

Review

# Comparison of the respiratory transition at birth or hatching in viviparous and oviparous amniote vertebrates<sup>☆</sup>

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## Abstract

Regardless of the mode of reproduction, three things must occur at birth or hatching in amniote vertebrates: initiation of breathing, pulmonary fluid elimination and reabsorption, and adequate perfusion of pulmonary circulation. Although data on these events are few, there appears to be no fundamental difference in them that can be associated with the oviparity to viviparity transition. There are, however, differences in the timing of these events in oviparous and viviparous amniotes. The transition to neonatal respiration tends to be very quick in viviparous species because the vascular support for oxygen uptake provided by the mother is rapidly disassociated from the mechanism for uptake by the embryo. By contrast, hatching often is a slow process, taking 24 h or more in some species, as chorioallantoic blood flow slowly gives way to clearing of the lungs and pulmonary gas exchange. Little is known of the mechanisms of pulmonary fluid elimination and reabsorption or lung inflation in reptiles, but the cellular structures and surfactant systems are similar in all amniote vertebrates. Nevertheless, there are differences, particularly of timing and maturation of various systems, but there has been no exploration of the functional (or phylogenetic) bases of these differences. Perfusion of the neonatal pulmonary system to support respiration in reptiles remains to be investigated. In mammals and birds, closure of the *ductus arteriosus* is important, but the role played by the *ductus arterioisus* in reptilian hatching or birth is not known.

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## 1. Introduction

Egg-laying (oviparity) and live birth (viviparity) are fundamentally different modes of reproduction that have major influences on life history strategies, reproductive physiology and behaviour of adults. The lizards and snakes

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(squamate reptiles) have been used as a major model to understand the evolution of viviparity in amniote vertebrates because viviparity has evolved at least 108 times in squamates (Blackburn, 2006), and different species exhibit different placental complexities ranging from very simple lecithotrophic (yolk-filled eggs) to placentae described as “eutherian-like” (Blackburn et al., 1984). By contrast, viviparity has evolved only once in mammals (Blackburn, 1992).

Fundamental differences in reproduction between oviparous and viviparous species have led to the term “hatching” being used to describe the embryo–neonate transition in oviparous species, and “parturition” in viviparous species. The term “parition” collectively describes the embryo–neonate transition, regardless of parity mode (Blackburn, 1992). Despite the obvious importance to the life of squamate reptiles, there has been only one direct attempt to compare features of respiratory changes associated with parition in oviparous and viviparous squamates (Johnston and Daniels, 2001), so I will draw heavily on information from birds and mammals to draw inferences about reptiles for other aspects of change at parition.

Comparisons between hatching in birds and birth in mammals must be taken with some caution because the structure and mechanism of operation of avian and mammalian lungs is fundamentally different (Maina, 2003). The respiratory system of birds consists of a series of air sacs with anastomosing air capillaries that allow unidirectional flow of air, compared to the blind sac and tidal flow in mammalian lungs (Maina, 2003). In that respect, reptilian faveolar lungs are more similar to mammalian bronchioalveolar lungs, although there are large differences in structural complexity, with reptilian lungs being simpler than mammalian lungs (Duncker, 1978; Maina, 1989; Maina et al., 1989; Adamson, 1997). The lungs of snakes are analogous in some ways to avian lungs, with some cross-current exchange between air flow and blood capillaries, and the ventilatory and respiratory regions of the lungs of both being uncoupled (air sacs in birds, avascular lung in snakes) (Maina et al., 1999). Regardless of mode of reproduction, phylogeny or lung morphology, the lung of amniote vertebrates must change from being a fluid-filled, non-functional organ to an air-filled, functioning gas exchange organ at birth or hatching (Orgeig et al., 2003) so cross taxon comparisons should allow for useful inferences to be drawn.

At birth, three things must occur: initiation of continuous external ventilation (breathing), pulmonary fluid elimination and reabsorption with establishment of a functional residual capacity, and adequate perfusion of pulmonary circulation (Mortola, 2001). My aim is to draw together information on these events in amniote vertebrates to establish possible changes that may be necessary in the evolutionary transition from oviparity to viviparity.

## 2. Initiation of continuous breathing

Hatching in birds is a lengthy and energetic process (Johnston and Daniels, 2001), consuming between 2.5 and 20% of the total energy consumption of development just in the physical exertion of hatching (Vleck and Bucher, 1998). An air

cell develops inside the blunt end of avian eggs during incubation, and the first breath of the embryonic chick is taken from the air cell on the day before hatching in chickens (Bellairs and Osmond, 2005). The chick first penetrates (or pips) the inner shell membrane to access the air space (internal pipping) and later breaks the eggshell (external pipping) prior to hatching. In contrast to placental amniotes, where ventilation and diffusion overlap for no more than a few minutes, gas exchange occurs both in the lungs and the chorioallantois between pipping and hatching in birds (Menna and Mortola, 2002) and presumably some reptiles. The ventilation rate increases as the lungs clear, even though the metabolic rate stays about the same, and the process takes more than 20 h in chickens (Visschedijk, 1968a; Rahn et al., 1974; Menna and Mortola, 2002). Heart rates generally increase during pipping, also (Tazawa et al., 1991, 1994).

Before parition, the fluid-filled lungs of amniote vertebrates are non-functional in gas exchange and hence is a non-essential organ (Mortola, 2001). Rhythmic contractions of the respiratory muscles and an associated decrease in pleural pressure occur from about the end of the first third of foetal development in mammals (Mortola, 2001) and well before internal pipping in birds (El-Ibiary et al., 1966; Vince and Tolhurst, 1975). Foetal breathing movements (FBM) increase in frequency throughout development, occurring about 30% of the time in the last few weeks at a rate that is similar to that of postnatal breathing in humans (Mortola, 2001). FBM decrease in the last few days before birth, and generally stop completely during birth in humans and lambs (Mortola, 2001). In chickens and pigeons, FBM become regular two to three days prior to hatching (but presumably after internal pipping), resulting in aeration of bronchial system, air sacs and parabronchi (Scheuermann et al., 1998). Regular breathing movements coincide with rapid development of the avian parabronchial gas exchange mantle, a rapid increase in capillaries between arterioles and venules, and a slow taking over from the chorioallantois in importance (Scheuermann et al., 1998 and references therein). There is no reason to expect that FBM do not occur during the later part of development in reptilian embryos, either.

The stimulus that initiates breathing is not properly known in mammals, birds or reptiles (Mortola, 2001). Lung ventilation begins slowly and somewhat erratically after internal pipping in birds, becoming regular 20 h before hatching in chickens, increasing in amplitude and frequency 12 h before hatching and then declining in amplitude and frequency after hatching (Vince and Tolhurst, 1975). Hence, the lungs do not suddenly become functional after the first breath, and complete aeration of the lungs takes many hours. A partial pressure gradient of 50 Torr between the air cell and arterial blood oxygen (Piiper et al., 1980; Pettit and Whittow, 1982) implies the presence of functional shunts (Piiper et al., 1980), but it is not known whether they persist after hatching. Increased hypercapnia and hypoxia towards the end of incubation provide stimuli for hatching (Visschedijk, 1968a,b,c; Pettit and Whittow, 1982). Metabolic rate rapidly rises when lung ventilation begins as a result of the release of hypoxemia and the hypoxic release of catecholamines in birds (Wittmann and Prechtel, 1991).

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