

SEA SNAKES, A CONTRAST TO OTHER VERTEBRATE DIVERS

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Sea snakes have a maximum capacity of diving to 100 metres depth and remaining submerged for two hours, after which they can rise rapidly to the surface, take only 1-3 breaths and then return to the bottom. Despite the depth and duration of submergence, they do not become anoxic, contract an oxygen debt or suffer the bends (Heatwole and Seymour, 1975 a ,b, 1976, Seymour 1974, Seymour and Webster, 1975, Heatwole et al., 1977). The means whereby such diving feats are possible would seem to be of interest to specialists in diving medicine and consequently are outlined in the present paper.

Although there are special adaptations involved in the diving physiology of sea snakes, there are certain characteristics of the general reptilian mode of life which differ from that of mammals in ways conducive to long periods under water. The chief of these is ectothermy.

Reptiles rely primarily upon external sources for body heat. Their body temperature may merely approach that of the external environment and fluctuate with it, but more often there are behavioural means (such as basking, shade seeking, etc.) of maintaining it within a certain range (Heatwole 1976). Although a variety of physiological, especially cardiovascular, adjustments aid in maintenance of body temperature (White 1976), endogenous production of heat is not a very important factor. Much of the food energy consumed by endotherms (mammals and birds) goes into chemical thermogenesis and the maintenance of a relatively high body temperature. Consequently, they have a high metabolic rates in comparison to reptiles which do not have such an energy requirement. It is for this reason that reptiles can go weeks, or even months, without food and not suffer nutritional problems. In general, the resting metabolic rate (and the resting oxygen consumption) of reptiles is only about 14-29% that of a mammal of comparable size (Figure 1: Bennett and Dawson 1976). In diving terms, this means that a reptile could be expected to remain submerged 3-7 times as long as a similar sized mammal on an equivalent amount of air before becoming anoxic, or requiring special mechanisms such as anaerobic glycolysis. This effect is further enhanced by the fact that reptiles have larger lung volumes than do mammals of equivalent size (Figure 2: Wood and Lenfant 1976). Combining the effect of low metabolic rate and large lung volume, the advantage a reptile would have over mammals in terms of aerobic diving time would be many fold, even without any social physiological adaptations. It would appear that even most land reptiles could be accomplished divers if they chose to do so. Indeed, a variety of species that are otherwise terrestrial or arboreal will jump into water and submerge for long periods as a means of escaping predators or man (see Heatwole 1975). In many aspects, sea snakes do not show any modification of the general reptilian plan. For example, the metabolic rate of sea snakes is not lower than that of an equivalent sized land snake at the same body temperature (Heatwole, in press). Similarly, the haemoglobin content, blood oxygen capacity, oxygen dissociation curve, degree of Bohr shift and other blood characteristics of potential importance to divers does not seem to differ markedly among sea snakes and land snakes (Heatwole and Seymour 1976, Heatwole in press).¹

There are several ways, however, in which sea snakes differ from land snakes that would seem to be of advantage to the diver. The lung of most snakes is a simple tube. The anterior region (really an expanded trachea known as the "tracheal lung") and middle portion (bronchial lung) are highly vascularized and are involved in exchange of respiratory gases. The posterior portion (Saccular lung) is membranous and receives only nutritive blood vessels. Consequently, it is not involved in respiratory gas exchange. Surgical ligating and deflating of this portion decreased

the voluntary submergence times in sea kraits whereas it had little effect on locomotion or ability to move upward or downward in the water (Seymour and Heatwole, in press) suggesting that its prime function is respiratory (perhaps air storage) rather than buoyancy control. Land snakes have respiratory problems (during prolonged swallowing of large prey, or when buried in sand) and the above lung structure is not unique to sea snakes. However, lung volume seems to be larger in sea snakes than in terrestrial species; often the lung extends from the neck to the posterior part of the body cavity.

The main physiological diving adaptation that sea snakes have is the degree of cutaneous respiration.² Land snakes have a very low rate of cutaneous gaseous exchange, and only a small proportion of their respiratory requirements are met in this way. In contrast, in sea snakes as much as one fifth or in some individuals one third of the resting oxygen requirements can be met by uptake through the skin and most if not all of the CO₂ can be eliminated via this route (Graham 1974, Heatwole and Seymour 1975; a,b, 1976).

Because of the combination of cutaneous respiration, large lung volume and low metabolic rate, sea snakes can remain aerobic under water for long periods of time. Seymour and Webster (1975) have shown that during extended voluntary dives snakes remain aerobic and do not produce much lactate. Indeed, sea snakes are just as sensitive to anoxia as are land snakes and lizards and are much more sensitive than are freshwater turtles (Heatwole, in press). Only in emergencies (ie. when forced to remain under water longer than the voluntary submergence time) do sea snakes resort to anaerobiosis.

Cutaneous gas exchange is not only important directly in respiration, but has implications for a number of other aspects of diving. For example, loss of CO₂ via the skin means that it fails to replace the gas volume lost through utilization of lung oxygen and thus snakes decrease in buoyancy with increased submergence time. Similarly, one of the major influences preventing the bends is probably the loss of blood nitrogen directly to the water via the skin.

One of the most important effects of cutaneous respiration is that it alters the significance of the circulatory system in diving. In order to understand this relationship it is necessary to contrast two major modes of circulatory adaptation to underwater life.

Most vertebrate divers (including mammals, birds and perhaps some reptiles) respond to submergence or apnea by (1) vasoconstriction of the peripheral and splanchnic vessels, resulting in (2) anaerobic glycolysis during which accumulation of lactic acid occurs, and an oxygen debt is incurred which must be paid back during breathing at the surface. Accompanying this is (3) bradycardia with the blood-flow circuit reduced to serving vital areas such as the heart and brain (Andersen 1966).

As indicated above, the last is characteristic of sea snakes only in emergencies; usually they produce very little lactic acid, remain aerobic throughout their dive, and do not breathe at the surface long enough to dissipate an oxygen debt. Although there are heart rate changes during the diving cycle. Heatwole (1977) has pointed out that they are not associated with the rest of the above syndrome and consequently they cannot be considered as diving bradycardia. Rather, they represent brief elevations of heart rate just prior to and during breathing (breathing tachycardia) which results in rapid lung perfusion and gaseous exchange during ventilation.

Cutaneous gaseous exchange would seem to be incompatible with the above syndrome because of the opposing demands for perfusion of peripheral tissues.

For cutaneous respiration to be effective, the skin must be perfused and peripheral vasoconstriction would be a disadvantage. For peripheral anaerobic glycolysis and husbanding of lung oxygen for vital centres, vasoconstriction is essential. Most vertebrate divers seem to respond in the latter way whereas the sea snakes have opted for the former strategy.

The circulatory system of reptiles also plays another role in diving. The reptilian heart is unique in vertebrates in that (1) there are two separate systemic arches leading from the ventricle, and that (2) the ventricle is divided into several subchambers which can communicate with each other at least under certain conditions and at certain points of the heart beat cycle. Alteration of intracardiac pressure relations result in some of the systemic venous return bypassing the pulmonary circuit and leaving the heart via the left systemic arch (right-to-left) shunt).³ Thus a reptilian heart permits a flexibility of function lacking in the mammalian heart in which the systemic and pulmonary venous returns are mandatorily completely separate.

In terms of diving⁴, the significance of such shunting is probably that low perfusion of the lung, when submerged, results in a gradual uptake of lung oxygen over a long time without a large elevation in blood oxygen levels. The lower the blood oxygen level, the greater would be the oxygen gradient across the skin and the more effective would be cutaneous oxygen uptake, and the greater the proportion of the total oxygen requirements that would be obtained via the skin. Also, a low perfusion rate of the lung would result in a reduced rate of nitrogen uptake from lung air and would decrease the risk of bends.

In summary, the reptilian mode of life with its associated ectothermy, low metabolic rates, large lung volume, and functionally flexible heart has in a real sense been a pre-adaptation for a diving existence not enjoyed by mammals. In sea snakes, development of cutaneous respiration has served to enhance those basic characteristics and has resulted in a different type of circulatory response to diving than that found in most divers; cutaneous respiration is also related to buoyancy control and prevention of the bends.

Footnotes:

- 1 By contrast there are some aquatic snakes of the family Acrochordidae that do have a greater Bohr shift and a lower metabolic rate than do land snakes or sea snakes.
- 2 There are also a variety of morphological adaptations such as paddle-shaped tail, nostril valves, and valves forming a tight seal when the mouth is closed. Also, a major adaptation to the salinity conditions of the sea is a salt excreting gland under the tongue which aids in osmoregulation (Dunson 1976).
- 3 The right systemic arch carries blood to the head as well as the body and tends to receive primarily oxygenated blood at all times. The left systemic arch supplies the posterior body and when oxygenated and unoxygenated blood is mixed it tends to exit from the heart via the left rather than the right arch (see Webb et al. 1971 and White 1976 for a detailed discussion of the anatomy and blood flow pattern of reptile hearts). During ventilation, perfusion is sometimes enhanced by a left-to-right shunt.
- 4 The significance of such shunting also lies in the ability to alter the heat transport function of the blood during basking and other thermoregulatory behaviour and still maintain oxygen transport capabilities (see White 1976).

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