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Physiological Adaptations of Aquatic Turtles

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Naturalists have long noted the remarkable ability of aquatic turtles to remain submerged for long periods of time. Only recently, though, has much serious attention been given to discovering the mechanisms which enable turtles to survive for so long in the relatively hypoxic aquatic environment.

Although all turtles are officially considered ~~to~~ be air breathers, several species are well adapted to an aquatic existence through special mechanisms. It is the purpose of this paper to explore some of these mechanisms and propose some direction for future study.

The most significant early work was done by S. H. Gage and S. P. Gage[1] in 1886, who demonstrated that two species of soft-shelled turtles (Trionyx) were able to extend their dives through the utilization of certain body surfaces to extract dissolved oxygen from the water. Gage also deduced that the pharyngeal cavity was the main site for oxygen exchange noting the prescence of filamenteous processes located near the glottis on the hyoid apparatus, which, along with the rest of the lining of the pharynx, is richly supplied with blood vessels. They also noted the regular movements of the hyoid apparatus, producing a rythmic intake and expulsion of water from the pharynx, comparing these to the gill movements of the fish.

Later workers substantiated this work. Cahn[2], in 1937, showed the path of water currents in and out of the pharynx as well as the cloaca. In 1960, experiments by Dunson[3] demonstrated that dissolved oxygen was indeed being utilized by Trionyx spinifer asper, the bulk of it being absorbed through the pharynx. More recent studies, such as those of Belkin[4] (1961) and others have brought into focus changes occuring in the metabolism of diving turtles while exposed to anoxic conditions.

The survival of turtles for extended periods under water under anoxic and hypoxic conditions has been noted frequently in the literature. Belkin's[5] (1963) work shows that fresh water turtles (six families, twenty five species) have a mean tolerance time for N_2 asphyxia of 14.75 hours. Mussachia[6] (1959) reports that turtles had survival times of up to 2.5 days when submerged in water. D. G. Penney[7] (1973) reports anoxic dives of 30 hours which the turtles survived. Pseudemys scripta is reported to have survived two weeks at 16°C-18°C under anaerobic conditions (Robin, etal 1964)[14]. Clearly, the turtle employs some sort of metabolic alteration in order to survive conditions lethal to most vertebrates.

Although all aquatic turtles seem to show a certain degree of anoxic tolerance; the ability to extract dissolved oxygen from the water apparently varies greatly from genus to genus. Carr[8] (1952) notes that soft-shelled turtles are susceptible to the fish poison rotenone while other turtles are not affected. Pseudemys scripta elegans is reported by Belkin[9] (1968) to be unable to take up significant quantities of O_2 . The wide variation seen in this aspect of the ~~trutle's~~ turtle's adaptive mechanism is to be expected, though, since habits of different genera vary widely.

For instance, *Pseudemys* is a basking turtle which prefers still or slow-moving bodies of water. Like other basking turtles, it spends much of its time out of the water, retreating to the water when danger threatens and at night. Prolonged dives at normal activity levels are the exception, and not the rule. In contrast, *Trionyx*, a river turtle, habitually buries itself in sediment, only its head extending, for long periods of time. The facility of an oxygen-obtaining mechanism is easily seen for the soft-shell. *Pseudemys*, though, obviously has less use for such a well-developed method. Moreover, the low dissolved oxygen concentrations found in stratified bodies of water, expecially in the hypolimnion, require that the extraction mechanism be a highly developed one in order to be of any value to the active turtle.

To suggest that these are the only factors, though, is certainly misleading. As was indicated above, turtles have been shown to be able to survive long after all sources of oxygen are absent in laboratory studies. In nature, most aquatic turtles are known to hibernate deep in the mud of lakes and streams for three to five months in conditions which approach anoxia.

Histochemical studies by Penney[10] (1974) and others have revealed a least a partial view of the metabolic shifts occuring during anoxia. Clark and Miller[11] (1973) performed chemical assays on the blood, brain, heart and liver of *Pseudenys scripta elegans* after varying times of anaerobiosis. They reported that liver glycogen fell and blood glucose increased. They also found that cardiac glycogen was exhausted after three hours and brain glycogen levels had remained the same. The rate of glycolysis was found to increase during the first six hours of anaerobiosis and then decrease progressively. ATP stores began to decline and were nearly exhausted after fifteen hours. Belkin[4] (1961) had earlier demonstrated that the prolonged anaerobic survival of Sternothaerus is facilitated by glycolytic energy.

Clark and Miller in the afore mentioned study hypothesized that the energetic innefficiency of glycolysis, as well as buildup of acids in tissue were the two main limiting factors in the tolerance of anoxia.

That acid buildup occurs was ascertained in a subsequent study by Penney[10] (1974) in which blood lactate was found to rise thirty seven times its initial level. Liver lactate increased by eight times. This study also ascertained the findings of Clark and Miller seen above. Penny also noted that bradycardia occurs eventually if not immediately, upon submersion. This infers a lowered energy metabolism in the turtle.

Jackson[12] (1968) showed by calorimetric methods that temperature independent suppression of metabolism occurs in submerged turtles. He reports a rapid decline in the rate of heat loss upon submersion. He also reports a heat loss after two-three hours to be only 15% of that in air. Penney's study reported data which showed the extent of glycogen depletion and increase in blood glucose and tissue lactate to be less than in previous studies like Clark and Miller.[11] These differences may have significance when viewed in the light of experimental conditions. The Clark and Miller study, as well as some others were carried out in N_2 atmospheres, while Penney"s[10] work was done by submersion in oxygen free water. This fact suggests that there certainly are temperature independent suppression mechanisms which are initiated involuntarily upon submersion.

Lahiri[13] (1972) et al who performed a study on free fatty acid uptake by isolated perfused turtle heart under aerobic and anaerobic conditions, found that free fatty acids, normally an important source of myocardial energy are instead incorporated into tissue triglyceride during anaerobiosis, especially when high glucose levels are maintained.

DISCUSSION

The results of the studies listed above reveal a few conclusions about the matabolic responses to anoxia:

(1) Glycolysis becomes the source of energy during anoxia.

(2) Low energetic efficiency of Glycolysis eventually takes its toll on the metabolic processes.

(3) Buildup of Lactic acid in blood and tissue occurs

(4) Temperature independent suppression methods possibly have role.

There are several important factors to be considered when interpreting these observations, though. Although the results obtained from the work on Pseudemys can probably be applied to other aquatic turtles, one must not ignore the probability that wide variations exist in metabolic adaptations. The fact that glycolysis has been shown to occur as an anaerobic metabolic response in two distinct families, Kinosternonidae and Emydidae, seems to indicate the universal nature of this response, but to say it is true for all aquatic types would be an unsound induction. It is clear to this writer that much more work needs to be done in the investigation of metabolic pathways during ~~anozia~~ anoxia. All this, of course, must be viewed with the knowledge that these experiments performed under anoxic conditions do not duplicate conditions commonly encountered in nature. The use of supplementary aquatic respiration by some turtles certainly would have an effect on the metabolic adaptaions mentioned above.

The highly variable habits of fresh-water turtles indicate that the adaptations of each species vary to meet the needs of that turtle. To make broad statements about physiological adaptations to an aquatic environment would therefore be generalizations which need to be narrowed down to species - by - species or genera by - genera studies to have any credibility. This is an area of study which is just beginning to take its first steps, though, and presents challenge to those in scientific community interested in this important area.

There is significance in the possibility that turtles may be able to shift metabolic pathways automatically upon immersion. this would certainly be an unusual phenomenon in the vertebrate world. If this is so, several new questions appear: What is the full extent of these shifts in pathways? What specific stimulus produces this response? What is the absolute limit to the facility of these adaptations? How long can a turtle survive under a given set of natural conditions?

It is this writer's hypothesis that most (if not all) aquatic turtles employ some sort of alternative metabolic course such as glycolysis as well as suppression of certain processes during extended dives. These internal physiological changes probably act in concert to varying extents with supplementary aquatic respiration and stored oxygen to produce some aerobic metabolism.

It is likely that O_2 concentration produces shifts in metabolic equilibria toward one pathway or another. Here another question arises: Does submersion produce a total shift to an alternate pathway as an automatic response or is the amount of shift dictated by the amount of oxygen available?

Several specific areas for research are proposed:

(1) Comparison of dissolved O_2 consumption for different genera and species

(2) Length of survival under varied conditions

(3) Comparative anatomical and histological studies of oxygen absorbing organs

(4) Relative importance of various oxygen-absorbing surfaces in extraction

(5) Detailed studies of natural history and ecology of turtles in correlation with their known respiratory adaptations

(6) Chemical assays of tissues following hypoxia done under "natural" conditions

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