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# Water Relations of Crocodilian Eggs: Management Considerations

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**Abstract:** This paper reviews knowledge about water relations of the eggs of *Crocodylus porosus* and makes it clear that, for a crocodile farmer, more information is needed to establish the relationship between the visible signs that occur at different incubation humidities and the fitness of resultant hatchlings. It may turn out that water availability, like temperature, has subtle but important effects which should not be overlooked.

For a crocodile farmer, the aim of carefully controlling the conditions of egg incubation is to maximize hatching rate and hatchling fitness. Ideally, no embryos should die from any cause related to management. Success will be determined by the conditions of transport between the nest and the incubator and by the physical conditions of incubation, particularly temperature and humidity, the gaseous environment and, probably to a lesser extent, whether the incubating eggs are surrounded by natural nesting material, other materials such as vermiculite, or just humid air.

In the wild, the nest provides the physical conditions of incubation. Regardless of whether a species is a mound-nester or a hole-nester, a diversity of materials is used for nest construction and some are better than others at providing optimum conditions for incubation. Hence, in the wild, crocodilians develop under a diversity of physical conditions, with varying success. In a farm, where precise artificial control can be maintained over all variables, it should be possible to do very much better.

What, however, are the best incubation conditions? An obvious starting point for determining this has been by reference to the conditions in successful field nests. Temperatures in the low thirties and a humid atmosphere allow successful development and the emergence of apparently fit hatchlings.

From this starting point, refinement has proceeded by experiment - the only way to determine the best conditions for a particular species. It is worth remembering, however, that success is usually scored with the production of apparently healthy hatchlings. The fitness of individuals subsequent to hatching has rarely been assessed in such a way that shortcomings might be correlated with incubation conditions. When this has been done, with incubation temperature, the results have been spectacular (see Lang Chapter 30; Joanen *et al.* Chapter 51).

Most of the refinements of physical conditions of incubation have been with respect to ambient temperature, and the subject is discussed in numerous chapters within this book. Incubation temperature determines not only the sex (Ferguson and Joanen 1982) of hatchlings, but also their post-hatching fitness (see Joanen *et al.* Chapter 51). In the wild, through naturally occurring variation of incubation temperatures, hatchling crocodiles of both sexes are produced. However, the discovery of sex-dependent growth rates will almost certainly lead to crocodile farmers favouring one sex and we shall undoubtedly see increasing attention being paid to precise and accurate control over incubation temperatures.

Apart from temperature, the nest mound or hole also influences humidity and respiratory gases. This chapter discusses several aspects of the water relations of crocodilian eggs that may be significant to farm management and draws attention to some deficiencies in our knowledge.

## INCUBATION HUMIDITY-HATCHING SUCCESS AND FITNESS

By comparison with temperature, the determination of optimum humidity during incubation has received little attention. Like temperature, we do know that successful hatching will occur over a wide range of humidities, but the upper and lower limits of water availability which allow successful hatching have not been quantified.

Bustard (1971) observed a small number of *Crocodylus novaeguineae* eggs and found that apparently normal hatchlings resulted from incubation in moist sand (7.8% water) and dry sand (2% water), despite weight changes of plus and minus 25% respectively. In some *Crocodylus porosus* nests I have observed, successful hatching occurred from eggs which have dried out sufficiently to leave large air spaces under the shell, perhaps 20% of the egg volume, with the shell membrane shrinking right away from the shell. In

others, conditions appear to be almost dripping wet, with eggs swollen from the uptake of water - yet successful hatching of such eggs is commonplace.

It seems reasonable to ask whether or not the fitness of hatchlings depends on the ambient water environment during incubation across the range over which hatchlings are produced successfully. Work by Packard et al. (1980, 1981a,b, 1982) and Tracy et al. (1978) has shown that the water conditions of incubation have a strong influence on the size of hatchlings in species with flexible-shelled eggs. It is quite probable that this, in turn, has an influence on overall fitness subsequently. However, in *Trionyx spiniferus*, the soft-shelled turtle (which has a hard-shelled egg) variability in the hydric environment during incubation has little effect on the developing embryos (Packard et al. 1979,1981c). This observation has been extrapolated to rigid-shelled eggs in general (Packard and Packard 1984), although my own observations and those of Grahame Webb and Peter Whitehead (pers. comm.) suggest that very dry eggs produce smaller hatchlings.

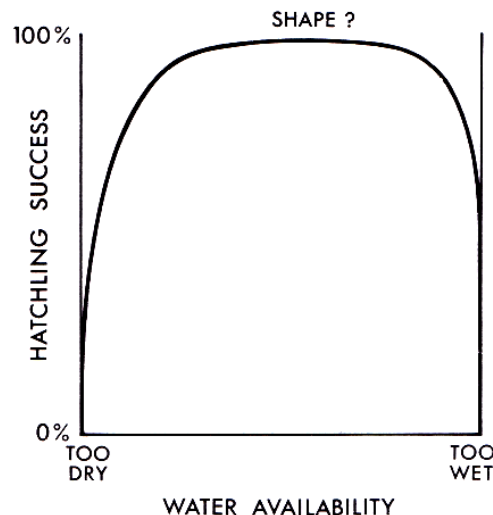


Fig. 1. Schematic representation of the possible relationship between hatching success and water availability during incubation of crocodilian eggs. The humidity limits of successful hatching are unknown, as is the shape of the survival curve and the level of humidity and other factors at which longitudinal cracking and subsequent swelling occurs.

The sort of information that ideally needs to be obtained is illustrated on Figure 1 for hatching success and Figure 2 for hatchling fitness (at any given temperature). Concerning Figure 1, the shape of the curve is unknown, as are the points on the "water availability" axis where success is severely reduced and at which longitudinal cracks develop. From Bustard (1971) and from personal experience, it is clear that crocodilian eggs tolerate a broad range of water availability, so the curve is likely to have a broad plateau. At the upper end, death of the embryo results from asphyxia when pores in the eggshell are blocked to oxygen diffusion. Grigg and Beard (unpublished data) measured oxygen diffusion through the shell-shell membrane complex and it is clear that the presence of a free water coating over the egg surface reduces diffusion drastically. At late stages of development particularly, when oxygen consumption of the developing embryo is high, inhibition of oxygen diffusion will result in death. This is undoubtedly the main cause of egg mortality due to flooding. The lower limit of water availability at which hatching is not compromised is also unknown but, from a management point of view, it is not of great concern as it seems to be easy to avoid. The lower limit, as well as the shape of the curve, is bound to be temperature-dependent.

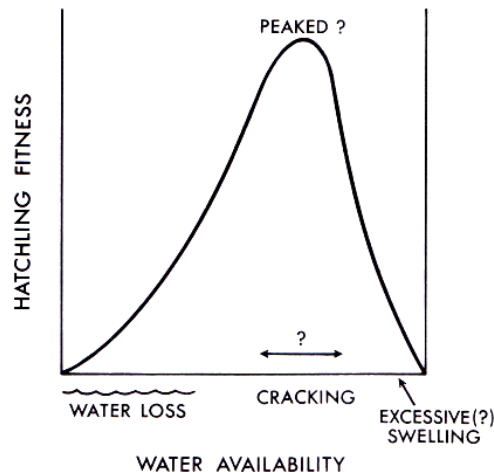


Fig. 2. Schematic representation of the possible relationship between hatchling fitness and water availability during incubation of crocodilian eggs. The extent to which hatchling fitness may depend upon the water environment during incubation is unknown as yet.

More important than the hatching success curve, which is obviously tolerant, we need to know about the possible dependence of hatchling fitness on water availability during incubation (Fig. 2). Is it markedly peaked by contrast with Figure 1? If so, then much more effort may need to be put into the regulation of specific humidities within farm incubators. Unlike its temperature, a developing embryo can regulate its body water content from available resources (water and albumen). Hence, one might predict a broad and flat rather than peaked curve, but the matter is in need of clarification.

#### RATES OF WATER LOSS AND GAIN

The eggs of crocodilians comprise a tough shell membrane underlying a calcareous shell which is pierced by pores. The whole structure has been described in elegant detail by Ferguson (1981, 1985). Grigg and Beard (1985) have described various aspects of water loss and gain at different stages of embryonic development, and those results are drawn upon here.

In thinking of water loss and gain by crocodile eggs, it is helpful to envisage the calcareous shell as an impermeable barrier to gases, including water vapour, pierced by numerous small pores through which diffusion of water vapour, oxygen and carbon dioxide occurs. The shell is the major barrier to water loss, as can be seen readily by the dramatic increase in the rate of water loss in a dry atmosphere after development of the longitudinal cracks that are typical of crocodile eggs incubated in a moist environment.

Comparing cracked and uncracked eggs from a single clutch, the former lost water at the rate of  $2120 \pm 180 \text{ mg d}^{-1}$  (SE;  $N = 8$ ), the latter at  $1260 \pm 50 \text{ mg d}^{-1}$  ( $N = 9$ ) (Grigg and Beard 1985). Compared to birds eggs, the eggs of crocodilians are more porous and uncracked eggs lose water four to five times more rapidly when measured under equivalent drying conditions (Packard et al. 1979; Grigg and Beard 1985). Naturally the rate of water loss depends on the vapour pressure gradient as well as the porosity, hence the need to incubate crocodilian eggs under humid conditions. (It is an interesting, but separate, topic to speculate upon why eggs of crocodilians should be so porous in comparison to those of birds.)

There are two sources from which an egg can regain lost water; by direct uptake and by the production of metabolic water. Grigg and Beard (1985) measured rates of water uptake by eggs replaced in a moist environment after a period of desiccation. There is considerable variability between clutches, but eggs from one clutch (#19) which lost approximately 1300 mg of water per day in drying conditions, regained almost 500 mg per day when replaced in a moist environment. By calculation, metabolic water production by a late term egg from the same clutch would approximate only 65 mg per day at  $30^{\circ}\text{C}$ . This emphasizes the importance of ambient water vapour conditions in determining the success or failure of a crocodilian egg. In contrast, the less porous eggs of birds retain water much more easily and the relative importance of metabolic water is much greater.

#### SHELL POROSITY AND INCUBATION IN NATURAL NESTING MATERIAL

In *Alligator mississippiensis* eggs, Ferguson (1981) described the progressive degradation of the outside of the shell during development, under the influence of microorganisms and/or carbonic acid formed from water and respiratory carbon dioxide. He predicted that this would result in both increased porosity of the shell as incubation proceeded, which would facilitate gas exchange in the later stages of development

(when oxygen demands are highest), and cause a weakening of the calcareous shell, making for an easy exit from the egg when incubation was complete. Accordingly, Ferguson has recommended that crocodile farmers should incubate eggs in natural media in order to promote the extrinsic degradation of the shell.

Whereas this may be desirable in *A. mississippiensis*, its value for *Crocodylus porosus* is uncertain because, even though surface pitting and 'rusty' erosion craters develop in *C. porosus*, just as in *A. mississippiensis* eggs, unaided hatching occurs routinely and spontaneously in the many eggs of *C. porosus* which show no sign of extrinsic degradation. Ferguson (1981) suggested for *A. mississippiensis* that failure to promote increasing porosity by incubation in natural media will leave hatchlings suffering mortality from asphyxia. However, Grigg and Beard (1985) found no sign of increased rates of water loss in older eggs, unless longitudinal cracking had developed. Measurements of rates of water loss may be an indication of shell porosity, but may not necessarily reflect shell-shell membrane gas conductance to respiratory gases (discussion in Grigg and Beard 1985), so whether oxygen conductance increases with incubation age is unknown. Increase in oxygen conductance of the eggshell of *Crocodylus johnstoni* eggs with increasing incubation time appears to be unrelated to degradation of the mineral layer (Whitehead Chapter 47). However, the hatching of *C. porosus* routinely from eggs without any visible extrinsic degradation shows that it is very doubtful that oxygen supply is limited in such circumstances.

The removal of calcium and other salts from the shell by the developing embryo will reduce shell strength and assist the breakout of the hatchling. Any additional weakening of the shell by extrinsic degradation, when it occurs, would be an advantage. However, in *C. porosus*, the significance of extrinsic degradation does not appear to be as great as has been suggested for *A. mississippiensis* and the extra time, effort and space required to incubate eggs in natural media, with the concomitant higher risk of infection, is unlikely to be justified.

In nature, the elaborate behaviour pattern by which mother crocodiles facilitate hatching by gently rolling unhatched eggs in the mouth (Pooley 1977) suggests that parental assistance for at least some eggs has been a normal circumstance for the last few million years at least. The crocodile farmer who plays that role from time to time appears to be maintaining a fine tradition!

The development of longitudinal cracks in eggs incubated under moist conditions may also facilitate exit by the hatchling, although whether or not this enhances survival significantly is unknown. As the egg swells, taking up water after the first cracks form, the adhesions between the calcareous shell and the underlying shell membrane are loosened so that the calcareous shell plates exfoliate more easily. The wriggling movements of the hatchling within the egg often speed the exfoliation and the shell membrane is then cut from below by the caruncle as the hatchling drags its head upwards and backwards. Grigg and Beard (1985) have measured internal pressures up to 122 torr (16.3 kPa) within swollen eggs and speculate that the development of longitudinal cracks may result from a build-up of hydrostatic pressure internally, in response to an increasing osmoticity as development proceeds. This question will be pursued in future work.

## CONCLUSION

It is clear that, for a crocodile farmer, more information is needed to establish the relationship between the visible signs that occur at different incubation humidities and the fitness of resultant hatchlings. It may turn out that water availability, like temperature, has subtle but important effects which should not be overlooked.

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