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978-0-521-11289-5 - Diving and Asphyxia: A Comparative Study of Animals and Man

Robert Elsner and Brett Gooden

Excerpt

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# 1 THE BIOLOGICAL SETTING

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The diving mammals offer the physiologist a natural experiment which shows how long and by means of what respiratory adjustment a mammal can endure asphyxia (Laurence Irving, 1939).

Depriving living organisms of oxygen and of the opportunity to rid themselves of carbon dioxide leads inevitably to progressive disruption of cellular biochemical processes, physiological dysfunction and the undoing of biological integrations which are collectively essential for homeostatic life. This condition, asphyxia, is a threat which lurks never far away from living vertebrate organisms. The so-called lower animals are generally more resistant to it than the higher, more complex forms which, for that complexity, are dependent upon a nearly continuous respiratory exchange. Asphyxia, and responses to it, can take several forms. It can characterize the disturbance of blocked respiration in a whole animal and it can take place in a regional tissue which is deprived of the perfusing blood required for the exchanges that are necessary for cellular survival. It is what the diving seal or duck experiences when it holds its breath and submerges in water. That exposure is usually brief and non-threatening, but if asphyxia continues without interruption, it leads inevitably to cellular disruption and organism death. In the considerations which follow, examples will be drawn from phenomena other than diving, and from both aquatic and terrestrial species, including man.

Resistance to asphyxia varies with species, age and special adaptation. Tolerance to ischaemia, the occlusion of blood flow, also varies within the animal according to the type of cells in the tissue deprived of circulation. Just as the time during which an animal can hold its breath and remain under water varies from species to species, so does the tolerance of

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tissues to ischaemia vary from organ to organ. The harbour seal can remain under water for a maximum diving time of 25 min. The Weddell seal of Antarctica can remain submerged for at least 60 min. Some ducks can dive for 10–15 min. Humans, with some practice, can breath-hold under water for about 2 min.

Similarly, a hierarchy exists among the tissues of the body. For example, the tissues in human limbs can be deprived of blood for 30 min or more without damage. On the other hand, it is obvious that the central nervous system, more specifically those portions of it involved in maintenance of consciousness, cannot sustain activity for more than a few seconds without a continuous supply of blood rich in oxygen. The potentially disruptive effects in these examples result from interruption in the supply of oxygen and its subsequent decline in the tissues, the accumulation of carbon dioxide and of other metabolic products, and the increasing acidity. The pathophysiological consequences of insufficient oxygen were eloquently discussed by Barcroft (1920) in a landmark article.

Pure hypoxia, that is, oxygen depletion with normal blood and tissue concentrations of carbon dioxide and hydrogen ions, is rare in nature. Acute altitude exposure, for instance, usually results in hypoxia together with hypocapnia and alkalosis produced by an associated increase in pulmonary ventilation. But asphyxial interference with respiration, as in breath-holding, diving, suffocation and loss of consciousness, leads to hypoxia, hypercapnia and acidosis, all of which increase progressively and relentlessly as asphyxia develops.

Adaptations which permit seals, ducks and other naturally diving animals to tolerate long submersions provide good examples of physiological and biochemical specializations. However, as they are understood today, these adaptations suggest no fundamentally new or previously unrecorded mechanisms. They are qualitatively related to reactions and regulatory mechanisms common to vertebrates, but species differ in their quantitative development. They can perhaps be best considered as extensions of the normal responses which guarantee stable conditions of life. In more general terms, asphyxial adaptations apply to invertebrates as well.

The train of events that takes place as seals dive de-

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monstrates these adaptations. Seals of the family Phocidae, capable of long dives, have special capabilities for oxygen storage. Their circulating blood volume is elevated, and their blood is richer in circulating haemoglobin than that of most other mammals (Lenfant, 1969). Further oxygen storage is accomplished by the high myoglobin contents in skeletal muscles (Robinson, 1939; Scholander, Irving & Grinnell, 1942a; Blessing & Hartschen-Niemeyer, 1969). Their lung volumes are not unusually different from those of terrestrial mammals, and some species usually exhale before diving. Thus, the major oxygen source which is readily available to central organs is stored within the blood itself. Accordingly, the total oxygen-storage capacities of harbour seal and Weddell seal blood, normalized for differences in body weight, are approximately two and three times, respectively, that of man (Lenfant *et al.*, 1969b).

The resting metabolic rates of seals are somewhat higher than those of comparably sized terrestrial mammals, some being approximately twice as high, while body temperatures are similar to those of land mammals. The elevated metabolic rate and thick subcutaneous blubber (representing 25–50% of body weight) provide the heat production and insulation necessary for maintenance of normal internal temperature in the cooling water environment (reviewed by Irving, 1969, Elsner *et al.*, 1977b and Blix & Steen, 1979). It can be readily calculated that if the submerged seal were to continue metabolizing at the same rate as before diving, its oxygen storage, despite its magnitude, would not be sufficient to maintain that rate during long dives. Clearly, some other responses must be essential for its survival.

The mammalian species which are adapted to aquatic habitats range in size from the blue whale to the water shrew, thus including the biggest animal ever to have lived and one of the smallest. Their maximum diving times vary from less than 1 min to 1- to 2-h submersions of sperm and bottlenosed whales (Irving, 1939). Some turtles can remain underwater for days on end (Belkin, 1963; Robin *et al.*, 1964). Weddell seals can dive to 600 m, sperm whales to more than 1000 m. Pathological accumulation of inert gas (decompression sickness), which might occur in repetitive diving, is avoided by

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virtue of structural adaptations which allow for thoracic compression and isolation of pulmonary air from perfusing blood during dives. These include a flexible rib cage, stiffened alveolar ducts and attachments of the diaphragm such as to permit some shifting of abdominal contents into the thorax (Scholander, 1940; Kooyman, 1972; Kooyman *et al.*, 1972).

### **Natural observations and laboratory experiments**

There has been a tendency through the years to look upon the reactions of aquatic species, such as seals and ducks, to diving experiments as constituting a fixed set of physiological events. The dogma suggests that all examples of diving, whether occurring in nature or in the laboratory, result in similar responses. Cessation of breathing, slowing of the heart rate and changes in the distribution of the circulating blood to favour the most vital organs have become fixed concepts to an extent greater than is warranted by the results of critical studies extending over several years. That view of diving physiology is not the whole story; rather, the responses vary in timing and intensity, just as do most biological phenomena.

In his classical work of 1940, Scholander pointed out that a seal freely submerging in water sometimes failed to show diving bradycardia. However, seals reacted to startle and loud noise with sudden heart rate slowing. Experimental diving studies in which animals were trained to dive upon a signal resulted in variable responses in the sea lion (Elsner, Franklin & Van Citters, 1964*a*), the harbour seal (Elsner, 1965; Elsner *et al.*, 1966*a*) and the dolphin (Elsner, Kenney & Burgess, 1966*b*). There was usually less decline in heart rate during trained immersion than during forced immersion (sea lion and harbour seal), but in dolphins the bradycardia was intensified during trained dives. The generalization which appears to apply is that some major component of the diving response is determined by the intention, conditioning or psychological perspective of the animal being studied. Thus, the diver acts as though it produces the most intense diving response when the need for achieving maximum diving duration is anticipated.

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Perhaps trained dolphins are more highly motivated than trained seals.

Kooyman *et al* (1980) described dives of up to 20 min in Weddell seals (which are capable of maximum dives exceeding 60 min) in which little or no dependence upon the anaerobic resources required for longer dives was made, although cardiovascular changes, signalled by bradycardia, presumably occurred (Kooyman & Campbell, 1972). Oxygen reserves were apparently sufficient to allow the dives to be made aerobically. If, as seems likely, these reserves are principally contained within the blood and oxygenated myoglobin of skeletal muscle, then the reactions of the voluntarily diving Weddell seals resembled those of restrained diving harbour seals in a previous study in which myoglobin oxygen was rapidly depleted before lactate production commenced in about 10 min, earlier in seals which struggled (Scholander *et al.*, 1942a: Fig. 1.1). One is struck by the similarity of the responses in the two examples, rather than by differences. Authors of both studies remarked upon the observation that the preponderance of free dives in nature are brief and aerobic, indicating that anaerobic responses, which are more exhausting and require longer recovery, are seldom brought into operation. Some, perhaps most, marine mammals are able, by virtue of efficient pulmonary gas exchange, to recover promptly from such dives, replenish oxygen stores and prepare for the next dive (Olsen, Hale & Elsner, 1969; Denison & Kooyman, 1973).

Butler & Woakes (1979) and Kanwisher, Gabrielsen & Kanwisher (1981) showed that freely diving birds make many short dives without changes in heart rate. Clearly, most of the dives performed by aquatic animals in nature are of short duration, and they apparently depend largely upon oxygen-sustained rather than anaerobic mechanisms. Ducks and seals doubtless find it uncomfortable and exhausting to push their diving habit to the anaerobic extreme of their reserve capabilities. Although that physiological reserve is rarely invoked, it is, nevertheless, a resource upon which survival may depend. From these considerations there emerges the concept of graded responses to diving, varying in intensity depending upon severity of the imposed stress and of the

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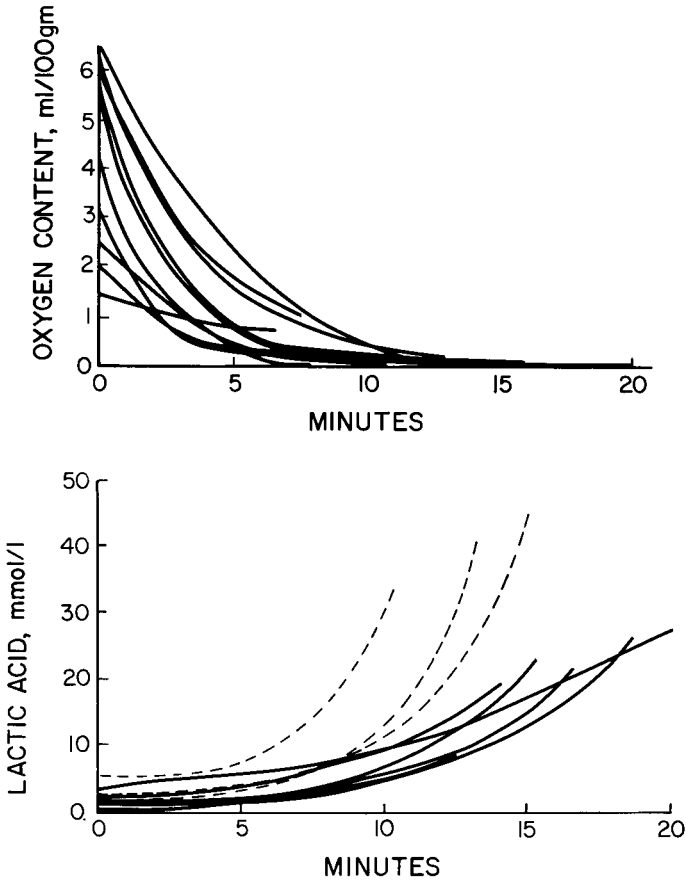
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Fig. 1.1. Depletion of myoglobin-bound oxygen (above) and increase in lactic acid concentration (below) in skeletal muscle of harbour seals *Phoca vitulina* during restrained dives. The solid lines represent dives of individual seals; the dashed lines represent dives during which the seals struggled against the restraint. (Redrawn from Scholander *et al.*, 1942a.)

degree to which control is exercised by higher cortical functions.

The understanding of diving biology is enhanced by examining the natural history of diving species. It is equally important that we study the full range of physiological responses of which these animals are capable by submitting

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them to experimental dives. Controlled laboratory investigations require either the use of trained animals or, more drastically, the interventions of restraint and anaesthesia. These approaches have all been usefully employed in various studies. Some success has been achieved in combining laboratory and fieldwork in natural settings.

A major response to most diving situations, natural and experimental, is the selective redistribution of the circulation. Inasmuch as many of the tissues of the body can tolerate oxygen deprivation for longer than the more vital ones, the heart and the brain, the available blood oxygen could be conserved by its preferential distribution to those vital organs for their immediate needs while the remaining organs, deprived of circulation, survive on anaerobic metabolic processes or, in the case of skeletal muscle, on oxygen bound to myoglobin. Modern understanding of these diving responses rests on the foundation of classical research reports by Irving (1934, 1939) and Scholander (1940) and their later collaborative publications. Some aspects of these adaptive mechanisms exist in many species which are not habitual divers when they are exposed to asphyxia. (General reviews: Scholander, 1962, 1963, 1964; Irving, 1964; Andersen, 1966, 1969; Elsner *et al.*, 1966a; Robin, 1966; Harrison & Kooyman, 1968; Strauss, 1970; Jones & Johansen, 1972; Ridgway, 1972; Galantsev, 1977; Kooyman, Castellini & Davis, 1981; Butler & Jones, 1982; Blix & Folkow, 1983).

The term 'diving response' refers to a sequence and collection of physiological events, including apnoea, bradycardia and redistribution of cardiac output, which are all under the control of multiple reflexes rather than forming a single 'diving reflex'. This latter term, which enjoys some popularity, conveys the incorrect impression that the events seen in diving constitute one reflex rather than many reflexes functioning together through their interactions.

**Hypometabolism, a strategic retreat**

Restricting the circulation of blood to a tissue or an organ results in a steady decline of the oxygen available for support of oxidative metabolic processes and subsequent dependence

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upon whatever anaerobic resources are available. Eventually, a depression of metabolism takes place. This lowering of the rate at which the many complex chemical processes can occur, thus conserving metabolic energy, is, in fact, a central feature of the adaptations to asphyxia. Viewed in this context, the diving response represents but one specialized example of a widespread and general response of many living animals, invertebrate as well as vertebrate, to life-threatening situations. There are abundant examples in nature.

The phenomenon of dormancy, which is characterized by a lowering of metabolic activity, is widespread in nature. Marine invertebrates such as intertidal molluscs, which require submersion in water to obtain an optimum gas exchange, are regularly subjected to cyclic tidal conditions which leave them high and dry. They retreat from those threatening situations into a state of lowered metabolism, thus decreasing the need for immediate dependence upon life-supporting functions (Newell, 1973). Fish removed from water show the reduced and redistributed circulation typical of the diving response (Leivestad, Andersen & Scholander, 1957; Garey, 1962; Scholander, Bradstreet & Garey, 1962*b*). The marine invertebrate *Aplysia* responded to air exposure with bradycardia (Feinstein *et al.*, 1977). A warm-water species, *A. brasiliiana*, showed a 43% average decrease in heart rate (Fig. 1.2), whereas a cold-water species, *A. californica*, showed only a 16.5% decrease. The bradycardia response in the warm-water species was shown to be largely neurally controlled via the abdominal ganglion. *Aplysia* are occasionally stranded on beaches or in tidal pools and are sometimes able to survive this asphyxial stress until they are once again submerged in the next tide. Hibernators and aestivators likewise retreat from the threats of decreased food supplies and thermal conflicts by lowering their metabolic rates. The highly active hummingbirds and bats experience nocturnal and daytime declines, respectively, in metabolic rate which provide them with an economical means of avoiding the necessity for obtaining a continuous food supply.

Snails react to dehydration by sealing off their shell openings and entering a dormant state (Schmidt-Nielsen,



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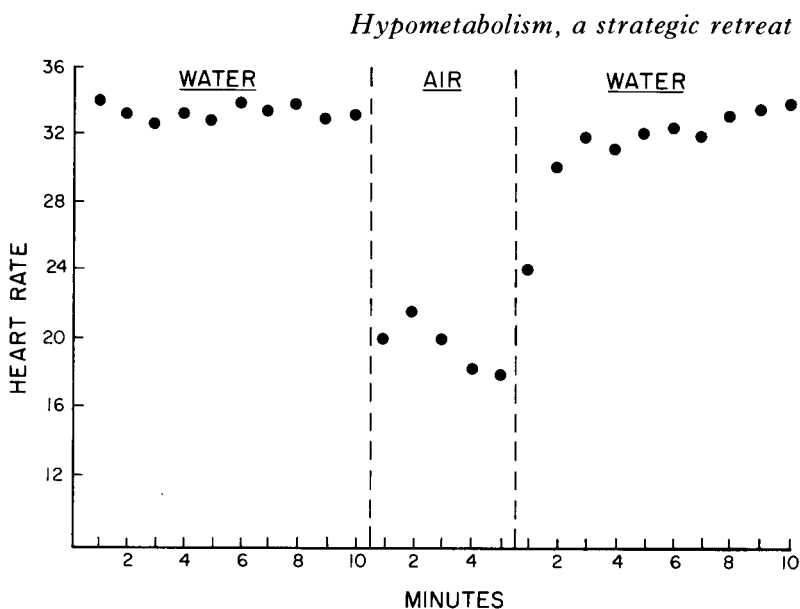
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Fig. 1.2. Heart rate (beats/min) of *Aplysia brasiliana* during removal from water, which induces asphyxia. (Redrawn from Feinstein *et al.*, 1977.)

Taylor & Shkolnik, 1971). Desert frogs respond to threatened dehydration by torpor. They can remain sealed off, buried in the ground, awaiting the next rainfall, which may be months or years away. The African lungfish *Protopterus* similarly lies dormant in dried mud-holes during long dry periods (Smith, 1930). Diapause is a well-known dormant condition in insects (Lees, 1955).

In addition to those examples that have been mentioned here, it is now appreciated that conditions of lowered metabolic activity occur in a great variety of mammalian, bird and invertebrate species, culminating perhaps in the phenomenon of cryptobiosis, a death-like state entered into by several species of primitive animals when they become thoroughly dehydrated. They can remain in this depressed state for years and can then be revived by rehydration. Certain species of rotifers and nematodes are examples (Crowe & Cooper, 1971). Scholander *et al.* (1953) described similar metabolic responses in frozen arctic plants and animals.

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The spectacular physiological events which take place in the process of mammalian birth provide yet another example of the implementation of a set of responses designed to protect the integrity of the central nervous system during a threat of asphyxia. The infant animal is exposed to asphyxia sometimes by disruption of placental blood flow and gas exchange, sometimes by compression of the umbilical cord and during the interval from the moment when it loses its gaseous lifeline to the maternal placental circulation until the moment when it first inflates its lungs. Its protection during these critical minutes depends upon adaptations for just that brief once-in-a-lifetime event. These include its anaerobic reserves and cardiovascular adjustments that favour its central nervous system at the expense of less sensitive tissues (Chapter 6).

An example of human hypometabolic retreat from disturbing environments is demonstrated by certain practitioners of Yoga in India. This voluntary reduction of metabolic rate was first documented by Anand, Chhina and Singh (1961) who studied a Yogi subject enclosed within an air-tight box. The investigation was inspired by reports of experienced Yogis who commit themselves to burial for several days in small subterranean chambers in order to achieve deep meditation in the absence of sensory stimulation. The burial chambers are most likely not air-tight, and recent evidence shows that the metabolic effects can be produced by the meditating Yogi without recourse to burial or enclosure. R. Elsner and H. C. Heller (unpublished results) studied a well-practised Yogi during 4 h of meditation in which his basal oxygen consumption was reduced by 45% (Fig. 1.3). Brief hypometabolic states have been described by Wallace, Benson & Wilson (1971) in subjects trained in Transcendental Meditation.

The most remarkable hypometabolic states in mammals are displayed by hibernators. They attain low metabolic rates as a consequence of lowering the body temperature, and this involves a resetting of the hypothalamic regulator of body temperature. The threshold temperature for thermoregulatory responses is much reduced, as is the gain of the regulator (Heller & Hammel, 1972; Heller & Colliver, 1974). Humans and other mammals usually experience slightly