

The Nest Environment of the American Crocodile (*Crocodylus acutus*)

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In the southern tip of the Everglades, Florida, a small population of the American crocodile, *Crocodylus acutus* builds nests in two quite different substrates, sand/shell and marl. Changes in temperature, soil water and gaseous composition were monitored in selected nests throughout incubation, and the gaseous resistance of the soils measured. Temperatures increased from approximately 30 C to a maximum of 34 C over incubation and no differences were found between the two nest types. The marl nests had a higher water content than the sand/shell nests and had a significantly higher resistance to gaseous diffusion. In both nest types there was a decline in PO_2 and an increase in PCO_2 over incubation, with greater extremes reached in the marl nests. In sand/shell nests, eggs lost 15% of initial wet weight over incubation. It is suggested that the crocodile embryo adapts to the characteristics of the different substrates by matching its metabolic rate to the gaseous environment of the nest. Important similarities in bird and crocodilian egg development suggest that the birds have been highly conservative in this feature of their biology.

THE American crocodile (*Crocodylus acutus*) population in southern Florida has shown a steady decline over the last century. It has been suggested (Ogden, 1978) that recent protective efforts may not have been successful in reversing this trend, although the population has been stabilizing in recent years (Kushlan, 1982). On the assumption that adults are adequately protected, any decline would most likely be due to inadequate recruitment from younger stock. Causes for the latter could be a decreased reproductive success resulting in fewer eggs laid, or an increased mortality at some stage in development between the embryo and the juvenile.

The small population of crocodiles in southern Florida (estimated at 100-400 nonjuvenile adults by Ogden, 1978) live at the northernmost limits of the range for that species and are probably near the limit of certain ecological tolerances (Kushlan, 1982). Ogden (1978) suggested that embryonic mortality was an important factor in population limitation. The conditions found in the nest microhabitat are likely to have a significant influence on embryonic development such that inappropriate changes or circumstances could be a major cause of egg mortality. For example, Ferguson (1981) has shown that alligator eggs (*Alligator mississippiensis*) incubated without nesting media fail to hatch. Unfortunately, there is little information on the nest environment of *C. acutus* in its natural hab-

itat and therefore no objective grounds for assessing this risk. To the best of our knowledge this is the first report on the gas and water conditions in incubating crocodile nests.

Nest gases.—The crocodile egg, like that of birds and a few turtles, is cleidoic; the eggshell and its membranes act as resistances to water and gas exchange between the egg and the nest environment (Lutz et al., 1980). In the cleidoic egg, changes in the internal gaseous environment are brought about by embryonic development, a phenomenon well documented in birds where, as development proceeds, respiratory metabolism increases with the result that the partial pressure of oxygen (PO_2) in the air cell decreases and the partial pressure of carbon dioxide (PCO_2) increases (Tazawa et al., 1980).

Diffusion is the primary means of gas exchange in closed soil nests. This has been shown both for mound nesting birds (megapods) and for hole nesting green (*Chelonia mydas*) and loggerhead sea turtles (*Caretta caretta*) (Seymour and Ackerman, 1980; Ackerman, 1981). The rate of diffusion is fixed by the gas partial pressure gradient between nest and the atmosphere, the permeability of the soils used in the nest mound, and the depth at which the eggs are laid. As a consequence the internal gaseous changes are exacerbated for eggs laid in an enclosed nest (Seymour and Ackerman, 1980).

There are, presumably, significant physiolog-

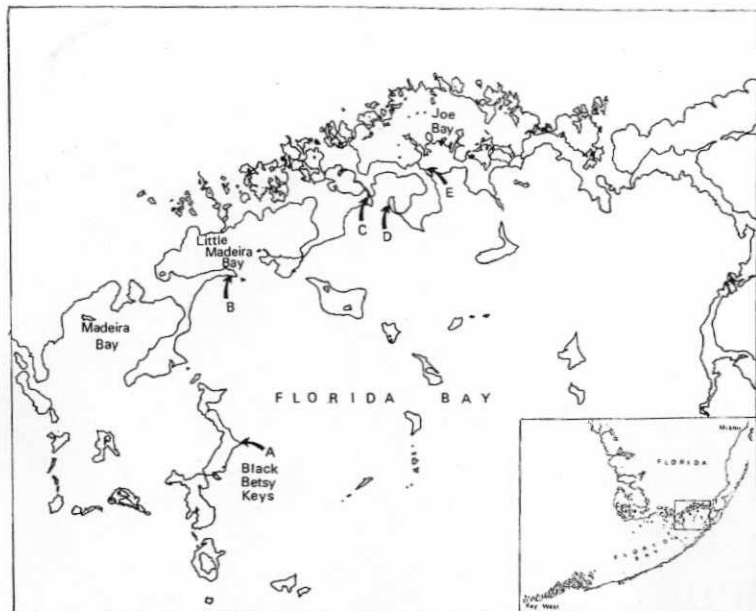


Fig. 1. Portion of Florida Bay showing positions of monitored nests. A: Black Betsy Point Nest, B: Madeira Point Nest, C: Mud Creek Nest, D: Alligator Bay Nest, E: Davis Creek Nest.

ical adaptations which allow, for example, the brush turkey embryo to survive and grow in environments where the CO_2 concentration reaches levels as high as 12% (Seymour and Rahn, 1978), while, for the domestic fowl an atmosphere containing more than 1% CO_2 causes significant decreases in hatching success (Lundy, 1969).

Nest water relationships.—Water immersion is a known hazard to soil incubated eggs. According to Grahame Webb (pers. comm.) it is a major cause of mortality for both salt and fresh water Australian crocodiles, and 48 hour submergence produced total mortality in clutches of *A. mississippiensis* eggs (Joanen, McNease and Perry, 1977). Still, some percentage of water in the nest soil may be beneficial to the eggs. A 100% humidity incubation environment may be necessary for *A. mississippiensis* eggs (Ferguson, 1981) and it appears that crocodile eggs can either take up water or decrease their weight throughout incubation. Bustard, for example (1971) recorded water loss by *Crocodylus novaeguinae* eggs in soils that had up to 3.9% water content, and the eggs increased in weight in soils of 7.8% water content. He recorded that most of the weight change had occurred within the first week of incubation. McIlhenny (1934) found that eggs

in the nest of *A. mississippiensis* increased in circumference and cracked over development. However, Moore (1953) reported that under normal field conditions, a *C. acutus* clutch lost 8.6% of its initial weight by the 70th day. Bustard (1971) also indicated that the eggs of *C. novaeguinae* were extremely tolerant of desiccation, being able to sustain at least 24.7% water loss and produce normal hatchlings. Water uptake may not only aid directly in the development of the embryo but under certain circumstances it may facilitate shell cracking near hatching through the absorption of water by the shell membranes (Lutz et al., 1980).

It would seem likely that if the above considerations apply to the American crocodile, then the site chosen by the female would be of some importance as it has to provide the proper environment needed by the growing embryo. However, in Florida Bay the American crocodile utilizes two very different soil substrates as nest sites: marl creek banks and sand/shell beaches. First impressions suggest that the sand/shell soil is a "clean" very porous soil while the marl nests have very fine particle sizes and a high organic matter content. Despite these differences, nests in both substrates are reused year after year and produce viable young (Moore, 1953; Ogden, 1978).

TABLE 1. CLUTCH MEASUREMENTS, 1979 AND 1980.

Clutch	Depth to top of clutch (cm)	Depth to middle clutch (gas probe) (cm)	Depth to bottom clutch (cm)	Number eggs	Size of egg chamber (cm)
1979					
Alligator Bay	42	51	59.5	43	
Black Betsy				41	40 × 30 × 40
Davis Creek				41	
Madeira Point				43	
Mud Creek	43	52	61	34	18 × 19
1980					
Madeira Point-1	28	36	45	40	
Madeira Point-2	36	45	53.5	32	
Mud Creek	18.5	27.2	36	39	

It is likely then, that the microclimate of the nest has a powerful influence on embryo development and hatching success. This is particularly true of the gas and water conditions throughout incubation. The aim of this study was to measure these factors in the natural nests of *C. acutus* in different soil substrates in order to gain some understanding of the microhabitat requirements of the developing crocodile egg.

METHODS

The study took place over two nesting seasons, in 1979 and 1980. Five nests were used in 1979 consisting of 3 sand/shell (Madeira Point, Black Betsy Point, Alligator Bay), and two marl nests (Mud Creek and Davis Creek) (Fig. 1). In 1980, two nests were used, one sand/shell (Madeira Point—two clutches) and one marl (Mud Creek). In order to insert the sampling tubes and probes, the eggs were removed (carefully) from the nests, weighed, measured and nest dimensions recorded. As the eggs were replaced in the nest chambers the tubes were positioned. Particulars are given in Table 1.

Temperature was monitored with a Markson Digital Thermometer and YSI probes placed in the center of the clutches. Gas was sampled using lengths of PE150 tubing that led from the center of each egg clutch to the nest surface. In order to prevent sand from entering the tubing each end in the clutch was covered with cheese cloth and the ends protruding above the nest were fitted with a 23 gauge "Luer-Stub" adapter or a cut off syringe needle and a plastic plug. The end above the nest was buried to prevent destruction by the female crocodiles.

The length of PE tubing ranged from 93–223 cm. After evacuation of the tube dead space, gas samples were collected in glass syringes equipped with "Luer-Lok" stop-cocks. They were locked by fitting the syringes with needles inserted in rubber stoppers. The syringes were transported back to the laboratory in a water filled cooler fitted with syringe holders to minimize temperature changes. The gases were analyzed in a BMS Mk2 Radiometer blood/gas analyzer and a Scholander 0.5 cc Gas Analyzer.

In 1979 soil samples were collected on a weekly basis. The soil was taken from the nest mound at the approximate depth of the clutch and placed in sealed glass containers. The samples were taken to the laboratory for soil water analysis. Percent soil water was determined by weighing soil samples before and after drying at 105 C for 24 hr. Salinity of the samples was calculated from chloride content. This was determined on oven dried soil by adding 5 to 10 ml of water to the soil, mixing well and the chloride concentration read on an Aminco chloride titrator. Salinity was also measured in 1980 soil samples taken from Mud Cr., Madeira Point and Alligator Bay nests.

Particle size distribution was determined on two soil samples from Mud Creek and Alligator Bay nests by mechanical analysis. The soil was dried at 105 C and then passed through a series of sieves. Total organic matter was measured by ashing these oven-dried soils at 450 C for 24 hours and reweighing.

Oxygen diffusivity measurements were made on soil samples collected from Alligator Bay and Mud Cr. nests in Oct. 1979 using techniques similar to those of Kutchai and Steen (1971).

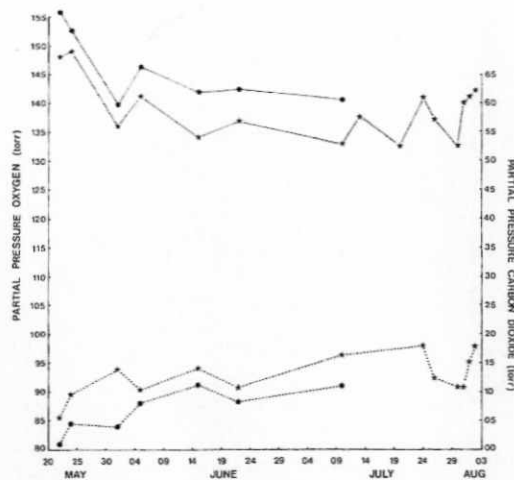


Fig. 2. P_{O_2} and P_{CO_2} changes in Alligator Bay (★) and Madeira Point (●) sand/shell nests, 1979. —, P_{O_2} ; ---, P_{CO_2} .

In essence a subsample of soil of known uniform depth formed one wall of a chamber. Oxygen was flushed from the chamber using nitrogen and the chamber sealed. The rate of increase of oxygen diffusing in from the atmosphere was monitored by an O_2 electrode (Radiometer) and the oxygen permeabilities (K) calculated using the equation of Wangenstein et al. (1970/1971):

$$K = \frac{0.693V}{t_{1/2}AT} \text{ cm sec}^{-1}$$

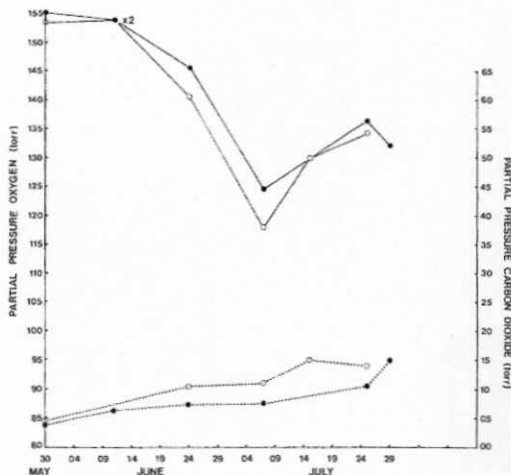


Fig. 3. P_{O_2} and P_{CO_2} changes in Madeira Point sand/shell nest, 1980. ○ Clutch 1; ● Clutch 2. —, P_{O_2} ; ---, P_{CO_2} .

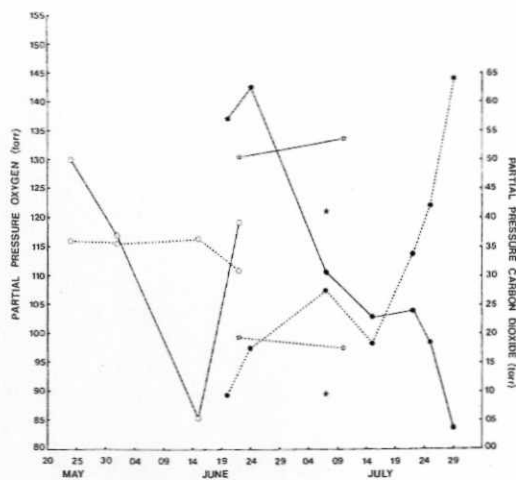


Fig. 4. P_{O_2} and P_{CO_2} changes in Mud Creek and Davis Creek marl nests, 1979 and 1980. ○, Mud Creek, 1979; ●, Mud Creek, 1980; ☆, Davis Creek, 1979; ★, Davis Creek, 1980. —, P_{O_2} ; ---, P_{CO_2} .

where V = volume of chamber (cm^3)

A = area of soil wall (cm^2)

T = absolute temperature

$t_{1/2}$ = time (sec) for the partial pressure of oxygen inside the chamber to reach one half of the partial pressure of oxygen outside the chamber.

The soil diffusivity (D) was then calculated from the equation $D = xK \text{ cm}^2 \text{ sec}^{-1}$, where x = the depth of the soil sample (cm).

Diffusivities were obtained from soil that had been oven dried at 105 C for 24 hrs and on soil

TABLE 2. MARL AND SAND/SHELL NEST COMPOSITION.

Mesh size	% particle type	
Sand/shell nest		
.5 mm–3.3 mm	59.89	Shell, coarse sand
250 μ –.5 mm	22.40	Medium sand
17.7 μ –25 μ	17.71	Fine sand and
<250 μ	100.00	Very fine dust
Marl nest		
>.6 mm	0.43	Wood
246 μ –.6 mm	0.27	Sand
<246 μ	99.3	Fine sand and
	100.00	Very fine dust

TABLE 3. DIFFUSIVITY (D) OF OXYGEN FOR ALLIGATOR BAY AND MUD CREEK SOILS (CM²·SEC⁻¹).

Alligator Bay (sand/shell)		Mud Creek (marl)	
% H ₂ O	D	% H ₂ O	D
		16	1.51×10^{-5}
10	7.21×10^{-3}	20	1.32×10^{-2}
15	1.96×10^{-2}	28	6.5×10^{-2}
40	1.54×10^{-2}	32	6.21×10^{-2}

to which different known quantities of water were added.

RESULTS

Temperature.—The range of nest temperatures measured was fairly narrow. In May and early June the mean temperature (both years) was 30.9 C (range 29.6–33 C) in the fertile nests. By late June the mean was 31.4 C (range 31–32 C), and in July \bar{x} = 32.7 C (range 28.6–34 C). Alligator Bay hatched on 3 Aug.; for those three days in Aug. the temperature averaged 34.3 C (range 34–35.1 C). A similar range (29–35 C) has been found for the nests of *A. mississippiensis* (Ferguson and Joanen, 1982). The incubation temperature of crocodiles overlaps with those of birds where the egg temperatures typically vary between 30–40 C with a mean value of 35.6 C for 27 species (Drent, 1975).

Soil comparison.—Comparison of marl and sand/shell nest soil composition is shown in Table 2. It can be seen that the sand/shell nests are considerably coarser (60% of the particles are greater than 0.5 mm) than the marl (99% of the particles less than 0.02 mm). The Mud Cr. soil also had almost 4 times the organic matter of the Alligator Bay soil (3.52% in Alligator Bay vs 13.43% in Mud Cr.). Similar differences between marl and sand/shell soil composition are reported in Buckman and Brady (1969).

Perhaps in consequence, the marl nests proved to have a consistently higher percentage of water than the sand/shell nests ($t = 2.035$, $P > 0.001$) (Table 4). Madeira Point (a sand/shell nest) in 1979 had the lowest amounts of water (5.06–13.0%) of any nest measured.

Nest oxygen and carbon dioxide profiles.—Nest oxygen and carbon dioxide profiles throughout the incubation periods of 1979 and 1980 are shown in Figs. 2, 3, 4. The initial values in the

TABLE 4. PERCENTAGE SOIL WATER, CROCODILE NESTS, FLORIDA BAY, 1979.

Date	Nests				
	Sand			Marl	
	BB	AB	MPt	MC	DC
4-28				36.14	
5-5		16.8			
5-17	10.96				
5-22	6.62	15.26			
5-30					32.8
6-5	7.89	19.35	13.30	32.09	33.74
6-15	13.92	18.6	8.78	31.32	22.59
6-22	10.40	13.75	12.90	28.83	
7-10	9.00	6.63	8.84	—	19.97
7-20	9.51	5.24	9.22		
7-24	7.98	4.89	9.32		
7-30	12.31	5.51	9.39		
7-31	12.52	5.60	5.06		

newly laid nest would be those of ambient, i.e. about 154 torr PO₂, 0 torr CO₂. Although the results are extremely variable, there is a trend of decline in oxygen and rise in carbon dioxide as incubation proceeds.

The most complete set of data was obtained from the sand/shell nests (Figs. 2, 3). It can be seen that in many nests a gradual fall in PO₂ was marked by rather sharp and irregular fluctuations, and the minimal PO₂ values were recorded several days before hatching. The average PO₂ in these nests was around 130–150 torr and the minimum was 116 torr. The gradual rise in PCO₂ was also accompanied by irregular, though lesser, fluctuations, that tended to mirror the PO₂ pattern. On established incubation the PCO₂ was about 5–10 torr and the highest value recorded was 16 torr.

Unfortunately the marl nests had a varying success. The data from Davis Cr. were incomplete. Interestingly, the 1979 PO₂ values increased as hatching approached (129–132 torr), suggesting as in the sand/shell nests, that minimal PO₂ values had been obtained some time before hatching. A single 1980 sample from Davis Cr. yielded a PO₂ of 120 torr and a PCO₂ of 13 torr. The most heavily monitored nest was in Mud Cr. In 1979 most of the Mud Cr. eggs were infertile, the nest later destroyed by raccoons, and in 1980 this site was flooded and the eggs apparently drowned (Mazzotti, Kushlan and Dunbar-Cooper, in prep.). The gas profiles for these nests are therefore probably strongly influenced by bacterial decay. As a con-

TABLE 5. EGG AND HATCHLING WEIGHTS (g): ALLIGATOR BAY, 1979.

Initial 5-5-79	7-30-79	Eggs			Hatchlings
		% weight lost	Full term 8-03-79	% weight lost	
91		—	77	15.4	59
86	75	12.8	72	16.3	54
98		—	83	15.3	66
93		—	80	14.0	64
91	82	9.9	80	12.1	63
88		—	79	10.2	56
89		—	75	15.7	57
93		—	83	10.7	63
93		—	65	30.1	51
$\bar{x} \pm SD$	91.3 ± 3.5		77.1 ± 5.8	15.5 ± 5.9	56.2 ± 5.1

sequence a relentless fall in PO_2 and rise in PCO_2 can be seen for the 1980 Mud Cr. clutch with the PCO_2 reaching as high as 64 torr.

Oxygen diffusivity.—The diffusivity values found in this study for sand/shell soil are very similar to those derived by Ackerman (1980) for the sand surrounding his green turtle nests, i.e., $1.5 \times 10^{-2} \text{ cm}^2 \cdot \text{sec}^{-1}$ for nests in Costa Rica and $2.5 \times 10^{-2} \text{ cm}^2 \cdot \text{sec}^{-1}$ for nests in Florida (Table 3).

The oxygen diffusivity of sand/shell soil from Alligator Bay was greater than that of the marl soil from Mud Cr. (Table 3) and at a typical water content of 10% sand and 30% for marl (Table 4), the marl would have an almost 9 fold lower oxygen diffusivity than the sand. Increase in the water content resulted in a fall in diffusivity in both soil types. However the effect was very much greater in the marl soil compared to sand/shell. For example a 10% increase in hydration caused a fall of $6.09 \times 10^{-3} \text{ cm}^2 \cdot \text{sec}^{-1}$ for the marl compared to $0.92 \times 10^{-3} \text{ cm}^2 \cdot \text{sec}^{-1}$ for the sand/shell.

Egg water loss.—Egg weight was monitored in the Alligator Bay sand/shell nest in 1979. The initial average weight of a random sample from the batch of eggs was $91.3 \text{ g} \pm 3.5$ (SE) (Table 5). This sample (Table 5) yielded weight losses over incubation, ranging from 10.8% to 30.1% (mean 15.5 ± 2.4 $n = 9$). Interestingly, at the end of incubation all the eggs from this clutch had "caved in" and had cracked shells. The hatchling weight at birth ranged from 54–64 g (average 59.2 ± 5.1), and the weight did not appear related to the initial egg weight or to the amount of water loss ($r^2 = 0.52$). For this

nest the birth weight of the crocodile hatchling was 0.64 ± 0.01 of the initial egg mass, an almost identical value to that found for eggs of bird species measured over a wide weight range (0.65) (Romanoff, 1967; Rahn, 1982). However, in contrast to the Alligator Bay nest, the eggs from the Madeira Point sand/shell nest were taut and spherical in appearance toward the end of incubation. Perhaps significantly the soil from the latter nest had a higher water content during the last twenty days of incubation ($\bar{x} = 8.4\%$) than that of Alligator Bay which averaged only 5.6%. Although only a single egg was weighed from the Madeira Point clutch, the weight loss found (7.4%) was considerably less than that for any of the eggs from the Alligator Bay nest.

DISCUSSION

Crocodylian nest and egg.—It would appear that during development *C. acutus* is tolerant of low PO_2 and high PCO_2 . In general, the values are rather similar to those found in green and loggerhead turtles towards the end of incubation i.e., PO_2 80–100 torr, PCO_2 35 torr (Ackerman 1977, 1980), and are also similar to those found in the bush turkey, *Alectura* of $PO_2 = 100$ torr and PCO_2 of 62 torr (Seymour and Ackerman 1980). Ackerman (1980) makes the interesting point that similar gas values are found toward the end of incubation inside the eggshell, i.e. in the air space, of the domestic fowl. Perhaps adaptations to the hypoxic/hypercapnic environment of the pre-pipping bird embryo is heritage of their pre-avian ancestry. In *C. acutus*, as in other enclosed-nest species, the high gaseous conductance of the eggshell may be

adaptive to compensate for the high humidity and high CO₂ environment soil resistance to diffusion (Lutz et al., 1980; Seymour and Ackerman, 1980). On artificially incubated sea turtles hatching success is increased if the gaseous conditions of the nest are mimicked and both egg mortality is increased and growth rate is slower if gas exchange is impeded (Ackerman, 1980). In both green and loggerhead sea turtle nests a decrease in gaseous conductance can result in a reduction in embryo growth rate, a prolonged incubation time and increase in egg mortality (Ackerman, 1981). From this consideration marl may be a less suitable substrate than sand during excessively wet seasons.

With these features in mind some interesting comparisons can be made between the developing green turtle and *C. acutus* sand/shell nests. Both nests contain a similar egg mass (5.5 kg green, 5.2 kg *C. acutus*). The nests are incubated at similar average temperatures (28–30 C green, Ackerman, 1977, 1980; 28–31 C *C. acutus*, this study), the eggs are laid at similar depths, the surrounding sands of both species have similar oxygen conductances and the nest gas tensions towards the latter part of incubation are also similar. The incubation times of both species are, however, markedly different (58 days in the green, Ackerman, 1980, and 90 days in *C. acutus*). This suggests that the intrinsic rate of increase in oxygen consumption is less in the *C. acutus* egg mass than in that of the equivalently sized egg mass of the green turtle. In the green turtle, Ackerman (1977) noted excursions in both CO₂ and O₂ levels at the end of the nesting period and attributed this phenomenon to the activity of the hatchlings struggling to free themselves from the nest. He suggested that when they worked hard their oxygen consumption would be high which would deplete oxygen from the nest cavity. This could result in quiescence until oxygen was replenished by diffusion when activity would start again. As we have noted in the crocodile nests, wide excursions in PO₂ were also found, however these occurred well before hatching and are therefore not likely to be due to the activity of hatching but the cause perhaps is similar, i.e., that towards the latter half of incubation a high rate of oxygen consumption by the egg mass outstrips diffusional exchanges. This would result in a fall in PO₂ or increase in PCO₂, and either could act as a metabolic suppressant to reduce oxygen consumption until the gaseous environment returned to more favorable conditions.

Such a strategy could be of advantage considering the nature of the nest sites used by *C. acutus*. Sea turtles appear to be highly selective in choosing nest sites, possibly selecting those beaches that have the necessary gas transport properties for optimal gaseous environments for the embryos (Ackerman, 1980; Seymour and Ackerman, 1980). *C. acutus*, on the other hand, nests in 2 quite different substrates and nest soil diffusivity will vary markedly, depending on the nature of the soil matrix and its water content. Under these circumstances different nests could only achieve optimal gaseous conditions, and avoid harmful changes, by continually matching the clutch respiration to the internal conditions of the nest. If the oxygen consumption of developing crocodile embryos is controlled by ambient levels of O₂ or CO₂ then such a strategy would allow nesting in a wider variety of substrates.

Crocodiles and birds.—In general, bird eggs lose water during incubation, and over a wide range of species the amount is similar i.e., around 15–20% of initial wet weight (Rahn and Ar, 1974). Struck by this uniformity, Ar and Rahn (1980) hypothesized that a constant water concentration in the egg, similar to that of the newly laid egg, may be necessary for optimal hatching success. They suggested that as dry matter is metabolized and metabolic water is produced throughout incubation, water concentration can only be maintained by losing a fixed portion of water. For evidence they calculated that the fractional loss for eggs ($F = \text{total weight loss} / \text{initial weight}$) for a wide variety of birds (81 species) was remarkably constant ($F = 0.150 \pm 0.02580$). This, they suggest, is the result of evolutionary selection for an appropriate pore structure in the shell. While some reptile eggs typically gain water (Packard and Packard, 1980) the hard-shelled crocodile egg appears to lose water, and interestingly, for the eggs of the one nest sampled in our study, the F value ($F = 0.154$) is almost identical to that found for birds. If this is not just a coincidence, then Ar and Rahn's hypothesis may also apply to the crocodile egg. In this context, it may be significant that unlike most reptiles, which have soft shelled eggs (Packard, Tracy and Roth, 1977), the crocodilian egg shell is remarkably similar, even in detailed structure, to those of birds (Ferguson, 1982).

Crocodile incubation is about 90 days compared to 27–28 days for a bird with similar sized

eggs (e.g., the Herring gull 82–94 g) (Drent, 1970). Similar total water losses would be achieved by the bird having a much higher daily water loss ($450\text{--}470\text{ mg}\cdot\text{day}^{-1}$ Ar and Rahn, 1980) compared to that of the crocodile egg ($157\text{ mg}\cdot\text{day}^{-1}$ this study). Water is lost by transpiration through the pores of the shell of bird eggs. The rate of water loss ($M_{\text{H}_2\text{O}}$, $\text{mg}\cdot\text{day}^{-1}$) is dependent on the water vapor conductance of the shell ($G_{\text{H}_2\text{O}}$, $\text{mg}\cdot\text{torr}\cdot\text{day}^{-1}$) and the water vapor partial pressure gradient across the shell ($\Delta P_{\text{H}_2\text{O}}$, torr). Presumably the same physical processes determine the rate of loss of water for the crocodile egg, and the low values would be due to having a reduced $G_{\text{H}_2\text{O}}$ and/or $\Delta P_{\text{H}_2\text{O}}$. Interestingly, many sea birds have greatly extended incubation times compared with similar sized eggs of land birds and have shells with reduced water vapor conductance (Whittow, 1980) in proportion to the extended incubation. The crocodile, on the other hand, has an egg shell with a water vapor conductance twice that of a similar sized bird egg (Lutz et al., 1980) so that, for a similar F value, long incubation periods require a reduced PH₂O. According to Rahn and Ar (1974), the mean PH₂O can be calculated from equation:

$$\Delta P_{\text{H}_2\text{O}} = M_{\text{H}_2\text{O}}/G_{\text{H}_2\text{O}}$$

For birds the average value is 34 torr (Rahn and Ar, 1974). In the crocodile the mean $\Delta P_{\text{H}_2\text{O}}$ can only be 7.5 torr. At an average incubation temperature of 30 C the water vapor tension inside the eggshell would be 31.8 torr and the effective vapor tension in the nest cavity would be 24.3 torr (31.8–7.5). This corresponds to an effective relative humidity of 76.4%. As a corollary: for the same relative humidity eggs with different incubation temperatures will experience different degrees of water loss. It has been determined that the temperature of egg incubation can determine sex for several reptilian species including *A. mississippiensis* (Ferguson and Joanen, 1982), but the role of differential water loss appears to have been ignored. This could be a factor of some importance.

Finally, we have seen that the bird and crocodile eggs show remarkable similarities both in structure and function. As the crocodile group is ancestral to birds (Romer, 1970) then it can be considered that perhaps birds have been highly conservative in this feature of their biology, retaining an essentially crocodylian poikilothermic egg and as such, the essential avian

advances in physiology and their morphological correlates are only manifested after hatching.

ACKNOWLEDGMENT

This work was funded by the Everglades National Park contract number CX5280-9-2129. We would like to thank James A. Kushlan and Frank Mazzotti for their generous assistance and advice on the project and Grahame Webb for his comments on the manuscript.

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FLORIDA 33149. Accepted 3 May 1983.