ± 23.6 h after star-fracture of the shell. A distinct pip-hole occurred in the shell 31.2 ± 10.7 h ($n = 9$) before hatching. This interval was also measured, with less precision, in 28 additional eggs, and had a mean value of 1.3 ± 0.5 days. The mean daily water loss ($\dot{M}_{H_2O}$) from unpipped eggs was 112.0 ± 22.6 mg/day ($n = 51$). The mean daily water loss from eight eggs that were unpipped when first weighed, but star-fractured during the second weighing, was considerably greater—192.1 ± 51.8 mg/day. The water loss from eggs that were star-fractured on both occasions when they were weighed was even greater (318.4 ± 43.0 mg/day, $n = 10$). The mean length of 116 eggs was 46.3 ± 1.6 mm and the width 32.6 ± 1.0 mm. The mean mass of 12 freshly-laid eggs was 28.69 ± 1.27 g, while the volume of 32 eggs was 25.35 ± 1.90 ml. The mean central egg temperature of six eggs was 36.5 ± 0.7°C. The measured water-vapor conductance (G_{H_2O}), mass (M_{sh}), thickness (L), and pore density (P_D) of the shells of Gray-backed Terns were 4.54 ± 0.77 mg/day·torr ($n = 12$), 1.6611 ± 0.1512 g ($n = 15$), 0.16 ± 0.01 mm ($n = 113$), and 77.1 ± 12.8 pores/cm^2 ($n = 10$), respectively. The shell thickness does not include the shell membranes. When they are included, the shell thickness is 0.21 ± 0.02 mm ($n = 26$). The thickness of the outer shell membrane was 0.04 ± 0.01 mm ($n = 17$) and that of the inner membrane 0.004 ± 0.001 mm ($n = 4$).

DISCUSSION

Using the allometric equation of Ar and Rahn (1980) and the mean mass of the freshly-laid eggs, the daily rate of water loss of unpipped eggs of Gray-backed Terns was predicted to be 166.4 mg/day. The *measured* daily water loss (112.0 mg/day), however, was only 67.3% of the predicted value.

The rate of water loss from the egg (mg/day) is determined by the G_{H_2O} of the shell (mg/day·torr) on the one hand, and the difference in water-vapor pressure across the shell (ΔP_{H_2O}; torr), on the other, using the equation $\dot{M}_{H_2O} = G_{H_2O} \cdot \Delta P_{H_2O}$ (Rahn and Ar 1974). The measured G_{H_2O} (4.54 mg/day·torr) was 76.9% of the value predicted on the basis of the mass of the freshly-laid egg (5.90 mg/day·torr; Ar and Rahn 1978). Consequently, the low $\dot{M}_{H_2O}$ may be due, in large part, to the low G_{H_2O}.

The low value for G_{H_2O} might, in theory, be related to the thickness of the eggshell (L), because the latter determines the length of the pathway along which water-vapor diffuses out of the egg. Thus, other things being equal, a thick eggshell would result in a low G_{H_2O}. The measured L including the shell membranes (0.21 mm), however, was only 90% of the value (0.24 mm) predicted by the equation of Ar et al. (1974) based on fresh-egg mass. Consequently, the relatively low G_{H_2O} cannot be explained in terms of shell thickness. On the other hand, the relatively thin shell may explain why shell mass (1.66 g) was only 77.2% of the

TABLE 1. 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 numbers of pores in the shell (N) of the Gray-backed Tern. M = fresh egg mass (g); I = incubation period (days); L = shell thickness (mm).

Characteristic of the egg	Measured values	Predicted values					
$\dot{M}_{H_2O}$ (mg/day)	112.0	$\dot{M}_{H_2O} = 13.243\ M^{0.754}$ (Ar and Rahn 1980)	=	166.4	$\dot{M}_{H_2O} = 151\ M/I$ (Rahn and Ar 1980)	=	143.0
G_{H_2O} (mg/day·torr)	4.54	$G_{H_2O} = 0.384\ M^{0.814}$ (Ar and Rahn 1978)	=	5.90	$G_{H_2O} = 2.32\ M^{0.976}/I^{0.730}$ (Hoyt 1980)	=	5.09
A_p (mm²)	0.46	$A_p = (9.72) \cdot 10^{-3}\ M^{1.249}$ (Ar and Rahn 1978)	=	0.64	$A_p = 2.2\ ML/I$ (Ar and Rahn 1978)	=	0.44
N (pores/egg)	2,975	$N = 1{,}041\ M^{0.504}$ (Hoyt et al. 1979)	=	5,651	$N = 3{,}390\ M^{0.96}/I$ (Rahn and Ar 1980)	=	3,217

value predicted by Paganelli et al. (1974) for an egg the size of that of the Gray-backed Tern.

The low G_{H_2O} may also be related to the total area of the pores in the shell, through which water vapor diffuses, which was less in Gray-backed Tern eggs than in eggs of similar size produced by other species. Total functional pore area (A_p; mm²) may be calculated from the measured values for L and G_{H_2O}, using the equation of Paganelli (1980), $A_p = 0.478\ G_{H_2O} \cdot L$. The value so calculated (0.46 mm²) was 71.9% of the value predicted from the mass of the freshly-laid egg (Ar and Rahn 1978). This relatively low value for A_p could mean that the eggs of the Gray-backed Terns have fewer or smaller pores than have eggs of similar size produced by other species. The pore density may be used to calculate the total number of pores (N) in the eggshell, since the mean surface area of the egg (38.59 cm²), computed from its fresh-egg mass (Tullet and Board 1977), multiplied by the pore density (77.1 pores/cm²) yields N(=2,975 pores). This number is only 52.6% of the 5,651 predicted on the basis of fresh-egg mass (Hoyt et al. 1979). Therefore, the low N of the Gray-backed Tern's egg may be responsible for the low A_p of its eggshell. Dividing A_p by N yields an average pore area (P_A) of 154.6 μm², which is almost twice the area expected from the predictive equation of Tullet and Board (1977), based on fresh-egg mass.

The difference in water-vapor pressure between the contents of the egg ($P_{H_2O,egg}$) and the microclimate of the incubated egg ($P_{H_2O,nest}$), calculated according to the equation of Rahn and Ar (1974; see above) was 24.7 torr. Assuming that the contents of the egg are saturated with water vapor, $P_{H_2O,egg}$ may be calculated from the egg's temperature, yielding a value of 45.3 torr. Consequently, $P_{H_2O,nest}$ is 20.6 torr, a value that is close to the 19 torr presented by Ar and Rahn (1978) for 23 species of birds. This is of interest because the Gray-backed Tern does not construct a nest.

The incubation period of the Gray-backed Tern (30.3 days) was 124% of that expected on the basis of the fresh-egg mass (Ar and Rahn 1978). Prolonged incubation is a common feature of tropical seabirds. In previous analyses (Whittow 1980, 1984), many characteristics of tropical seabird eggs have been related not only to their mass, but also to their long incubation periods (Table 1). Table 1 shows clearly that predictions incorporating the incubation period, as well as the fresh-egg mass, more closely approximate the measured characteristics of the unpipped egg of the Gray-backed Tern than predictions based solely on the egg's mass. Thus, the data obtained from the Gray-backed Tern add to the evidence (Rahn et al. 1976, Whittow 1980, 1984) that the values for $\dot{M}_{H_2O}$, G_{H_2O}, and N in the unpipped eggs of tropical terns are related to the relative duration of the incubation period.

Using information on 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, the total water loss from the egg over the entire incubation period can be estimated. Star fracture of the shell occurred 4.1 days before hatching. The water loss from star-fractured eggs was 318.4 mg/day. Consequently, the total water loss from pipped eggs was 1,305.4 mg, whereas the cumulative pre-pipping water loss was 112.0 × (30.3 − 4.1) = 2,934.4 mg. Hence, the total water loss from the egg over the entire incubation period was 4,239.8 mg or 14.7% of the mass of the freshly-laid egg. This is probably an underestimate, since the water loss from eggs with a pip-hole was not measured (for reasons presented elsewhere, Pettit and Whittow 1983) and was probably greater than that from star-fractured eggs (Pettit and Whittow 1983). Although most of the water loss (69.2%)

occurred during the pre-pipping phase, it is significant that 30.8% occurred during the pipped phase, which represented only 13.5% of the total incubation period. Comparison of these data with those from the White Tern and Sooty Tern does not suggest any simple relationship between the duration of the incubation period and either the partition of water loss between the pre-pipping and pipped periods, or the total water loss expressed as a fraction of the fresh-egg mass. Such a relationship between incubation period and total water loss was indicated in a small series of tropical Procellariiformes (Pettit and Whittow 1983).

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