

# NEST MICROCLIMATE, WATER-VAPOR CONDUCTANCE, AND WATER LOSS IN HERON AND TERN EGGS

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**ABSTRACT.**—Rates of water loss ( $\dot{M}_{\text{H}_2\text{O}}$ ) were measured in eggs of seven species of tree-nesting Ciconiiformes and three species of ground-nesting Charadriiformes during natural incubation. Measurements of egg temperature, conductance of the egg shell to water vapor, and nest and ambient humidity allow one to calculate the difference in water-vapor pressure ( $\Delta P$ ) between egg and nest and between nest and ambient air.  $\Delta P$  between egg and nest was significantly lower in ground-nesting species (23 torr) than in tree-nesting species (31 torr). We suggest that low  $\Delta P$  in ground-nesting species was due to relatively high humidity (ca. 27 torr) in nests built on the ground compared to the humidity in loose stick nests of tree-nesting species (ca. 14 torr). Water-vapor conductance of eggs from more humid nests is relatively higher than that of eggs from less humid nests (107% and 78% of predicted values, respectively), resulting in similar fractional losses in mass for the whole incubation period in both groups of birds.  $\dot{M}_{\text{H}_2\text{O}}$  was not always constant throughout incubation. We suggest that changes in  $\dot{M}_{\text{H}_2\text{O}}$  may be due to changes in ambient humidity and/or egg temperature. Received 29 December 1980, resubmitted 5 January 1982, accepted 5 July 1982.

AVIAN eggs lose water by diffusion through pores in the shell. Total water loss during incubation must be within certain limits for successful development. Hatchability of chicken eggs is optimal when total water loss is 10–12% of initial egg mass (Lundy 1969), and water loss of naturally incubated eggs of a wide variety of birds averages about 15% (Drent 1975, Ar and Rahn 1980). The rate of water loss from eggs is determined by: (1) the pore geometry (length, cross-sectional area, and number of pores) of the eggshell, which determines water-vapor conductance; (2) egg temperature, which determines water-vapor pressure within the egg; and (3) parental behavior, nest structure, and ambient conditions, which interact to determine water-vapor pressure in the nest.

We investigated the interaction of these factors in the water economy of 10 species of birds. Although all the species studied nest in colonies on small islands off the coast of North Carolina, their nesting habits fall into two distinct categories. The herons, egrets, and ibis build their nests in trees, usually 2–5 m above the ground. Their nests consist of loosely woven

sticks and twigs and are sometimes so flimsy that the eggs can be seen through the bottom of the nest. The terns and gulls nest on the ground. The terns lay their eggs in a scrape on exposed sand, whereas the gulls construct nests of vegetation that are usually placed under cover of grass or small shrubs.

We measured rates of water loss and water-vapor conductance of naturally incubated eggs in each species and also measured egg temperature, nest humidity, and ambient humidity in four of these species. Results of this study suggest that the difference in water-vapor pressure between an egg and its microenvironment is less in the ground nests of gulls and terns than it is in the tree nests of herons.

## MATERIALS AND METHODS

*Birds and study area.*—We studied eggs of 7 species of herons, egrets, and ibis (Table 1), and 3 species of gulls and terns. The Ciconiiformes were nesting in trees on two small islands in the estuary of the Newport River near Beaufort, North Carolina. Royal Terns (*Sterna maxima*), Sandwich Terns (*S. sandvicensis*), and Laughing Gulls (*Larus atricilla*) nested on Morgan Island, a dredge spoil island near the tip of Cape Lookout, North Carolina. The two terns nested together in dense colonies on sparsely vegetated or bare sand, and Laughing Gulls nested on the ground in nearby vegetation.

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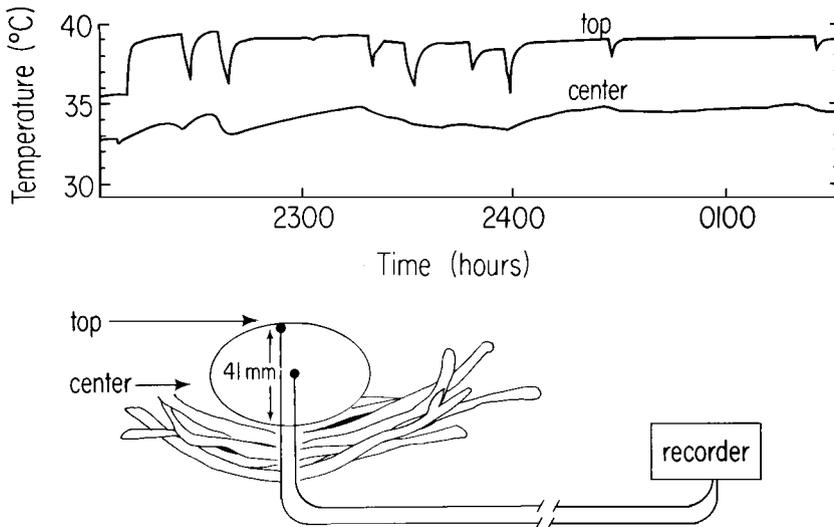


FIG. 1. Great Egret egg temperature. The top trace is the temperature at the top of the egg, adjacent to the brood patch, and the lower trace is the temperature at the center of the egg. Egg position was maintained in the nest by the thermocouples, which were threaded through the nest and run to the chart recorder.

*Rates of water loss.*—The change in egg mass during incubation is due almost entirely to water loss (Drent 1970). We determined rates of water loss ( $\dot{M}_{H_2O}$ ) from naturally incubated eggs by weighing the eggs in the field at 2- to 6-day intervals with a Torbal torsion balance readable to  $\pm 0.01$  g.

*Physical characteristics of the egg.*—The water-vapor conductance ( $G_{H_2O}$ ) of eggs was measured using the method of Ar et al. (1974) in which water loss of eggs in a desiccator at constant temperature is monitored by measuring change in mass.  $G_{H_2O}$  varies with egg temperature and barometric pressure. To permit comparison with other published data we converted all our reported values to 25°C and 760 torr (101.3 kPascals) using the procedures described by Paganelli et al. (1978). The  $G_{H_2O}$  at an incubation temperature of 37°C is 1.02 times the value at 25°C.

The initial mass of eggs that were collected was measured by refilling the air cell with water at the conclusion of the experiment. For eggs that were not collected, we calculated initial mass from the egg's dimensions by the method of Hoyt (1979), using species-specific weight coefficients ( $K_w$ ) determined from the collected eggs.

*Egg temperature during incubation.*—We measured egg temperatures with forty-gauge copper-constantan thermocouples implanted in eggs of Great Egrets (*Casmerodius albus*), Cattle Egrets (*Bulbulcus ibis*), White Ibis (*Eudocimus albus*), and Royal Terns. Two thermocouples were glued into the bird's own egg using fast-setting epoxy, one at the top of the egg and one in the center of the egg (see Fig. 1). In egret and ibis nests the thermocouple egg was placed as close as possible to the center of the 2- to 4-egg clutch,

with the top thermocouple adjacent to the brood patch of the adult. The egg was anchored in place by the thermocouple leads passing through the bottom of the nest. Royal Terns usually lay a single egg, and orientation of the thermocouple egg in the nest cup was fixed by burying the thermocouple leads in the sand under the egg.

Egg temperature was recorded continuously with an Omega thermocouple D.C. millivolt amplifier and a battery-operated Linear chart recorder. We calibrated the recorder-thermocouple system before and after each series of measurements against an NBS-certified mercury thermometer. All the species studied incubated essentially continuously, so egg temperatures did not vary by more than a few degrees. The egg temperatures we report are means of temperatures taken at 30-min intervals from continuous records made during uninterrupted incubation.

*Water-vapor pressure.*—Water-vapor pressures in the macroenvironment around the nests ( $P_i$ ) were measured in two ways. We calculated  $P_i$  from the relative humidity and temperature record of a clock-driven Serdex hygrothermograph situated about 0.5 m above the ground in the vicinity of the nests. The hygrothermograph was calibrated using saturated salt solutions (Winston and Bates 1960), and was found to be accurate within 1 torr (= 133 Pa) in the range of temperatures and relative humidities encountered. We also measured mean  $P_i$  using "egg hygrometers" (Rahn et al. 1977). These consisted of chicken eggshells of known  $G_{H_2O}$ , filled with silica gel and weighed to the nearest 0.1 mg in the laboratory before and after the period of measurement. Because the desiccant holds humidity inside the shell near

TABLE 1. Initial egg mass ( $M$ ), incubation period ( $I$ ), water-vapor conductance ( $G_{H_2O}$ ), and rate of water loss in the nest ( $\dot{M}_{H_2O}$ ) of 10 species of birds.  $F$  is the fractional mass loss during incubation, calculated as  $F = I \cdot \dot{M}_{H_2O} / M$ .  $\Delta P_{H_2O}$  is the gradient in water-vapor pressure between egg and nest [ $\Delta P = M_{H_2O} (1.02 G_{H_2O})^{-1}$ ]. Values given are means  $\pm$  SD. Sample sizes, as number of eggs followed by number of clutches, are in parentheses.

	Initial egg mass (g)	$I$ (days)	$G_{H_2O}$ ( $\text{mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}$ )	$\dot{M}_{H_2O}$ ( $\text{mg} \cdot \text{day}^{-1}$ )	$F$	$\Delta P_{H_2O}$ (torr)
TREE NESTS						
Great Egret ( <i>Casmerodius albus</i> )	48.6 $\pm$ 2.8 (26, 15)	27 <sup>a</sup>	7.6 $\pm$ 1.2 (27, 15)	231 $\pm$ 26 (9, 4)	0.13	30
Snowy Egret ( <i>Egretta thula</i> )	22.6 $\pm$ 1.5 (6, 2)	22 <sup>b</sup>	3.8 $\pm$ 0.7 (6, 2)	121 $\pm$ 33 (9, 4)	0.12	31
Tricolored Heron ( <i>Egretta tricolor</i> )	26.6 $\pm$ 1.5 (8, 4)	23 <sup>b</sup>	3.6 $\pm$ 1.8 (8, 4)	126 $\pm$ 30 (18, 6)	0.11	35
Cattle Egret ( <i>Bulbulcus ibis</i> )	27.8 $\pm$ 2.8 (19, 14)	23 <sup>a</sup>	5.4 $\pm$ 1.5 (19, 14)	163 $\pm$ 25 (16, 10)	0.14	30 (26-31) <sup>c</sup>
Black-crowned Night-Heron ( <i>Nycticorax nycticorax</i> )	38.8 (1, 1)	24 <sup>a</sup>	6.2 (1, 1)	175 $\pm$ 17 (9, 4)	0.11	28
Glossy Ibis ( <i>Plegadis falcinellus</i> )	37.4 $\pm$ 4.4 (6, 6)	23 <sup>a</sup>	7.6 $\pm$ 2.0 (6, 6)	207 $\pm$ 42 (23, 7)	0.13	27
White Ibis ( <i>Eudocimus albus</i> )	50.8 $\pm$ 5.7 (30, 22)	22 <sup>a</sup>	7.8 $\pm$ 3.4 (30, 22)	290 $\pm$ 30 (18, 6)	0.13	36 31
GROUND NESTS						
Laughing Gull ( <i>Larus atricilla</i> )	44.6 $\pm$ 1.6 (12, 4)	23 <sup>c</sup>	9.8 $\pm$ 2.2 (12, 4)	230 $\pm$ 41 (25, 10)	0.12	23
Royal Tern ( <i>Sterna maxima</i> )	68.0 $\pm$ 5.2 (17, 17)	28 <sup>a</sup>	13.3 $\pm$ 3.0 (17, 17)	321 $\pm$ 75 (21, 21)	0.13	24 (21-25) <sup>e</sup>
Sandwich Tern ( <i>Sterna sandwicensis</i> )	36.1 $\pm$ 2.6 (6, 6)	25 <sup>d</sup>	8.3 $\pm$ 1.6 (6, 6)	190 $\pm$ 40 (14, 14)	0.13	22 (21-24) <sup>e</sup>
					$\bar{x} = 0.13$	23

<sup>a</sup> Observed incubation period, this study.

<sup>b</sup> Maxwell and Kale (1977).

<sup>c</sup> Oppenheim (1972).

<sup>d</sup> Langham (1974).

<sup>e</sup> Range of  $\Delta P_{H_2O}$  given range in  $\dot{M}_{H_2O}$  (Fig. 2).

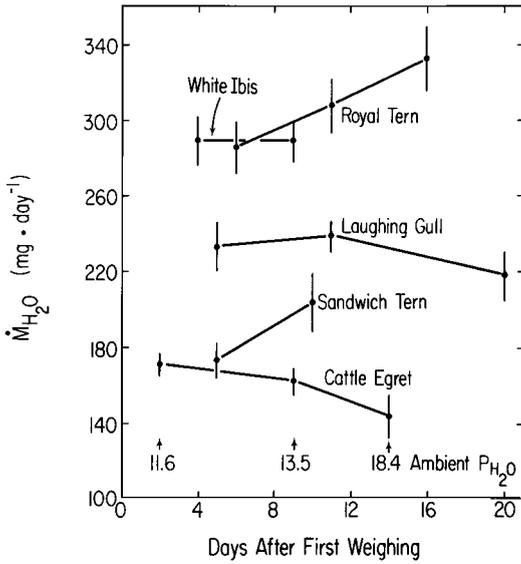


FIG. 2. Rates of water loss from eggs as a function of time. Lines connect mean values during each interval plotted at the midpoint of the interval. Vertical bars extend only  $\pm 1$  standard error for clarity of presentation. Number of eggs in each group are: Royal Tern (12), Sandwich Tern (12), Cattle Egret (13), White Ibis (8), and Laughing Gull (13). Numbers under the values for Cattle Egret eggs are the mean ambient water-vapor pressures for the same interval.

zero, mean water-vapor pressure ( $P_{H_2O}$ ) around such a hygrometer egg can be calculated from the equation  $P_{H_2O} = \dot{M}_{H_2O} / G_{H_2O}$ , where  $\dot{M}_{H_2O}$  is the rate of water absorption of the egg in  $mg \cdot day^{-1}$  and  $G_{H_2O}$  is water-vapor conductance in  $mg \cdot (day \cdot torr)^{-1}$ . We placed egg hygrometers under nests of Great Egrets and White Ibis for 2–3 days to determine mean  $P_i$  and at the same time placed another egg hygrometer in the nests to determine water-vapor pressure around the eggs in the nest ( $P_N$ ). The chicken-egg hygrometers differed in color and were slightly larger than the birds' own eggs, but with the exception of one Great Egret that destroyed a hygrometer, the adult birds incubated hygrometer eggs along with their own.

RESULTS

Mean daily rates of water loss varied directly with egg size, ranging from  $121 mg \cdot day^{-1}$  in Snowy Egret (*Egretta thula*) eggs to  $321 mg \cdot day^{-1}$  in Royal Tern eggs (Table 1). The  $\dot{M}_{H_2O}$  of Sandwich Tern and Royal Tern eggs increased significantly (paired *t*-test,  $P < 0.01$  and  $P < 0.001$ , respectively) from each interval to the next (Fig. 2). The  $\dot{M}_{H_2O}$  of Cattle Egret eggs

TABLE 2. Ambient and egg temperatures measured at the center and top of the egg from two Great Egret nests and one nest of each of the other species. Numbers shown are means of temperatures taken at 30-min intervals  $\pm$  SD; number of hours of observation in parentheses.

Species	Temperature ( $^{\circ}C$ )		
	Ambient	Center	Top
Great Egret	16.7	$34.3 \pm 1.4$ (27.5)	$36.9 \pm 1.6$ (28.5)
Cattle Egret	21.7	$36.8 \pm 0.8$ (44)	$37.5 \pm 1.1$ (25)
White Ibis	20.5	—	$37.1 \pm 1.0$ (20)
Royal Tern	24.3	$37.8 \pm 0.7$ (13)	$39.2 \pm 1.2$ (9.5)

declined between intervals and declined significantly ( $P < 0.001$ ) during the last interval. There was no consistent trend in  $\dot{M}_{H_2O}$  of the other species. Mean values for each species are listed in Table 1.

The  $G_{H_2O}$  values for the various species are listed in Table 1. White Ibis eggs had an unusually wide range of  $G_{H_2O}$  values, from 3 to 15  $mg \cdot (day \cdot torr)^{-1}$ .

Mean temperature in the middle of the egg ranged from  $34.3^{\circ}C$  in Great Egret eggs to  $37.8^{\circ}C$  in Royal Tern eggs (Table 2). A significant vertical temperature gradient existed through all of the eggs measured. Temperature at the top of the egg, that part in closest contact with the brood patch of the incubating adult, averaged  $1.6^{\circ}C$  higher than at the middle. Temperatures were recorded simultaneously at the center and top of one Great Egret egg for 14 h, and a mean gradient of  $4.5^{\circ}C \pm 1.2$  ( $\bar{x} \pm SD$ ) was found over a distance of 20.5 mm (Fig. 1).

Ambient and nest water-vapor pressures for Cattle Egret, Great Egret, White Ibis, and Royal Tern nests are shown in Table 3. Mean  $P_i$  values determined with the hygromograph and with egg hygrometers placed directly under heron nests over the same time interval were not significantly different ( $P > 0.5$ ), and no distinction is made between the two methods.

The  $P_N$  values were calculated as follows. Water loss from an egg can be expressed by a form of the Fick diffusion equation as

$$\dot{M}_{H_2O} = G_{H_2O}(P_A - P_N), \quad (1)$$

TABLE 3. Mean water-vapor pressure in eggs ( $P_A$ ), in nests around eggs ( $P_N$ ), and in ambient air around nests ( $P_I$ ) during incubation in four species of birds.  $T_{egg}$  is estimated egg-surface temperature. See text for discussion of calculations.

Species	$T_{egg}$ (°C)	$P_A$ (torr)	$\Delta P = P_A - P_N$ (torr)	Estimated $P_N$ (torr)		$P_I$ (torr)
				$P_A - \Delta P$	Egg hygrometer	
Great Egret	35.6	44	30	14	15	12
Cattle Egret	37.2	48	30	18 (17–22) <sup>a</sup>	—	16
White Ibis	37.1	47	36	11	14	11
Royal Tern	38.5	51	24	27 (26–30) <sup>a</sup>	—	15

<sup>a</sup> Range of  $P_N$  given range in  $\Delta P$  (Table 1).

where  $P_A$  is the water-vapor pressure in the egg and  $P_N$  is the water-vapor pressure in the nest around the egg (Rahn and Ar 1974). The term  $\Delta P = (P_A - P_N)$  is the driving gradient for water loss and can be estimated as  $\Delta P = \dot{M}_{H_2O}/G_{H_2O}$  (Table 1). The  $P_N$  is then equal to  $(P_A - \Delta P)$  and can be calculated in two ways. First, for hygrometer eggs incubated with the natural clutch,  $P_A = 0$ , so  $P_N = \dot{M}_{H_2O}/G_{H_2O}$ . Here,  $\dot{M}_{H_2O}$  is the rate of water uptake, not water loss. Second, for a natural egg,  $P_A$  approximates the water-vapor pressure at saturation at egg temperature, so  $P_N = P_A - \dot{M}_{H_2O}/G_{H_2O}$ . Both techniques yield similar estimates of  $P_N$  in Great Egret and White Ibis nests. We used only the second method to estimate  $P_N$  in Royal Tern and Cattle Egret nests. Because average  $\dot{M}_{H_2O}$ , and thus  $\Delta P$ , varied over time in these two species, we calculated a range of  $P_N$  using the highest mean  $\dot{M}_{H_2O}$  and the lowest mean  $\dot{M}_{H_2O}$  (Table 3).

Egg-surface temperatures used to estimate  $P_A$  were assumed to be midway between temperatures recorded from the top and middle of continuously incubated eggs (Table 2), except for White Ibis eggs, for which we measured temperature at the top of the egg only. We suggest later that egg temperature, and thus  $P_A$ , may rise during incubation. If a temperature of 35°C was associated with the earliest and lowest measured  $\dot{M}_{H_2O}$  and a temperature of 39°C with the latest and highest measured  $\dot{M}_{H_2O}$  in the Royal Tern, then  $P_N$  would change from 21 to 28 torr over the course of incubation.

The  $\Delta P$  values for each of the 10 species we studied are reported in Table 1. For the three species in which  $\dot{M}_{H_2O}$  was not constant, the range in  $\Delta P$  is shown. The mean  $\Delta P$  for seven

tree-nesting Ciconiiformes was  $30.7 \pm 3.3$  torr ( $\bar{x} \pm SD$ ), whereas the mean for the three Charadriiformes was only  $23.0 \pm 0.6$  torr. The difference between the two groups is significant ( $t' = 5.95$ ,  $P < 0.01$ ).

#### DISCUSSION

*Nest humidity.*—The data we present can be used to compare the microclimate around eggs in the loose stick nests of herons, egrets, and ibis with that around eggs in the ground nests of gulls and terns. Our results show that ground nests are significantly more humid than tree nests in the same macroenvironment.

The difference in  $\Delta P$  between tree- and ground-nesters (Table 1) must result from differences in  $P_A$ ,  $P_N$ , or both between the two classes of nests. We did not measure  $P_A$  directly, but used egg temperatures to estimate  $P_A$  values (see Results). If incubation temperatures of gull and tern eggs were 3–4°C lower than incubation temperatures of egret, ibis, and heron eggs,  $P_A$  and  $\Delta P$  of the former would be reduced by enough to account for the observed difference (7.7 torr) in  $\Delta P$ . This is not the case, however. The average temperature of a Royal Tern egg was actually higher than temperatures of Great Egret, Cattle Egret, or White Ibis eggs (Table 2). For seven species of gulls and terns for which egg temperatures have been reported (Howell and Bartholomew 1962, Drent 1970, Morgan et al. 1978, Rahn and Dawson 1979, Pettit et al. 1981), average egg temperatures are in no case lower than those we measured in egrets and ibis.

We conclude that the difference between  $\Delta P$  values for the two groups must be due to a

difference in  $P_N$ . That is, the ground nests of gulls and terns are more humid than tree nests of herons, egrets, and ibis in the same macroenvironment. In four species, we have the data necessary to estimate  $P_N$  itself, and not just  $\Delta P$  (Table 3). The estimated mean  $P_N$  around a Royal Tern egg is 9–16 torr higher than that around Great Egret, Cattle Egret, or White Ibis eggs.

High  $P_N$  in ground-nesters initially seems surprising. To the human observer the bare open sand on which the terns nest is a more desiccating environment than are the often shaded nest sites of herons. Both groups of birds incubate nearly continuously, so differences in parental attentiveness are unlikely to account for the differences in  $P_N$ . Rather, the likely explanation for the observed difference can be found from a consideration of the sources of water vapor in a nest and the avenues for water loss from the nest. Tree-nesting herons build loose stick nests that do not present much of a barrier to convective and/or diffusive gas exchange. Water vapor added to the nest from the egg or incubating adult is quickly lost to the ambient air. When ambient conditions are similar, ground nests have higher  $P_N$  than tree nests for three reasons: (1) the ground itself is an important source of water vapor (Geiger 1965), (2) the relatively solid surface of the ground reduces water loss from the nest by convection and diffusion, and (3) wind speed on the ground is less because nests are in the boundary layer. The  $P_N$  of the Great Egret and White Ibis nests measured with egg hygrometers was only 0–3 torr higher than water-vapor pressure in the macroenvironment ( $P_I$ ), while the calculated mean  $P_N$  in the Royal Tern nests was 12 torr higher than water-vapor pressure in the macroenvironment (Table 3).

Our data provide direct evidence that nest site and structure can have a significant effect on the gradient in water-vapor pressure between the nest and the macroenvironment. Data compiled by Walsberg (1980) provide an independent test of this hypothesis. In 10 ground-nesting species the mean gradient of water-vapor pressure between nest and ambient conditions ( $P_I - P_N$ ) was  $8.2 \pm 4.3$  torr ( $\bar{x} \pm \text{SD}$ ). For two tree-nesting species (*Anous tenuirostris* and *Gygis alba*) the mean gradients were 3 and 0 torr, respectively. Despite differences among investigators, their techniques, and the habitats in which they worked, the difference in

$P_I - P_N$  between ground nesters and tree nesters is marginally significant (Mann-Whitney  $U = 19$ ,  $P = 0.1$ ). If we include data from the four species reported here, the difference becomes highly significant ( $P < 0.01$ ).

*Egg water-vapor conductance.*—Nest humidity is of physiological significance to a developing embryo, because it affects  $\dot{M}_{\text{H}_2\text{O}}$  and the hydration state of that embryo, but  $\dot{M}_{\text{H}_2\text{O}}$  depends on  $G_{\text{H}_2\text{O}}$  as well as on  $\Delta P$ . In order to compare  $G_{\text{H}_2\text{O}}$  values between different species, it is necessary to take the effects of egg size and incubation period into account. Hoyt (1980) presented an equation that expresses the interrelation between these parameters for 143 species of birds:

$$G_{\text{H}_2\text{O}} = 2.32 (M^{0.976}/I^{0.73}), \quad (2)$$

where  $M$  is initial egg mass in g and  $I$  is incubation period in days. If our measured  $G_{\text{H}_2\text{O}}$  values are expressed as a percentage of the value predicted for eggs of the same  $M$  and  $I$  from equation 2,  $G_{\text{H}_2\text{O}}$  averages  $78 \pm 11\%$  ( $\bar{x} \pm \text{SD}$ ) of the predicted values for 7 tree-nesters and  $107 \pm 6\%$  for 3 ground-nesters. These two percentages are significantly different ( $t' = 5.36$ ,  $P < 0.01$ ). That is, eggs laid in stick nests in trees, which are incubated in less humid microenvironments, have relatively lower  $G_{\text{H}_2\text{O}}$  than eggs of ground nesters, which are incubated in more humid microenvironments. Lomholt (1976) and Birchard and Kilgore (1980) reported a similar relationship between  $G_{\text{H}_2\text{O}}$  and nest humidity in several other species of birds.

Because  $G_{\text{H}_2\text{O}}$  is high in ground-nesting species, where  $\Delta P$  is low, and low in tree-nesting species, where  $\Delta P$  is high, the total water loss during incubation, expressed as a fraction of initial mass ( $F$ ), is not significantly different between the two groups (Table 1,  $t = 0.44$ ,  $P > 0.5$ ). Estimates of  $F$  depend on  $\dot{M}_{\text{H}_2\text{O}}$ , which is not always constant (see below). The measurements of  $\dot{M}_{\text{H}_2\text{O}}$  that we used to estimate  $F$  extended over 45–90% of the incubation period for each species, however, so it is unlikely that  $\dot{M}_{\text{H}_2\text{O}}$  could vary enough during the remainder of the incubation to change the conclusions above.

*Changes in rates of water loss from eggs.*—In the Royal Tern, Sandwich Tern, and Cattle Egret daily rates of water loss during natural incubation changed with time (Fig. 2). Because few studies of egg water loss have been carried out

over the whole incubation period, it has generally been assumed that  $\dot{M}_{\text{H}_2\text{O}}$  remains constant. Drent (1970), however, showed that the  $\dot{M}_{\text{H}_2\text{O}}$  increased during the early stages of incubation in the Herring Gull (*Larus argentatus*), and  $\dot{M}_{\text{H}_2\text{O}}$  of eggs of four other gulls also varies over time (Morgan et al. 1978, Rahn and Dawson 1979). Change in rate of water loss from an egg can result from one or more of the following: (1) change in  $G_{\text{H}_2\text{O}}$ ; (2) change in nest humidity,  $P_N$ ; or (3) change in  $P_A$ , due to change in surface temperature of the egg.

Water-vapor conductance of eggs increases during the first few days of incubation in several species of passerines but is relatively constant after the development of the chorioallantois (Carey 1979, Hanka et al. 1979, Birchard and Kilgore 1980, Sotherland et al. 1980). Most of our measurements of  $G_{\text{H}_2\text{O}}$  were made using eggs that had been incubated at least 10 days (the same eggs in which we measured  $\dot{M}_{\text{H}_2\text{O}}$ ). Exceptions were the Laughing Gull eggs, which were all freshly laid, and some White Ibis eggs. We could detect no significant change in  $G_{\text{H}_2\text{O}}$  of White Ibis eggs during development ( $t = 0.98$ ,  $P > 0.2$ ). The  $G_{\text{H}_2\text{O}}$  of 12 freshly laid eggs was  $8.59 \pm 2.20 \text{ mg}(\text{day} \cdot \text{torr})^{-1}$  ( $\bar{x} \pm \text{SD}$ ), and the  $G_{\text{H}_2\text{O}}$  of 13 eggs containing well-developed embryos was  $7.00 \pm 2.49 \text{ mg}(\text{day} \cdot \text{torr})^{-1}$ . It may be that  $G_{\text{H}_2\text{O}}$  increases with development of the chorioallantois only in small (<10 g) eggs, as Birchard and Kilgore (1980) suggested. Even if  $G_{\text{H}_2\text{O}}$  changes early in incubation, such changes cannot account for the variations in  $\dot{M}_{\text{H}_2\text{O}}$  of Royal Tern and Cattle Egret eggs very late in incubation.

In the absence of any evidence that  $G_{\text{H}_2\text{O}}$  changes during middle to late incubation, these changes in  $\dot{M}_{\text{H}_2\text{O}}$  are presumably due to changes in nest humidity, egg temperature (and hence  $P_A$ ) or both. Our measurements of egg temperatures and nest humidities did not extend over the entire period of  $\dot{M}_{\text{H}_2\text{O}}$  measurements, so we cannot be certain of what caused the observed changes in  $\dot{M}_{\text{H}_2\text{O}}$ . The available data, however, suggest that changes in  $P_N$  may be sufficient to account for the variation in  $\dot{M}_{\text{H}_2\text{O}}$  in Cattle Egret eggs, but not in the two tern species.

For 7 of the 10 species in which we measured  $\dot{M}_{\text{H}_2\text{O}}$ , neither  $\dot{M}_{\text{H}_2\text{O}}$  nor ambient humidity changed significantly during the period of measurement. The gradual decline in  $\dot{M}_{\text{H}_2\text{O}}$  of Cattle Egret eggs, however, was correlated with

a gradual increase in  $P_I$ , the average humidity in the macroenvironment (Fig. 2). The close correlation between  $P_N$  and  $P_I$  in ciconiiform nests (Table 3) suggests that  $P_N$  might have increased by an equivalent amount, about 7 torr. All other things being equal, this would reduce  $\Delta P$ , the gradient driving water loss from the egg, and therefore reduce  $\dot{M}_{\text{H}_2\text{O}}$  (see equation 1). The predicted reduction in  $\dot{M}_{\text{H}_2\text{O}}$  closely approximates the observed changes.

The observed increases of 20% and 17% in  $\dot{M}_{\text{H}_2\text{O}}$  in Sandwich and Royal terns, respectively (Fig. 2), cannot adequately be accounted for by changes in  $P_I$ . At least part of the increased rate of water loss may be due to an increase in surface temperature of the egg. Drent (1970) found that temperature in the nest of the Herring Gull and in the center of the egg rose steadily during the first two-thirds of incubation. In addition, heat production of the developing embryo late in incubation is sufficient to raise egg-surface temperature in some species (Drent 1970, Vleck unpubl.). Even at a constant nest humidity, the observed 17% increase in  $\dot{M}_{\text{H}_2\text{O}}$  in Royal Tern eggs could be accounted for by only a 1.3°C rise in mean surface temperature of the egg. A complete understanding of the causes of variation in  $\dot{M}_{\text{H}_2\text{O}}$  will require measurement of  $G_{\text{H}_2\text{O}}$ ,  $P_N$ , and egg temperature throughout the incubation period.

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