

## RESPIRATORY GAS EXCHANGE AND GROWTH OF WHITE TERN EMBRYOS

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**ABSTRACT.**—The parameters of respiratory gas exchange and growth in White Tern (*Gygis alba*) eggs were examined during natural incubation. The O<sub>2</sub> consumption of eggs (MO<sub>2</sub>) reached a plateau on day 32 of the 35.5-day incubation period resulting in an average MO<sub>2</sub> of 159 ml O<sub>2</sub> STPD·day<sup>-1</sup> immediately prior to external pipping, and air cell gas tensions of 100 torr for O<sub>2</sub> and 49 torr for CO<sub>2</sub>. MO<sub>2</sub> increased rapidly during the 5.2-day pip (star fracture)-to-hatch interval, achieving an O<sub>2</sub> uptake of 470 ml O<sub>2</sub> STPD·day<sup>-1</sup> in hatchling chicks. The level of pre-pipping MO<sub>2</sub> appears to be adaptive to prolonged incubation and is related to the extent to which the incubation period deviates from the expected value based on initial egg mass. The mean pre-external pipping daily water loss (MH<sub>2</sub>O) was 78.7 mg·day<sup>-1</sup> but increased to 275 mg·day<sup>-1</sup> in externally pipped eggs, yielding a 17.5% total fractional mass loss over the entire incubation period. The pre-pipping cost of prolonged semi-precocial development, calculated by indirect calorimetry, was 2.71 kJ per gram yolk-free embryonic tissue. The total energy expenditure for embryonic development was 3.32 kJ per gram of hatchling tissue.

The White Tern (*Gygis alba*) is one of only two terns with prolonged incubation (Whittow 1980). It has the longest incubation time in relation to its egg mass of any tern (Rahn et al. 1976, Whittow 1980). Available data on the incubation physiology of the White Tern suggest that it is subject to the same constraints as are other seabirds with prolonged incubation (Rahn et al. 1976, Whittow 1980). In addition, the eggs are adapted for prolonged incubation through curtailment of daily water loss from the egg; this is related to the relatively low water-vapor conductance of the shell and a low egg temperature (Rahn et al. 1976, Howell 1978). In procellariiform seabirds, prolonged incubation is associated also with slow embryonic growth and an increased energy cost of incubation (Ackerman et al. 1980, Whittow 1980, Pettit et al. 1981a, b). However, the degree of development at hatching is greater in the White Tern (semi-precocial) than in the Procellariiformes, which are considered to be semi-altricial (Nice 1962). The White Tern and procellariiforms may therefore differ in the oxygen and energy cost of incubation. The present study was undertaken in order to provide information on the growth, embryonic oxygen consumption, and the energetics of in-

cubation in the White Tern. An important part of our study was to document the events occurring between pipping and hatching, signalling the transition from diffusive gas transport across the pores of the shell to the convective gas transport of the lungs.

### METHODS

The study was conducted from January to March 1980 on Sand Island, Midway Atoll (28°13'N, 177°23'W) in the northwestern Hawaiian Islands. Additional data were obtained during 1981. In late January and early February, possible nest sites in attendance by "prospecting" pairs of White Terns were checked daily for the appearance of eggs. Eggs from nest sites on tree limbs (*Casuarina*) and man-made structures such as window sills and roof tops were marked with the date of laying and nest number. No eggs were deserted as a result of egg-handling and the incubating adult quickly returned to the egg after it was replaced. In some cases, the eggs were removed briefly for measurements in the laboratory, and a chicken's (*Gallus gallus*) egg suitably marked as a White Tern egg was exchanged for it at the nest, to prevent desertion. Although the chicken's egg was much larger, it was readily accepted and incubated during the brief exchange period. Beginning on day 12 of incubation, oxygen uptake was measured with a modified Scholander respirometer (Ackerman et al. 1980) at a constant temperature of 35°C. Oxygen consumption of hatchling tern chicks was also determined using the Scholander respirometer. Beginning on day 27 of incubation, air cell gas tensions were analyzed with a 0.5 cm<sup>3</sup> Scholander

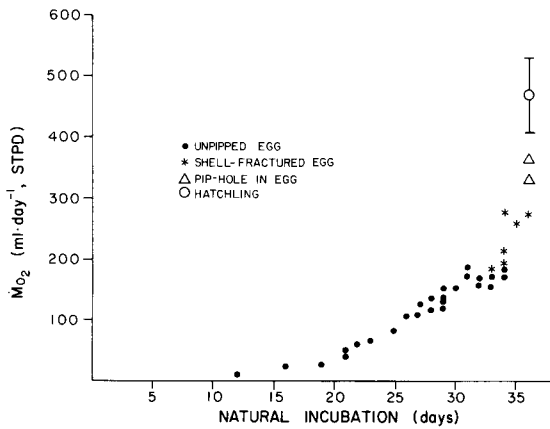


FIGURE 1. The relationship between egg oxygen consumption ( $\text{MO}_2$ ) and incubation time in the White Tern; 34 measurements on 17 eggs. The mean hatching  $\text{O}_2$  consumption ( $\pm$ SD) of 14 chicks is presented according to symbols given in the key.

micro-gas analyzer (Wangensteen and Rahn 1970/71), and air cells were filled with distilled water and weighed to approximate the initial egg weight (Grant et al., unpubl. data). The eggs were then dissected carefully to separate the embryo from the yolk and both were weighed to .01 g. Shell thickness, length and breadth of the egg, volume and density were measured (Morgan et al. 1978). Five fresh eggs were collected for determination of the relative yolk content; the eggs were boiled and the yolk:albumen ratio determined from the weights of the solidified yolk and albumen.

In order to determine daily water loss ( $\text{MH}_2\text{O}$ ), eggs were weighed periodically throughout incubation using a torsion balance. Ambient water vapor pressure surrounding the egg was measured with White Tern hygrometers (Rahn et al. 1977). The hygrometers were weighed to 0.01 g after a two-day period of continuous incubation. Temperatures of six eggs were obtained by inserting a thermocouple directly into the center of the egg, immediately after removal from under an incubating bird and reading directly from a Kane-May Ltd. Dependatherm recording device. Additional temperatures of two embryos were obtained by passing the thermocouple wire through a pip-hole in the shell and placing it against the thoracic region of the embryo.

## RESULTS

### PIPPING AND HATCHING

The exact sequence of events between pipping and hatching, and the embryonic age at penetration of the air cell must be known in order to evaluate levels of oxygen consumption immediately before pipping (pre-pip  $\text{MO}_2$ ). We sought evidence of pipping activity daily in 16 eggs by examining the shell for small pip-cracks or star fractures, and then by listening for respiratory or "peeping" sounds by placing the egg next to the ear. Furthermore, the eggs were candled and weighed and the air cell border was outlined in pencil as a reference mark for further observations. Two eggs were internally pipped (penetration of the air cell)

one day prior to external pipping (fracture of the shell), but 14 eggs were externally pipped (star fractured) prior to internal pipping. During internal pipping, "peeping" sounds and breathing were easily heard. The formation of a pip-hole in the shell occurred in nine eggs at one to two days prior to hatching. The mean external pip (star fracture)-to-hatch interval was 5.2 days  $\pm$  0.8 (SD), range 3 to 7 days ( $n = 16$ ). The mean incubation period for 18 eggs was 35.5 days  $\pm$  1.4 (SD).

### OXYGEN CONSUMPTION OF THE EMBRYO ( $\text{MO}_2$ )

$\text{MO}_2$  increased throughout the greater part of incubation, and reached a plateau on day 32 (Fig. 1). A logistic curve (Ricklefs 1967) was fitted to the data for 26 unpipped eggs up to day 32:  $\text{MO}_2 = 160/1 + e^{-0.284(t-23.5)}$ ,  $r = 0.975$ , where  $\text{MO}_2$  is the egg oxygen consumption ( $\text{ml O}_2 \text{ STPD} \cdot \text{day}^{-1}$ ), the numerator is the asymptote of the curve,  $e$  is the base of the natural logarithms,  $t$  is time of incubation (days), and  $r$  is the correlation coefficient. Pre-external pipping  $\text{MO}_2$  was calculated by averaging the data for seven unpipped eggs aged 32 to 34 days and was  $159.4 \text{ ml O}_2 \text{ STPD} \cdot \text{day}^{-1} \pm 13.0$  (SD). External pipping (shell fracture) occurred at a mean wet, yolk-free embryonic mass of  $11.0 \text{ g} \pm 1.0$  (SD),  $n = 5$ , and with a mean yolk reserve of  $5.4 \text{ g} \pm 0.7$  (SD). The oxygen uptake of 14 hatchlings with an average weight of  $16.1 \text{ g} \pm 1.6$  (SD) was  $470 \text{ ml O}_2 \text{ STPD} \cdot \text{day}^{-1} \pm 60$  (SD).

### AIR CELL GAS TENSIONS

The air cell gas tensions measured concurrently with pre-external pip  $\text{MO}_2$  (day 32–34) were  $100.3 \text{ torr} \pm 7.4$  (SD) for oxygen and  $48.5 \text{ torr} \pm 4.6$  (SD) for carbon dioxide. Air cell analysis began on day 27 of incubation at an embryonic mass of about 8 g. At this stage of development, a sample of about  $2.5 \text{ cm}^3$  was obtained, sufficient for gas analysis; the mean air cell gas tensions were  $99.7 \text{ torr} \pm 9.6$  (SD),  $n = 10$  for  $\text{O}_2$ , and  $49.2 \text{ torr} \pm 6.8$  (SD),  $n = 10$  for  $\text{CO}_2$  suggesting a long plateau stage of similar gas tensions from day 27 to 34 (Fig. 2).

Two eggs which were pipped externally (shell fractured), just below the border between the air cell and the embryonic compartment, were analyzed for air cell gas tensions. The air cell was intact in both eggs as the embryo had not yet penetrated it to begin lung inflation. The  $\text{O}_2$  and  $\text{CO}_2$  tensions of these two eggs averaged 117.3 torr and 41.4 torr, respectively, suggesting increased diffusion of gases due to the cracked shell.

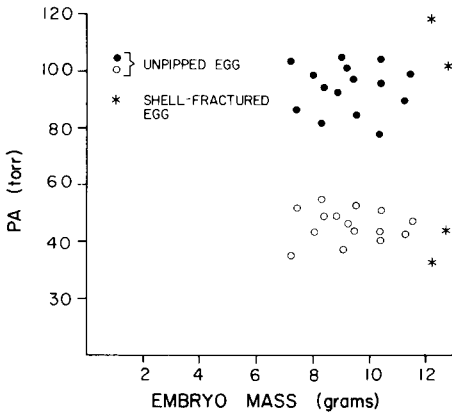


FIGURE 2. The air cell  $PO_2$  and  $PCO_2$  of White Tern eggs in relation to wet, yolk-free embryonic mass. Asterisks denote air cell gas tensions of two eggs that were shell-fractured prior to internal pipping. White and black dots denote  $PCO_2$  and  $PO_2$ , respectively, of unpipped eggs.

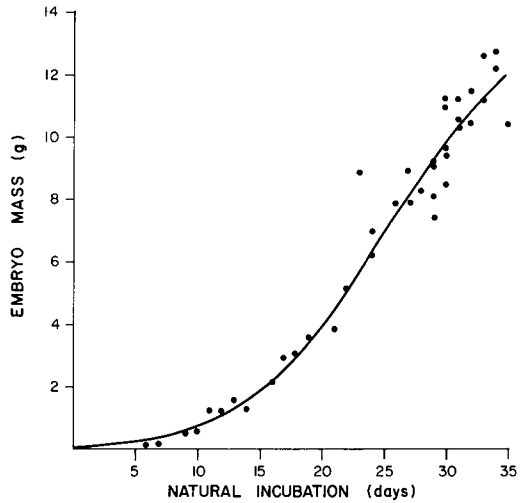


FIGURE 3. The relationship between wet, yolk-free embryonic mass and natural incubation of White Terns. The curve superimposed on the data was derived from the logistic equation presented in the text.

The respiratory quotient, R.Q., of the egg was calculated by the formula:  $R.Q. = 0.78 P_{ACO_2} / \Delta PO_2$  where 0.78 is the ratio of the diffusion coefficient of  $CO_2$  to that of  $O_2$  in air and  $\Delta PO_2$  is the partial pressure difference of  $O_2$  between the ambient environment and the air cell (Wangenstein and Rahn 1970/71). The R.Q. for eggs aged 27 to 34 days had a mean value of  $0.74 \pm 0.4$  (SD).

The oxygen conductance of the shell ( $GO_2$ , ml  $O_2$  STPD  $\cdot$  day $^{-1}$   $\cdot$  torr $^{-1}$ ), defined as  $MO_2 / \Delta PO_2$ , where  $\Delta PO_2 = PI_{O_2} - PA_{O_2}$  or the difference between the  $O_2$  partial pressure of fresh air ( $PI_{O_2}$ ) and the  $O_2$  tension in the air cell  $PA_{O_2}$  (Rahn et al. 1974), was 2.99 ml  $O_2$  STPD  $\cdot$  day $^{-1}$   $\cdot$  torr $^{-1} \pm 0.46$  (SD),  $n = 15$ .

#### GROWTH OF THE EMBRYO

A logistic growth curve (Ricklefs 1967) was fitted to the growth data for 40 embryos of known age (Fig. 3). The logistic equation is  $M_t = 14.1 / (1 + e^{-0.186(t-25.30)})$ ,  $r = 0.966$ , where  $M_t$  is the embryonic mass at time,  $t$ ;  $e$  is the base of the natural logarithms; the numerator is the asymptote of the curve (yolk-free hatchling mass);  $r$  is the correlation coefficient. The mean yolk reserve at external pipping (5.41 g) was 49% of the yolk-free embryonic mass (11.0 g),  $n = 5$ . The mean yolk-free hatchling mass in 6 eggs was  $14.1 \text{ g} \pm 1.5$  (SD) and the mean yolk reserve of hatchlings was  $1.01 \text{ g} \pm 0.6$  (SD). The mean total hatchling mass was  $15.5 \text{ g} \pm 1.5$  (SD),  $n = 18$ , or 66.5% of the mean initial egg mass.

The relative yolk content or percent of egg contents was  $38.0\% \pm 2.0$  (SD) and the

yolk-albumen ratio was  $0.61 \pm 0.05$  (SD),  $n = 5$ .

#### EGG WATER LOSS, NEST HUMIDITY AND EGG TEMPERATURE

Physical dimensions of the egg and shell are compared with values obtained by Rahn et al. (1976) (Table 1). Mean daily mass loss,  $M_{H_2O}$ , measured over a 14-day interval was  $78.7 \text{ mg} \cdot \text{day}^{-1}$ , and would result in a 10.2% loss over the pre-pipping incubation period. However, the daily water loss from eggs that were externally pipped was considerably greater than in the unpipped egg (Table 1). Multiplying the average duration of the pipped (external) – hatched interval (5.2 days) by the daily water loss of pipped eggs ( $327.0 \text{ mg} \cdot \text{day}^{-1}$ ), yielded a value of 1.700 g or 42% of the total water loss from the egg during incubation. The total fractional water loss over the entire incubation period was 17.5%. "Nest" vapor pressures, measured by egg hygrometry, averaged  $14.6 \text{ torr} \pm 3.5$  (SD),  $n = 9$ .

The mean brood patch temperature recorded over a 20-min period by a thermocouple placed on the upper surface of a rigidly-held styrofoam egg was  $36.7^\circ\text{C} \pm 0.1$  (SD) at an ambient temperature of  $20^\circ\text{C}$ . The mean proventricular body temperature in two adult birds was  $39.5^\circ\text{C}$ . The mean egg temperature of six incubated eggs measured by quickly inserting a thermocouple into the center of the egg, was  $35.3^\circ\text{C} \pm 0.8$  (SD). The age of these eggs ranged from 1 to 23 days. The embryo temperatures obtained from an egg with a pip-hole in the

TABLE 1. Physical dimensions and water loss in the White Tern egg. Mean values  $\pm$  SD. The figures in parentheses are the number of measurements.

	This study	Rahn et al. (1976)	
Egg	Egg wt. (g)	23.3 $\pm$ 1.6 (18)	21.4 $\pm$ 1.2 (14)
	Density (g cm <sup>-3</sup> )	1.053 $\pm$ 0.004 (18)	1.053 (14)
	Volume (cm <sup>3</sup> )	22.13 $\pm$ 1.6 (18)	20.3 $\pm$ 1.2 (14)
	Length (cm)	4.18 $\pm$ 0.11 (23)	4.07 $\pm$ 0.10 (14)
	Breadth (cm)	3.15 $\pm$ 0.10 (23)	3.11 $\pm$ 0.06 (14)
Shell	Shell wt. (g)	1.20 $\pm$ 0.08 (16)	1.13 $\pm$ 0.07 (14)
	Thickness (mm)	0.177 $\pm$ 0.7 (17)	0.17 $\pm$ 0.01 (14)
	GH <sub>2</sub> O (mg·day·torr <sup>-1</sup> )	2.48 $\pm$ 0.76 (12)	3.47 $\pm$ 0.68 (14)
	MH <sub>2</sub> O (mg·day <sup>-1</sup> ) unpipped eggs	78.7 $\pm$ 15.6 (19)	74.0 (6)
	externally pipped (shell fracture)	327.0 $\pm$ 49.3 (7)	—
	F, pre-pipping water loss constant	0.102	—
	F, total incubation water loss constant	0.175	0.12
	PH <sub>2</sub> O in egg (torr)	43	43
	PH <sub>2</sub> O in nest (torr)	14.6 $\pm$ 3.5 (9; measured)	22 (calculated)
	$\Delta$ PH <sub>2</sub> O	26.8	21
PH in nest (%)	—	51	
Egg temperature (°C)	35.3 $\pm$ 0.8 (6)	35.4	

eggshell were 35.1°C on day 35 and 36.1° on day 36.

## DISCUSSION

### OXYGEN CONSUMPTION OF THE EMBRYO AND HATCHLING

Hoyt and Rahn (1980) have shown for 28 species of birds that the pre-internal pipping (preIP) metabolic rate is a function of both egg mass and incubation period. Their equation,  $MO_2 = 139 W^{0.85}/I^{0.65}$ , predicts a preIP  $MO_2$  of 198 ml O<sub>2</sub> STPD·day<sup>-1</sup> for a 23.3-g egg and 35.5-day incubation period. Their analysis was based on species in which internal pipping presumably precedes external pipping. In the White Tern, however, external pipping is the initial event in the pipping process and the pre-external  $MO_2$  (159 ml O<sub>2</sub>·day<sup>-1</sup>) is the basis for comparison with other species. This comparison results in an embryonic O<sub>2</sub> uptake that is 80% of the predicted value. This prediction is better than one based on egg mass alone:  $MO_2 = 25.2 W^{0.73}$  (Hoyt et al. 1978) which predicts that pre-pip  $MO_2$  will

equal 251 ml O<sub>2</sub> STPD·day<sup>-1</sup> or 157% of our observed value.

The equations of both Hoyt and Rahn (1980) and Hoyt et al. (1978) were derived for birds that do not have incubation periods in excess of predictions based on egg mass. However, procellariiform birds, and the White Tern, are seabirds with prolonged incubation (Whittow 1980). Evidence has been presented elsewhere (Pettit et al. 1981a, b) that the level of pre-external pipping  $MO_2$  among Procellariiformes is adaptive to prolonged incubation: the more prolonged the incubation, the lower the pre-pipping  $MO_2$ . The data presented here suggest that the White Tern also conforms to this pattern.

The rate of oxygen uptake must increase rapidly during the hatching process. Pre-external pipping  $MO_2$  is 35% of the hatchling rate of O<sub>2</sub> uptake predicted for a 15.5 g chick ( $\dot{V}O_2 = 62 W^{0.73}$ ; Ackerman et al. 1980). This relative percentage is close to the relationship obtained in 39-g Bonin Petrel (*Pterodroma hypoleuca*) eggs (33%; Pettit et al.

1981b). Our measured rate of  $O_2$  uptake in 14 hatchling White Terns ( $470 \text{ ml } O_2 \text{ STPD} \cdot \text{day}^{-1}$ ) was 100% of the rate predicted by Ackerman et al. (1980) for a 16.1-g chick. During the hatching process the mass-specific metabolism increases by 200%. The plateau mass-specific rate, immediately prior to external pipping, may be calculated by dividing the embryonic mass at pipping into the pre-pip  $\dot{M}O_2$ . This value was  $14.5 \text{ ml } O_2 \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ , while the observed hatchling mass-specific rate was  $29.2 \text{ ml } O_2 \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ . In other words, the pre-pipping specific oxygen uptake is 50% of the observed hatchling mass-specific metabolism.

#### TOTAL OXYGEN CONSUMED AND ENERGETIC CONSIDERATIONS

The total amount of oxygen consumed throughout incubation was determined by measuring the area under the curve in Figure 1. These data are presented in Table 2 along with the energy equivalents (1 l  $O_2$  equals 20.08 kJ). The total amount of  $O_2$  consumed was 2.57 l  $O_2$  STPD or 51.6 kJ of energy. Approximately 110 ml  $O_2$  per gram of egg is consumed during incubation, which is slightly higher than the average value of 102 ml  $O_2 \cdot \text{g}^{-1}$  egg reported by Hoyt and Rahn (1980) for many avian eggs, but lower than the values for small procellariiforms (Pettit et al. 1981b). The White Tern's incubation period is 152% of the predicted incubation period based on egg mass (Ar and Rahn 1978) and it may use less total energy for development than does the Bonin Petrel and Wedge-tailed Shearwater (*Puffinus pacificus*; Ackerman et al. 1980). The incubation periods of the petrel and shearwater are 185% and 181%, respectively, of predicted. The oxygen consumed during the pip-to-hatch interval was 42% ( $1,075 \text{ ml} / 2,565 \text{ ml} \times 100$ ) of the total oxygen consumed during incubation, a proportion similar to that obtained in Procellariiformes (Pettit et al. 1981a, b).

A useful calculation for comparison with other species is the amount of energy required to synthesize one gram of tissue. By dividing the amount of oxygen consumed prior to external pipping (1,490 ml  $O_2$ ) by the wet, yolk-free mass at pipping (11.0 g), one obtains  $135 \text{ ml } O_2 \cdot \text{g}^{-1}$  tissue or  $2.71 \text{ kJ} \cdot \text{g}^{-1}$  tissue. This value is greater than the energetic requirements in the Herring Gull (*Larus argentatus*) of  $2.30 \text{ kJ} \cdot \text{g}^{-1}$  (Drent 1970). In procellariiform birds, the energy cost of pre-pipping development increases from  $2.12 \text{ kJ} \cdot \text{g}^{-1}$  for the Black-footed Alba-

TABLE 2. Energetic cost of embryonic development in the White Tern.

	l $O_2$	kJ
Cost pre-pipping incubation (per g embryonic tissue)	1.49 0.135	29.92 2.71
Cost total incubation (per g hatchling tissue)	2.57 0.166	51.61 3.33
Cost of hatching (pipping-hatching)	1.08	21.69
Total incubation cost (per g fresh egg mass)	0.110	2.22

tross (*Diomedea nigripes*) to  $2.58 \text{ kJ} \cdot \text{g}^{-1}$  for the Bonin Petrel. The energy cost of development increases as the incubation period becomes relatively longer than predicted on the basis of egg mass. In addition the high cost of embryonic development in the White Tern may be related to its semi-pre-social status at hatching.

#### AIR CELL GAS TENSIONS

Constant oxygen and carbon dioxide gas tensions in the air cell over a relatively long period prior to pipping conform with a relatively constant  $\dot{M}O_2$  and a slow rate of growth. However, the plateau in air cell gas tensions precedes that in  $\dot{M}O_2$ , suggesting that low levels of embryonic blood oxygen and high levels of carbon dioxide may prevail at this time. The pre-pipping metabolic rate may reflect primarily that  $O_2$  consumed for maintenance of the embryo and maturation of specialized tissues. The partial pressures of air cell gases measured at this stage are similar to those measured for other birds, including eggs with long incubation periods (Rahn et al. 1974, Hoyt et al. 1979, Ackerman et al. 1980, Pettit et al. 1981a, b). The values obtained for the White Tern are particularly significant as they have been measured directly from the smallest egg with a prolonged incubation period that has been studied to date. Embryonic respiration in small eggs with prolonged incubation appears to be constrained by the same limiting gas tensions that ensure embryonic development and acid-base balance in many avian eggs. These data provide additional evidence that air cell oxygen tensions are not lower in small eggs, as suggested by Vleck et al. (1979).

#### GROWTH OF THE EMBRYO

The growth constant (k factor; Ricklefs 1967) of a White Tern embryo is 0.186, which may be compared with the logistic k factors for other species with prolonged in-

incubation. Thus, the  $k$  factor is 0.170 in the shearwater (Ackerman et al. 1980), and 0.148 in the Bonin Petrel (Pettit et al. 1981b). This comparison indicates that the tern embryo grows slightly faster than procellariiform embryos. The factor  $t_{10-90}$ , which represents the amount of time required to grow from 10% to 90% of the asymptotic weight, is 23.7 days in the tern, 25.9 days in the shearwater, and 29.7 days in the petrel (Pettit et al. 1981b). The maximal amount of absolute growth ( $g \cdot day^{-1}$ ) is 0.66 g in the tern egg and occurs at the 76th percentile of incubation or day 27. The maximal rate of absolute embryonic growth may occur earlier in incubation with decreasing egg mass among species with prolonged incubation. Among Procellariiformes the maximal rate of absolute growth ranges from the 70th percentile in the Bonin Petrel to the 75th percentile in the albatross (Pettit et al. 1981a, b).

#### EGG WATER LOSS

Daily water loss of the White Tern egg is approximately one-half of that predicted from egg mass alone ( $M_{H_2O} = 0.015 W^{0.74}$ , Drent 1970) while the incubation period of 35.5 days is 152% of that predicted ( $I = 11.64 W^{0.221}$ , Ar and Rahn 1978). The observed fractional water loss of 10.2% prior to external pipping and 17.5% over the entire duration of incubation is similar to the 15% reported for other species (Rahn and Ar 1974, Drent 1975, Ar and Rahn 1980) and is achieved by decreasing eggshell water vapor conductance to 50% of that predicted ( $G_{H_2O} = 0.384 W^{0.814}$ , Ar and Rahn 1978) and by decreasing incubation temperature to values lower than those of many other species (Drent 1975).

The measurements related to the water loss from the egg, obtained in the present study, necessitate some qualification of conclusions made in a previous report (Rahn et al. 1976). In view of the considerable amount of water lost during the long interval between external pipping and hatching, it is not valid to multiply the pre-pipping daily rate of water loss by the entire incubation period. This was done previously, to arrive at the value for the fractional weight loss ( $F$ ) of the egg during incubation (Rahn et al. 1976). After the outer shell membrane and eggshell are pipped, the increased water loss during the pip-to-hatch interval should be measured and combined with the pre-pipping water loss to derive the total amount of water lost over the entire incubation period. This amount, divided by the

initial egg weight, results in a value for  $F$  in the White Tern egg which is considerably higher than the value presented previously (Table 1). A similar situation obtains in the Bonin Petrel and the Wedge-tailed Shearwater, which also have a long interval between external pipping and hatching (Whittow 1980, Grant et al. 1981).

In summary, the physiology of embryonic respiration in the White Tern shares many adaptive features for prolonged incubation with Procellariiformes. Thus, the low eggshell water-vapor conductance predictably ensures a reduced embryonic growth rate and low pre-pipping  $MO_2$ . The energetic cost of prolonged embryonic development as well as the oxygen cost of hatching, and the pre-pipping  $MO_2$  expressed as a percentage of hatching  $MO_2$ , are similar to those of procellariiforms that have been investigated.

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