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

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THE NEST ENVIRONMENT OF THE AMERICAN CROCODILE

(*Crocodylus acutus*)

Report T-671

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INTRODUCTION

The American crocodile (*Crocodylus acutus*) population in southern Florida has shown a steady decline over the last century, and it has been suggested (Ogden, 1978) that recent protective efforts may not have been successful in reversing this trend, although the population may be stabilizing in recent years (Kushlan, in press; Kushlan and Mazzotti, in prep.). 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 Odgen, 1978) live at the northernmost limits of the range for that species and are probably near the limit of certain ecological tolerances (Kushlan, in press). 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 habitat and therefore no objective grounds for assessing this risk.

Nest Gases

The crocodile egg, like that of birds and a few turtles, is cleidoic; and 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. This is well documented in birds where, as development proceeds, respiratory metabolism increases with the result that the partial pressure of oxygen (PO2) in the air cell decreases and the partial pressure of carbon dioxide (PCO2) increases (Tazawa et al., 1980). It has been suggested that the intensifying hypoxic (low PO2), hypercapnic (high PCO2) environment that develops in the bird egg air sac eventually stimulates pipping of the shell by the chick. This is turn allows the initiation of lung air respiration. The diffusion characteristics of the shell are important as they determine to a great extent the gaseous composition of the air sac, and there is evidence that in different bird species, shell diffusion properties are finely tuned to the gaseous and water vapor conditions of different nest microhabitats (Carey, 1980).

The internal gaseous changes are exacerbated for eggs laid in an enclosed nest, such as mound or hole nests. This has been shown in studies on mound nesting brush turkeys (*Alectura lathami*) and hole nesting green turtles (*Chelonia mydas*) where metabolic activity of the eggs causes an oxygen depletion in the nest cavity and a buildup of CO2, particularly towards the end of incubation when the metabolic rate is highest (Seymour and Ackerman, 1980).

The nest gas values will depend upon the rate of oxygen consumption and carbon dioxide production of the clutch as well as the gaseous resistence of the nest soil. Ackerman (1977, 1980) produced an interesting model of the relationship between the egg clutch of sea turtles and the surrounding sand, by considering the clutch as a single egg entity. He assumed that the respiratory interplay between an embryo and its shell would be, in essence, very similar to that between the total egg clutch and the soil around it. In this model the gaseous exchange between the nest and the external environment would be a function of the permeability of the soil, its water content, the temperature of the clutch and the metabolic activity of the clutch. The latter would depend on the size of the clutch and its stage of development. The soil acted as the hypothetical shell whose permeability was determined by the particle size, its degree of hydration and the depth to the egg clutch (Ackerman, 1977).

There are, presumably, significant physiological adaptations which allow, for example, the brush turkey embryo to survive and grow in environments where the CO2 reaches as high as 12% (Seymour and Rahn, 1978), while, in the domestic fowl an atmosphere containing more than 1% CO2 causes significant decreases in hatching success (Lundy, 1969). It is possible that one such adaptation is seen in the very thin egg shell of the brush turkey. The gas levels that the embryo "sees" are determined, to some extent, by the shell resistence. In the brush turkey the shell permeability is greater than that of a similar sized standard bird egg and the gradients of gaseous partial pressures across the shell is correspondingly reduced (Seymour and Rahn, 1978). This may be important with respect to CO2 as not only is CO2 intimately involved in acid-base metabolism, but a high CO2 concentration tends to act as a metabolic inhibitor. Interestingly, the eggshell of the crocodile C. acutus also has much higher permeabilities than bird eggs of similar size, although in this case, the shell is much thicker than that of an equivalent bird eggshell (Lutz et al., 1980). The permeability values of the crocodile egg shell are dependent on the water content of both the shell and shell membrane so that nest humidity, and indirectly, soil water content, are probably important (Lutz et al., 1980).

Nest Temperature

The temperature of the egg clutch/nest is, of course, crucial to development of the embryos. The temperature of the nest would be determined by the heat output of the clutch (itself a function of clutch size and stage of incubation), the thermal properties of the surrounding nest medium, the ambient temperature(s) and the extent and intensity of solar radiation. Nest temperatures, therefore, will vary throughout incubation. Ogden (1978) collected spot temperatures on C. acutus nests in Florida Bay and found that the sand nests had an average temperature of 27.8°C in May and 31.4°C in July and his mud nests were slightly cooler, with a mean temperature of 27.5°C in May and 27.7°C in July. Interestingly, in a subsequent study, Patty, Kushlan and Robertson (in prep.) found that mud nests were warmer than the sand nests. They also found that the nests display diurnal temperature variances with a high reached at night and a low during midday, and that the average nest temperature increases over the summer months (as does the ambient temperature).

The increase in metabolic rate that occurs throughout incubation can lead to a rise in nest temperature if metabolic heat output becomes greater than the heat dissipation capacity of the surrounding nest material. In sea turtles, egg clutch temperatures become higher than the nesting beach soil towards the end of incubation (Ackerman, 1977, 1980). Alligators also tend to have nest temperatures higher than the ambient, but this is thought to be helped in part by the effects of the breakdown of the vegetation of which the nest mound is made (Goodwin and Marion, 1978; Dietz and Hines, 1980).

The biological effects of temperature are profound. In reptiles the incubation temperature strongly influences the duration of incubation. For exmaple, in sea turtles (green *Chelonia mydas* and loggerhead *Caretta caretta*) the length of incubation increases approximately 5 days per 1°C below the optimal incubation temperature (Mrosovsky and Yntema, 1980). Bustard (1971a) found that incubation in green turtle nests in shady, wind-exposed areas was twice as long as that for nests in sunny protected areas. Temperature also affects hatching success. Bustard (1971b) found that the optimal temperature for *Crocodylus novaeguineae* development is 32°C, below which there was an increased mortality until at temperatures around 28°C, there were no survivors. The incubation temperatures may also have more subtle affects on the developing embryos. It appears that in some species of turtles, including sea turtles, sex is actually determined by incubation temperature, with higher temperatures causing femaleness and cool temperatures maleness (Bull *et al*., 1982). A similar phenomenon appears to operate in Alligators, though curiously in this species the higher temperatures produce males (Ferguson and Joanen, 1982).

As little as 1-2°C changes can make a considerable difference to the sex ratio of the hatchlings (Mrosovsky and Yntema, 1980). If true of turtles and alligators then it may also apply to crocodiles, so that differences in mean temperature of incubation could have profound effects on the sex ratio of the adult population. Clearly, it is of prime importance to have accurate data on temperature change in crocodile nests that occur throughout incubation.

Nest Water Relationships

Water immersion is also a known hazard and according to Webb (pers. comm.) is a major cause of mortality for both salt and freshwater Australian crocodiles. This flooding is mainly due to rainwater. Dietz and Hines (1980) found that at least 48 hrs of submergence in tap water were necessary to drown the eggs of *Alligator mississipiensis*. However, the submersion endurance for most species is not known.

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. mississipiensis* eggs (Ferguson, 1981) and it appears that crocodile eggs can take up water and increase their weight and volume throughout incubation. Bustard for example (1971b) recorded water loss by *C. 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. 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. novaeguineae were extremely tolerant of dessication, being able to sustain at least 24.7% water loss and produce normal hatchlings. However, turtle eggs incubated under low humidity dessicated and showed both low survivorship and some abnormal development (Packard et al., 1977) and both C. porosus and C. johnstoni are affected similarly (G. Webb, pers. comm.). Water uptake may not only directly aid 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).

Nest Substrate

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 different substrates, nests in both substrates are reused year after year and produce viable young (Moore, 1953; Ogden, 1978; Patty, Kushlan and Robertson, in prep.). Information on the water content of the nests and permeability characteristics of the soils is needed.

In summary, the microclimate of the nest has a powerful influence on embryo development and hatching success. This is particularly true of the temperature, 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 (Madeira Point, Black Betsy Point, Alligator Bay), and two marl nests (Mud Creek and Davis Creek). In 1980, two nests were used, one sand (Madeira Point - two clutches) and one marl (Mud Creek). At each of the sites investigated in 1980 two "control" nests were dug in the mounds at the same depth as the clutches. These served as controls in order to distinguish the effect of the metabolizing egg mass on the nest microclimate (see Appendix).

Gas was sampled using lengths of PE150 tubing that led from the center of each egg clutch to the nest surface (see Fig. 1). 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. 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

Table 1. Clutch measurements and age of eggs on day of probe placement, 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)	Age of Eggs at Probe Placement (days)
<u>1979</u>						
Alligator Bay	42*	51	59.5	43		1-2
Black Betsy				41	40x30x40	
Davis Creek				41		
Madeira Point				43		3-10
Mud Creek	43*	52*	61	34	18x19	1
<u>1980</u>						
Madeira Point-1	28	36	45	40		14-20
Madeira Point-2	36	45	53.5	32		1-2
Mud Creek	18.5	27.2	36	39		<14

* Calculated depths.

were transported back to the laboratory in coolers fitted with syringe holders and filled with water. This ensured that there was no gas leakage and maintained a steady temperature. The gases in 1979 and part of 1980 were analyzed in a BMS Mk2 Radiometer blood gas analyzer. In the latter part of 1980, a Scholander 0.5 cc Gas Analyzer was also used.

Four types of temperature instruments were used in the nests during the two nesting seasons. A Markson digital thermometer (Model 5650) with a YSI probe was used in both 1979 and 1980. The probe was introduced into the clutches through polyvinyl tubing (0.5 inch in diameter). The tubing was placed on the bottom of the egg chambers, in the middle of the clutch, and on top of the clutch (Fig. 1). The ends in the clutch were sealed with cheese cloth secured by rubber bands to prevent any damage to the eggs and closed off at the surface by rubber stoppers. As with the gas tubes, the external ends were away from the clutch and buried to prevent damage by the female crocodiles.

In 1979, we placed small (5 cm) mini-transmitters (Mini-Mitter Model L) into the center of the egg clutches. These were monitored by a Model CH Lafayette Receiver and calibrated against a mercury thermometer before and after insertion. In 1980, the temperature of Madeira Bay clutch 2 was monitored by a Rustrak 2-channel transister temperature recorder (Model 2133B) and two YSI general purpose thermistor probes. All temperature probes were calibrated against a NBS thermometer. One probe was buried into the center of the clutch and the second was buried in the nest mound at approximately the same depth as the center of clutch. Max-Min mercury thermometers were also buried in each clutch in 1980 (Mazzotti, Kushlan, and Dunbar-Cooper, in prep.).

In 1979 the sampling tubes were inserted on the following dates - Mud Creek, April 28; Davis Creek, 30 May; Alligator Bay, May 5; and Black Betsy Point, May 17. In 1980 the sampling tubes were inserted on Madeira Point, May 25; Mud Creek, May 24. Nest data are shown in Table 1.

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 probes and tubes were positioned. In 1979, the Madeira Point nest was reopened three times and Mud creek and Alligator Bay nests reopened once each to replace temperature probes. As opening the nests had the effect of reestablishing "atmospheric" gas tensions, only data from undisturbed nests were used in describing the natural changes in nest gas tensions. The other nests in 1979 and all the nests in 1980 were not reopened throughout the incubation period.

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 form Mud Creek, Madeira Point and Alligator Bay nests.

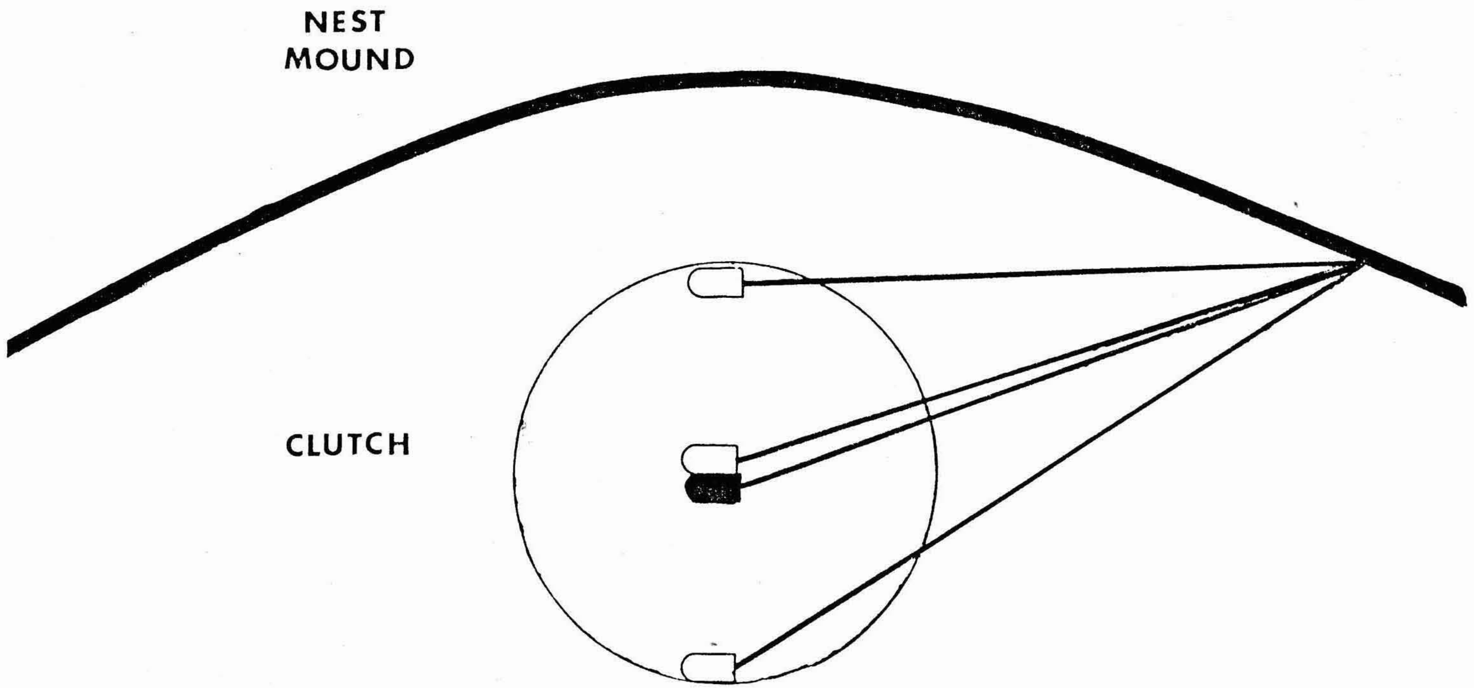

Fig. 1. Nest/clutch showing placement of probes. (Darkened probe = gas tube; plain probe = temperature tubes).

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 Creek nests in October 1979 using techniques similar to those of Kutchai and Steen (1971). In essence a subsample of soil of 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 Wangensteen et al. (1970/1971). Diffusivities were measured on soil that had been oven dried at 105°C for 24 hrs and soil to which different known quantities of water were added.

RESULTS AND DISCUSSION

Temperature

The nest temperature profile throughout incubation is shown in Figure 2. Raw data are given in Appendix 1. 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), and in July the mean was 32.7°C (range 28.6-34°C). Alligator Bay hatched on 3 August, for those three days in August the temperature averaged 34.3°C (range 34-35.1). However, greater temperatures than those found by our spot method were recorded by the max-min thermometers in 1980: 36.5°C was the maximum recorded for Madeira Beach nest (Mazzotti, Kushlan and Dunbar-Cooper, in prep.). Ogden (1978) believed that the low temperatures of his marl nest may have been the cause of nest mortality in those nests. The temperatures recorded by Ogden are lower than those we obtained for both sand and marl nests.

Noticeable from our 1980 data is the small diurnal fluctuation within the clutches (mean = 1.4 + 0.4°C) in over the 24 days monitored with the Rustrak recorder (Appendix 2). Figure 3 shows a typical example. The highest nest temperatures were reached at night (at approximately 2400 hrs) and the lowest at approximately 1200 hrs. This is, of course, opposite to the air temperature cycle. A long term increase and low daily fluctuation within the nest have been recorded previously for crocodilians (Patty, Kushlan and Robertson, in prep.; Ogden, 1978 for *C. acutus*, Chabreck, 1973; Goodwin and Marion, 1978; Dietz and Hines, 1980 for *A. mississippiensis*; Webb, Messel and Magnusson, 1977, for *C. porosus*). At any one time no difference was found between top, middle and bottom nest temperature measurements (four fertile nests monitored). In the sand Madeira nest no difference was also found between the nest and adjacent soil temperature ($p > 50\%$, $t = 0.03$, $df = 6$), however in the mud nest of Davis Creek, the mid-egg mass was 1.5°C warmer than the adjacent soil as determined in a spot check in the middle of incubation.

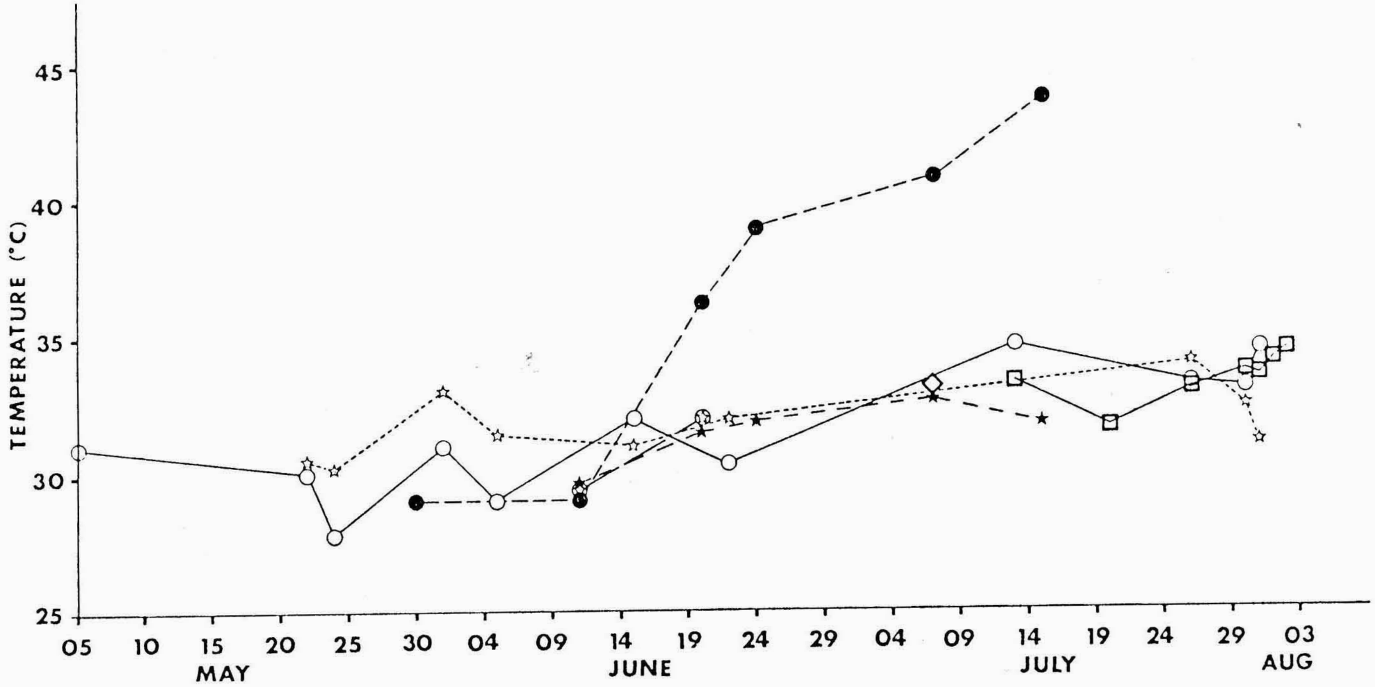

Fig. 2. Nest temperatures, 1979 and 1980. ○, Air, 1979; ●, Air, 1980; ☆, Madeira Point, 1979; ★, Madeira Point, 1980, Clutch 1; ⍟, Madeira Point, 1980, Clutch 2; □ , Alligator Bay, 1979; ◇ , Davis Creek, 1980).

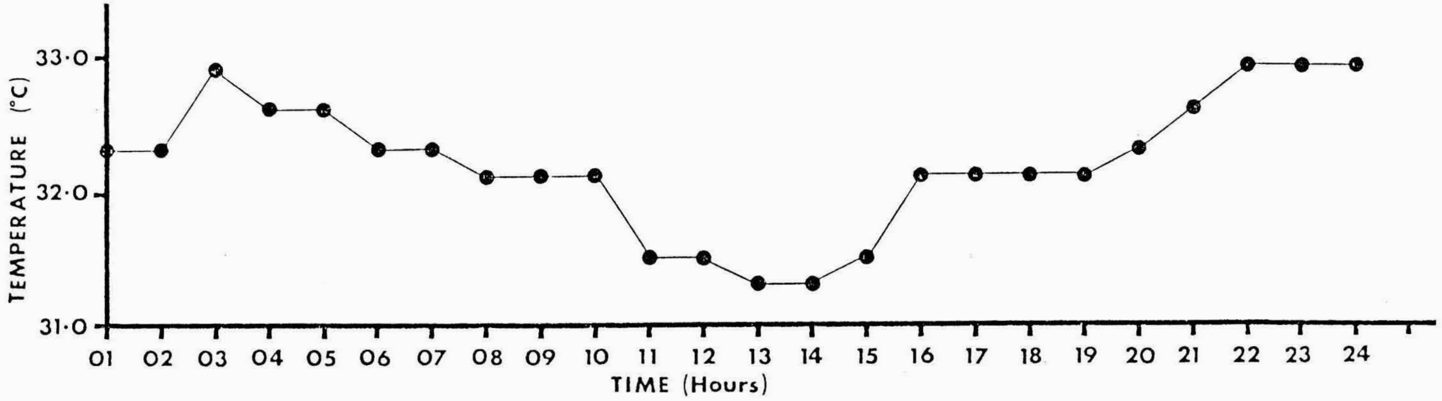

Fig. 3. Nest temperature, June 24, 1980, Madeira Point, Clutch 2.

Water Content and Soil Profile

Diffusion is the primary means of gas exchange in soil nests. This has been shown both for mound nesting birds (megapods) and for sea turtles (Prange and Ackerman, 1974; Ackerman, 1977; Packard et al., 1977; Seymour and Ackerman, 1980). The rate of diffusion is fixed by the oxygen gradient between nest and the atmosphere, the permeability of the soils used in the nest mound, and the depth at which the eggs are layed. It is possible that there is some maternal influence on nest permeability as the female crocodile churns up the soil in preparation for egg laying, presumably loosening the soil structure. After egg deposition she covers the eggs and smooths over the area. However, as incubation progresses, the soil structure settles out again, affected by factors such as water content and movement of the adult over the top of the nest.

Comparison of mud and sand nest composition is shown in Table 2. It can be seen that the sand 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 Creek soil also had almost 4 times the organic matter than that of the Alligator Bay soil (3.52% in Alligator Bay vs. 13.43% in Mud creek). Similar differences between marl and sand soil composition are reported in Buckman and Brady (1969).

Perhaps in consequence, the mud nests proved to have a consistently higher percentage H_2O than the sand nests ($t = 2.035$, $p > 0.001$) (see Table 3). Madeira Point (a sand nest) in 1979 had the lowest amounts of water (5.06-13.%).

Oxygen Diffusivity

The diffusivity values found in this study for sand soil are very similar to those derived by Ackerman (1980) for the sand surrounding his green turtle nests, i.e., 1.77×10^{-5} for nests in Costa Rica and 2.96×10^{-5} for nests in Florida (Table 4).

The oxygen diffusivity of sand soil from Alligator Bay was greater than that of the marl soil from Mud Creek (Table 4). 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 (0.11×10^{-5} for sand compared to 0.73×10^{-5} for mud for a 10% increase in hydration over the range measured).

At the percent water we found for the nest soils during incubation (2-19% sand, 36% mud; Table 3), the oxygen diffusion rates of marl soils would be considerably less than those found in the sand nests.

Nest Oxygen and Carbon Dioxide Profiles

Nest oxygen and carbon dioxide profiles throughout the incubation periods of 1979 and 1980 are shown in Figures 4-6 and Appendix 3. The initial values in the newly laid nest would be those of ambient, i.e. about 154 torr, PO_2, 0 torr CO_2. Although the results are extremely variable, there is a trend of a decline in oxygen and rise in carbon dioxide as incubation proceeds.

Table 2. Marl and sand nest composition.

Mesh Size	%	Particle Type
Sand Nest		
.5 mm - 3.360 mm	59.89	Shell, coarse sand
250 μ - .55 mm	22.40	Medium sand
17.7 μ - 250 μ	4.69	Fine sand and
< 250 μ	13.02	Very fine dust
	100.00	
Marl Nest		
	0.43	Wood
.6 mm	0.27	Sand
246 μ - .6 mm		Fine sand and
< 246 μ	99.3	Very fine dust
	100.00	

Table 3. Percentage soil water, crocodile nests, 1979.

Date	NESTS				
	Sand			Marl	
	BB	AB	MPt	MC	DC
4-28				36.14	
5-3		16.8			
5-17	10.96				
5-22	6.62	15.26			
6-5	7.89	19.25	13.30	32.09	33.74
6-15	13.92	18.60	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		

BB = Black Betsy, AB = Alligator Bay, MPt = Madeira Point, MC = Mud Creek, DC = Davis Creek.

Table 4. Diffusivity (D) of oxygen for Alligator Bay and Mud Creek soils ($cm^2.sec^{-1}.torr^{-1}$).

Alligator Bay (sand)		Mud Creek (marl)	
% H_2O	D	% H_2O	D
		16	1.81×10^{-5}
10	2.19×10^{-5}	20	1.58×10^{-5}
15	2.39×10^{-5}	28	7.9×10^{-6}
40	1.85×10^{-5}	32	7.44×10^{-6}

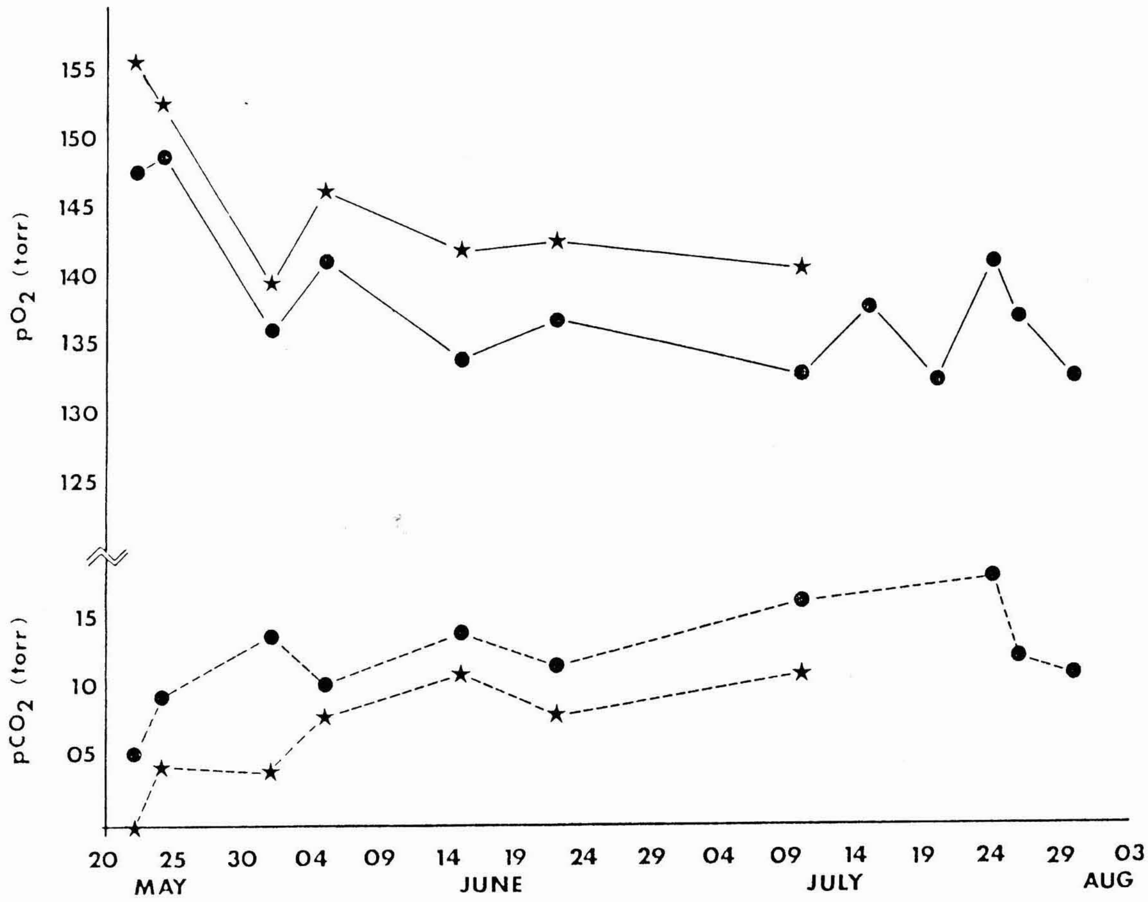

Fig. 4. PO_2/PCO_2 sand nests 1979. ___, PO_2; ---, PCO_2. ● , Alligator Bay; ★, Madeira Point.

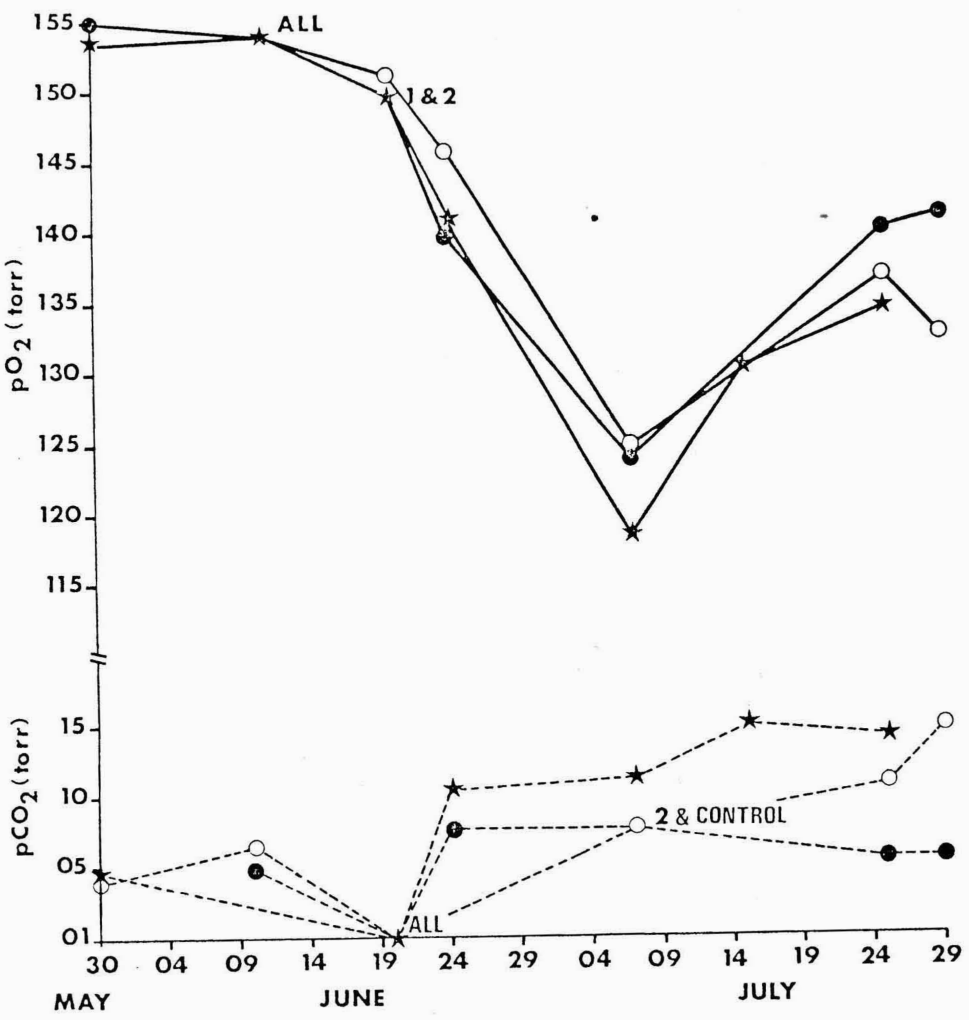

Fig. 5. PO_2/PCO_2 sand nests 1980. —, PO_2; ---, PCO_2. ●, Clutch 2; ○, Clutch 2, control; ★, Clutch 1.

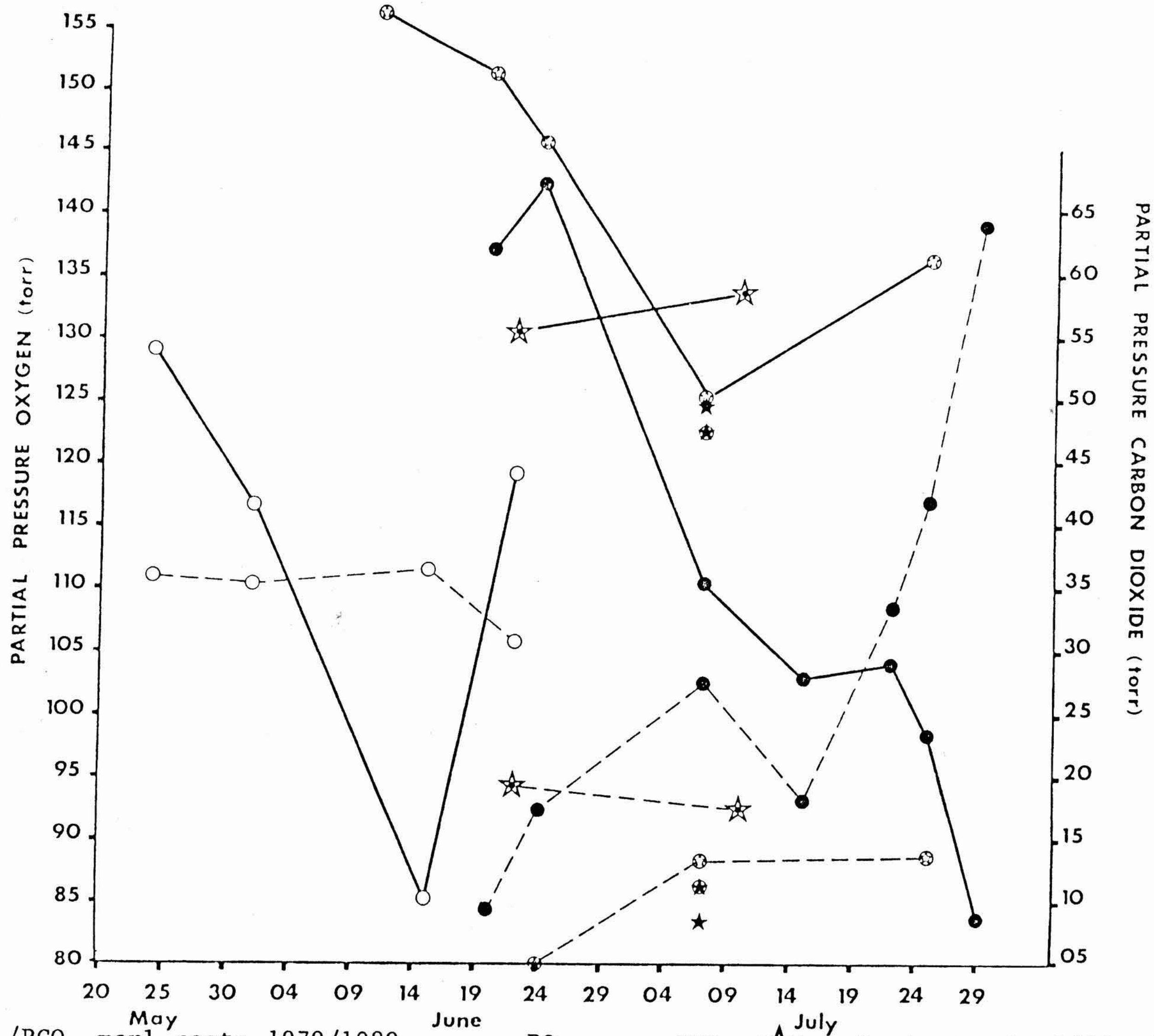

Fig. 6. PO_2/PCO_2 marl nests 1979/1980. ——, PO_2; ---, PCO_2. ☆, Davis Creek, 1979; ★, Davis Creek, 1980; ✪, Davis Creek, Control, 1980; ○, Mud Creek, 1979; ●, Mud Creek, 1980; ⍟, Mud Creek Control, 1980.

The most complete set of data was obtained from the sand nests (Figures 4 and 5). It can be seen that in many nests the 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 most heavily monitored nest was in Mud Creek. In 1979 most of the Mud Creek eggs were infertile and the nest was destroyed by racoons 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 probably the result of bacterial decay. A relentless fall in PO2 and rise in PCO2 can be seen for the 1980 Mud Creek clutch with the PCO2 reaching as high as 64 torr. The data from Davis Creek was incomplete. A single 1980 sample yielded a PO2 of 120 torr and a PCO2 of 13 torr, and the PO2 and PCO2 values towards the end of the 1979 incubation were around 125-140 torr and 17-20 torr respectively. Interestingly, the 1979 PO2 values gradually decreased as hatching approached, suggesting as in the sand nests, that minimal PO2 values had been obtained some time before hatching.

Egg Water Loss

Egg weight was monitored in the Alligator Bay sand nest in 1979. The initial average weight of a random sample from the batch of eggs was 91.3 g ± 3.5 (SE) (Table 5). The soil water ranged from 4.9 to 19.4% (Table 3). After about 80 days of incubation, two eggs were reweighed and found to have lost an average of 11% of their initial weight, which is approximately 0.36 $g.day^{-1}$. On the day before hatching (2 days later) this loss had increased to 14.2% of initial weight, i.e., for these two eggs the rate of loss was 2.4 g/day, suggesting that the great bulk of weight loss (presumably water) occurs over the final portion of incubation. The total sample (Table 5) yielded weight losses over incubation, ranging from 10.8% to 30.1% (mean 15.5 ± 2.4 n = 9). Interestingly, at this period 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 nest the birth weight of the crocodile hatchling is 0.64 ± 0.01 of the initial egg mass, an almost identical value to that found for the bird egg over a wide weight range (0.65) (Romanoff, 1967; Rahn, 1982). In contrast to the Alligator Bay nest, the eggs from the Madeira Point sand nest were taut and spherical in appearance towards the end of incubation. The soil had a higher water content during the last twenty days of incubation (8.4%) and although only a single egg was weighed from the batch, the weight loss found (7.4%) was considerably less than that for any of the eggs from the Alligator Bay nest. It is possible that the effect of water loss on the crocodile egg is, first of all, to cause the tough shell membrane to contract to a round, spherical shape thereby assisting in the cracking of the thick shell (Lutz et al., 1980), and then on further water loss (perhaps greater than 10%) for the membrane to collapse producing a concave appearance. It appears that all bird eggs lose water over

Table 5. Egg and hatchling weights (g): Alligator Bay, 1979.

	EGGS					HATCHLINGS
Egg Number	5-5-79	7-30-79	% Weight Lost	8-03-79	% Weight Lost	8-03-79
1	91		--	77	(15.4)	59
2	86	75	(12.8)	72	(16.3)	54
3	98		--	83	(15.3)	66
5	93		--	80	(14.0)	64
8	91	87	(9.9)	80	(12.1)	63
9	88		--	79	(10.2)	56
10	89		--	75	(15.7)	57
11	93		--	75	(15.7)	57
19	93		--	65	(30.1)	51

incubation (Ar and Rahn, 1980; Seymour and Ackerman, 1980), while reptile eggs typically gain water (Packard and Packard, 1980). However as we have shown the crocodile and perhaps also the rigid shelled eggs of the soft shell turtle <u>Trionyx spiniferus</u> (Packard et al., 1981) may lose water throughout incubation.

In general, bird eggs appear to lose a similar amount of water over incubation, i.e., around 15-20% of initial net weight (Rahn and Ar, 1974). Ar and Rahn (1980) hypothesize that a constant water concentration in the egg, similar to that of the newly laid egg, is necessary for optimal hatching success. They suggest 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 note that the fractional loss for eggs (F = total weight loss/initial weight) for a wide variety of birds (81 species) was remarkably constant (F = 0.150 ± 0.02580), and suggest that this is the result of evolutionary selection of an appropriate pore structure in the shell. Interestingly, the same calculation for crocodile eggs yields an almost identical F value (F = 0.154) and if this is not just 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 and Packard, 1979), the crocodile egg shell has well developed structural pores similar to those of birds (Marszalek et al., unpubl.)

Some comparison with birds suggests how water loss is achieved. In birds, water is lost by transpiration through the pores of the shell, and the total amount lost is the product of the average rate of loss per day (M H2O) and length of incubation (I). The rate of loss in turn, is dependent on the water vapor conductance of the shell (G H2O) and the water vapor partial pressure gradient across the shell (ΔPH2O). The herring gull, for example, has eggs of comparable size to those of the crocodile (82-94 g) but with much shorter incubation times (27-28 days) (Drent, 1970). The F value however is very similar (0.13-0.15) and this is achieved by having a high daily water loss of 450-470 mg day^{-1} (Ar and Rahn, 1980), compared to that for the crocodile egg (M H2O = 157 mg day^{-1}, this study). In order to arrive at the same F value with a larger incubation time, either the GH2O) must be reduced and/or the ΔPH2O must be reduced. Many sea birds have greatly extended incubation times compared with similar sized eggs of land birds and tend to have shells with reduced water vapor conductance (Whittow, 1980). The crocodile, however, 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 low water vapor pressure gradient (ΔPH2O).

The mean ΔPH2O can be calculated from the equation.

$$\Delta PH2O = \dot{M}\ H2O/GH2O$$

(Rahn and Ar, 1974). For birds the average value is 34 torr (Rahn and Ar, 1974). In the crocodile the mean ΔPH2O is 7.5 torr; however, as most water loss occurs at the end of incubation the actual gradient at this time must be somewhat greater.

Soil Water

The range of soil water contents in sand and marl nests (Table 3), show a considerable variation throughout the year. As expected, the marl nests appear to hold water with greater tenacity than the sand. This is reflected in the constant higher percentages of water found in these nests and is in agreement with work done previously on the differences between soil types and water carrying capacity (Buckman and Brady, 1969). As the effects on gas permeability is so much greater in the marl soil, the consequences to the nest environment are likely to be correspondingly influenced.

The extreme in water content is flooding, considered to be the major cause of nest failure in *C. porosus* (C. Webb, pers. comm.). Total loss of clutches by flooding also been reported for American alligators (Joanen et al., 1978; Goodwin and Marion, 1978), however alligator eggs can withstand up to 12 hrs of submergence in tap water (Joanen, McNeal and Perry, 1977). Most flooding of crocodilian nests is due to fresh water inundation and in the partially flooded nest in Alligator Bay (1980), salt analyses showed that this had been a fresh water phenomenon, presumably due to the exceptionally heavy rains. However, water taken from the nest of the flooded Mud Creek nest on 10 June 1980 was saline (Mazotti et al., in prep.), and on 29 July we found the chloride content of the nest soil water to be 642 M/L, i.e., approximately 125% full strength sea water (where sea water=35°/oo cl), indicating evaporative concentration of the original sea water inundation. The mortality in this nest was 100%.

The Crocodilian Nest and Egg

It would appear that during development *C. acutus* is tolerant of low PO2 and high PCO2. The values are rather similar to those found in green and loggerhead turtles towards the end of incubation, i.e., PO2 80-100 torr, PCO2 30-50 torr (Ackerman, 1977, 1980), and are also similar to those found in the bush turkey, *Alectina* of PO2 = 100 torr and PCO2 of 62 torr (Seymour and Ackerman, 1980). Ackerman (1980) makes the interesting point that similar gas values are found towards the end of incubation inside the eggshell, i.e., in the air space, of the domestic fowl, and perhaps this is a heritage of their pre-avian ancestry (our suggestion). In any case it is very likely that the species is adapted to develop optimally in these conditions and in *C. acutus*, as in other enclosed-nest species, the high gaseous conductance of the eggshell may be adaptive to compensate for the soil resistence to diffusion (Lutz et al., 1980; Seymour and Ackerman, 1980). In 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).

With these features in mind some interesting comparisons can be made between the developing green turtle and *C. acutus* sand nests. Both nests contain a similar egg mass (5.5 kg green, 5.2 kg *C. acutus*). The nests are incubated at similar temperatures (28-30°C green, Ackerman, 1977, 1980; 28-31°C *C. acutus*, this study). The egg nests are laid at similar depths, and as discussed above 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 *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. It is possible that the cause 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 results in a fall in PO2 or increase in PCO2, either acting as suppressants to reduce the metabolic rate until the gaseous environment returning to more favorable conditions.

The reason for such a strategy might lie in the nature of the nest sites chosen by *C. acutus*. Sea turtles appear to be highly selective in choosing nest sites and it has been suggested that one criterion could be those beaches that have the necessary gas transport properties which result in optimal gaseous environments for the clutches (Ackerman, 1980; Seymour and Ackerman, 1980). For *C. acutus*, on the other hand, 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. It is possible then that the oxygen consumption of developing crocodile embryos is controlled via a feedback process by ambient levels of O2 or CO2. This strategy would allow nesting in a wider variety of substrates but at the cost of some flexibility in incubation duration.

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 perhaps the bird has been highly conservative in this feature of its biology, retaining an essentially crocodilian type, poikilothermic egg. As such, the essential avian advances in physiology and their morphological correlates are only manifested after hatching.

Many questions have been raised by this study concerning the crocodile and its nest. At what level does PCO2 inhibit development and what is the lowest PO2 that can be tolerated? Are these results reached in the nest? At what percentage of soil water in the marl soil is gaseous exchange intereferred with? What is the amount of water an egg can lose before the embryo is harmed? Is a loss of water necessary for the release of the young from the eggs and if so, how much? If a low percentage of water in the soil increases the water loss in the eggs, will this effect the time of hatching of the young or prevent total absorption of the yolk before hatching? (Hatchlings were found in the 1981 nesting season which came from very dry nests with incompletely absorbed yolk sacs -- would this lower the viability of the hatchlings?). Clearly future study should be done on the effects of the gaseous environment on the growing embryo.

SUMMARY

1. In the nesting seasons of 1979 and 1980 selected crocodile nests from Florida Bay were studied to examine the nest environment throughout incubation.

2. Nest temperatures ranged from 29.0-35.5°C, the higher temperatures more associated with the latter part of the season. A small diurnal fluctuation was recorded over 25 days of monitoring a normal sand nest.

3. Nest soil water values varied considerably (4.89-36.14%). Marl tended to have higher amounts of water throughout the incubation period.

4. All eggs lost water over the incubation period. The greatest loss appeared to occur towards the end of the season. The amount of water loss is determined by the egg shell permeability and the water vapor gradient across the egg shell, the latter being dependent on the hydration of the soil. In the most complete set of data the average water loss found was very similar to that found for birds (15%). The average birth weight of the hatchlings was 0.64 of the initial egg mass, also very similar to that found for birds.

5. The oxygen diffusivity of sand was much greater than that of marl. In marl the diffusivity was strongly influenced by water content.

6. In all nests there was a decline in oxygen and rise in CO2 over incubation, i.e. developing embryos will naturally experience hypoxic, hypercapnic conditions. The changes were very variable between nests, though they appeared to be greater in mud nests. It appears that in several cases minimum nest oxygen levels were reached before the end of incubation.

7. It is suggested that the metabolic rate of the nest clutch of _C. acutus_ is regulated by oxygen and carbon dioxide levels in the nest. This allows _C. acutus_ to use soils of quite different and varying gas permeabilities for nesting sites.

CONCLUSIONS

There is no direct evidence provided from this study that over the two seasons monitored the internal nest enviornment was limiting to the American crocodile population in Florida Bay. This is particularly true with regards to temperature where only minor fluctuations were recorded. However, in some instances the excursions in nest oxygen and carbon dioxide levels were considerable.

It appears that an alteration in the gaseous composition of the crocodile nest is inevitable, the result of an interplay between the metabolism of the egg clutch and the resistance to gas diffusion provided by the nest soil. Some degree of hypoxia and hypercapnia in the internal nest environment might be necessary for optimal development and hatching, but excessive changes could be deleterious. The greatest changes, would probably occur in marl nests during heavy rainy seasons, as the wet marl soil has a very high resistance to gaseous diffusion, and the eggs in these nests might be most at risk. This effect would be compounded if any eggs drowned as it would lead to a substantial depletion of nest oxygen and accumulation of large amounts of carbon dioxide.

There is a clear need to gather more field data on undisturbed nests to investigate if there is a relationship between the changes in internal gaseous nest environment and hatching success. There is a necessity to investigate the respiratory physiology of the developing egg of a crocodilian species in order to establish the optimal levels of environmental PO2 and PCO2, and to identify harmful changes.

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APPENDIX I

Temperatures of Everglades Crocodile Nests (1979-1980)

I-A. MADEIRA POINT NEST

Date	Top	Middle	Bottom	Control	Air above nest
1979					
5-22		30.5#			30.0+
5-24		30.2#			28.5+
6-01		33.0#			29.0+
6-05		33.0#			29.0+
6-15		31.0#			32.0+
6-22		32.0#			33.0+
7-10					35.0+
7-26	34.2*		33.9*		31.0*
7-30	33.2*		31.5*		31.7*
	31.0*		30.8*		33.0*
			CLUTCH 1		
1980					
5-30		29.3*			30.6*
6-11		32.0*		29.5*	30.5*
6-20				31.6*	33.5*
6-24				31.5*	34.2*
7-07				32.4*	40.8*
7-15				32.0*	43.9*
			CLUTCH 2		
6-11	29.7*	29.6*	30.0*	29.5*	30.5*
6-20	32.3*	31.5*	31.5*	31.6*	33.5*
6-24				31.8*	31.6*
7-07	33.1*	32.7*	32.7*	32.4*	40.8*
		31.6x			
7-15	32.3*	31.8*	31.6*	32.0*	43.9*
7-26		30.6x			
7-27		32.8x			
7-28		32.5x			
7-29		37.8x			

#	Mini Meter Telemeters
*	Markson Digital Thermometer
+	Max-Min Thermometer
x	Rustrak Recording Thermometer

I-B. ALLIGATOR BAY NEST

Date	Top	Middle	Bottom	Control	Air above nest
1979					
7-13	33.0^{*}		33.5^{*}		39.5^{+}
7-20	31.3^{*}		32.1^{*}		
7-26	32.5^{*}		33.7^{*}		36.5^{+}
7-30	33.4^{*}		33.9^{*}		33.0^{+}
7-31	32.9^{*}		34.0^{*}		37.0^{+}
8-01	34.1^{*}		34.0^{*}		38.5^{+}
8-02	35.1^{*}		34.0^{*}		

#	Mini Meter Telemeters
*	Markson Digital Thermometer
+	Max-Min Thermometer
x	Rustrak Recording Thermometer

I-C. BLACK BETSY POINT NEST

Date	Top	Middle	Bottom	Control	Air above nest
1979					
5-22		30.2[#]			30.0[+]
5-24		31.4[#]			27.0[+]
6-01		31.5[#]			31.5[+]
6-15		29.4[#]			
6-22		31.3[#]			32.0[+]
7-10		33.5[#]			37.0[+]
7-13		32.5[#]			35.0[+]
7-24	28.6[*]		29.0[*]		30.5[+]
7-26	30.7[*]		30.6[*]		32.0[+]
7-30	31.2[*]		31.1[*]		34.6[+]
7-31	31.2[*]		31.2[*]		33.5[+]

[#] Mini Meter Telemeters

[*] Markson Digital Thermometer

[+] Max-Min Thermometer

X Rustrak Recording Thermometer

I-D. MUD CREEK NEST

Date	Top	Middle	Bottom	Control	Air above nest
<u>1979</u>					
5-03		$27.8^{\#}$			
5-05		$29.3^{\#}$			31.0^{+}
6-22		$31.0^{\#}$			33.5^{+}
<u>1980</u>					
5-30				30.1^{*}	
6-11	29.5^{*}	29.7^{*}	29.5^{*}	29.8^{*}	27.5^{*}
6-22	29.7^{*}	29.4^{*}	29.6^{*}		38.9^{*}
6-24				31.8^{*}	31.6^{*}
7-15				31.5^{*}	37.9^{*}

I-E. DAVIS CREEK NEST

Date	Top	Middle	Bottom	Control	Air above nest
<u>1980</u>					
7-07	33.2^{*}	33.1^{*}	32.2^{*}	31.6^{*}	42.7^{*}

\# Mini Meter Telemeters

* Markson Digital Thermometer

\+ Max-Min Thermometer

x Rustrak Recording Thermometer

APPENDIX II

Rustrak Temperatures - Madeira Point Nest

(1980)

Date	Nest °C	Date	Nest °C	Date	Nest °C
June 20		June 28		July 6	
1800	31.1	0600	32.8	0600	31.6
2400	32.2	1200	31.9	1200	31.1
		1800	31.9	1800	30.2
		2400	33.1	2400	29.7
June 21		June 29		July 7	
0600	31.7	0600	33.1	0600	32.7
1200	31.1	1200	31.9	1200	31.6
1800	31.7	1800	31.9	1800	32.2
2400	32.2	2400	29.7	2400	33.3
June 22		June 30		July 8	
0600	31.7	0600	31.9	0600	32.5
1200	31.7	1200	31.1	1200	31.1
1800	30.6	1800	30.3	1800	31.6
2400	31.7	2400	30.8	2400	32.2
June 23		July 1		July 9	
0600	31.7	0600	30.8	0600	31.6
1200	30.6	1200	30.0	1200	30.5
1800	31.7	1800	29.7	1800	31.6
2400	32.2	2400	29.7		
June 24		July 2		July 26	
0600	31.7	0600	29.7		
1200	31.1	1200	29.1		
1800	31.7	1800	28.6	1800	31.7
2400	32.5	2400	30.0	2400	32.8
June 25		July 3		July 27	
0600	32.2	0600	30.8	0600	32.5
1200	31.7	1200	30.5	1200	32.3
1800	31.7	1800	30.0	1800	32.8
2400	32.5	2400	30.2	2400	33.1
June 26		July 4		July 28	
0600	31.9	0600	30.5	0600	32.5
1200	31.1	1200	30.0	1200	32.5
1800	31.1	1800	29.4	1800	35.0
2400	33.1	2400	30.0	2400	35.8
June 27		July 5		July 29	
0600	32.2	0600	30.8	0600	37.2
1200	31.4	1200	30.0	1200	37.8
1800	31.1	1800	29.4		
2400	30.5	2400	30.2		

APPENDIX III

Gas Measurements of Everglades Crocodile Nests

1979-1980 (torr)

MADIERA POINT

Date	P_{O_2}	P_{CO_2}	Date	P_{O_2}	P_{CO_2}
1979			1980		
			Clutch 1		
5-22	156.0	1.0	5-30	153.5	4.6
5-24	152.8	4.5	6-11	154.0	-
6-01	139.8	4.0	6-20	149.5	0.8
6-05	146.5	8.0	6-24	140.5	10.4
6-15	141.9	11.2	7-07	118.1	11.1
6-22	142.4	8.2	7-15	129.8	14.9
7-10	140.6	11.0	7-25	134.2	13.9
7-13	147.8	-	Clutch 2		
7-20	153.3	12.0	5-30	155.0	3.9
7-24	154.0	8.9	6-11	153.8	6.3
7-26	145.9	-	6-20	149.5	0.8
7-30	129.8	8.3	6-24	145.5	7.3
7-31	144.1	10.4	7-7	124.6	7.6
			7-25	136.2	10.6
			7-29	132.0	14.8
			Control		
			6-11	153.8	4.8
			6-20	151.0	0.7
			6-24	139.5	7.6
			7-7	123.7	7.5
			7-25	139.8	5.4
			7-29	140.7	5.4

MUD CREEK

Date	P_{O_2}	P_{CO_2}	Date	P_{O_2}	P_{CO_2}
<u>1979</u>			<u>1980</u>		
			Clutch		
5-24	129.7	36.0	6-20	137	9.3
6-1	116.8	35.5	6-24	142.5	17.4
6-15	85.3	36.5	7-7	110.7	27.3
6-22	119.1	30.8	7-15	102.9	18.1
			7-22	103.9	33.6
			7-25	98.4	41.9
			7-29	83.7	63.9
			Control		
			6-11	156.0	-
			6-20	151.0	-
			6-24	145.5	4.3
			7-07	125.2	13.2
			7-25	136.2	13.6

DAVIS CREEK

Date	P_{O_2}	P_{CO_2}
<u>1980</u>		
Clutch		
7-07	121.2	9.5
Control		
7-07	122.5	11.2

ALLIGATOR BAY

Date	P_{O_2}	P_{CO_2}
1979		
5-22	148.1	5.5
5-24	149.1	9.6
6-01	136.2	13.8
6-05	141.2	10.4
6-15	134.2	14.2
6-22	136.9	11.6
7-10	133.1	16.3
7-13	137.7	-
7-20	132.5	-
7-24	141.0	18.1
7-26	137.0	12.3
7-30	132.6	10.9
7-31	140.1	10.8
8-01	141.0	16.1
8-02	142.3	17.8

BLACK BETSY POINT

Date	P_{O_2}	P_{CO_2}
1979		
5-24	152.5	6.6
6-05	149.5	4.8
6-22	145.4	5.4
7-10	146.4	6.8
7-13	150.4	-
7-20	146.6	8.8
7-24	151.0	8.2
7-26	140.9	-
7-30	136.2	5.4
7-31	149.6	7.2