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Development during the first seven days post-hatching

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INTRODUCTION

The neonate has basic needs that must be satisfied at the time of hatching if survivability and maximum potential are achieved. Some of these basic needs are fresh air, clean water, proper feed, and heat. The developmental state at hatching of the neonate differs among all avian species (Nice, 1962). The post-hatching period for altricial neonates is more critical than for precocial birds because they hatch in a less mature state. Differing amounts of maternal care are therefore essential for each species (Nice, 1962). Although embryonic growth among species is very similar, no two physiological systems seem to mature at the same rate (Ricklefs and Starck, 1998). In addition, maturity may be a function of the egg conductance constant (Ar and Rahn, 1978), which is determined by egg mass, eggshell conductance (or functional properties) and the length of the incubation period (see Box 1 later), all of which may constrain neonatal maturity. When viewed energetically, the difference between maturity types resides in the different water concentrations in eggs and hatchlings, in the density of chemical potential energy in the dry matter of true hatchlings, and in the different amounts of energy transferred from the egg to the spare yolk (Ar *et al.*, 1987).

On the basis of species comparisons of post-hatching growth of all birds (Lilja, 1983; Ricklefs, 1987), it has been suggested that the rate of growth after hatching is at least partially determined by the pattern of organ growth. It appears that a high rate of growth is correlated to early growth of ‘‘supply organs’’ (oesophagus, proventriculus, gizzard, intestines, heart and liver) at the expense of ‘‘demand organs’’ (breast, wings, legs and feathers). These changes begin very early in development (Lilja and Olsson, 1987), and Schmalhausen (1930) hypothesised that growth and organ function come into conflict when growth occurs too slowly or too rapidly.

Even under the most optimum conditions, a newly hatched bird is not free from stress. This is impossible because the absence of stress is death (Selye, 1951). However, hatchlings possess abilities to cope with stress via adrenal cortical hormones (Davis and Siopes, 1989). Hatchlings have different blueprints for growth and maturation that must occur within a predetermined time frame. Many times this blueprint does not include adjustments that need to occur in maturational and growth processes in an imperfect environment. The objective of this paper is to define a ‘‘physiologically normal’’ hatchling and to describe the principles involved in the maturation and growth of several organ systems during the initial stages of life.

At least six physiological systems exist that require maturation during the last week of incubation or, in the case of altricial species, the initial days of life outside the shell. These systems are: (1) the circulatory system (heart and blood); (2) the kidney and body fluids system; (3) the digestive system; (4) body temperature regulation; (5) the respiratory system; and (6) the immune system. These systems are discussed here using published data to help clarify important points.

CIRCULATORY SYSTEM

The heart and blood are among the first tissues to develop and mature in the embryo (see Baggott, 2001), and both function physiologically in the initial stages of embryonic development (Watterson and Sweeney, 1973; Tazawa and Whittow, 2000). The number of red blood cells increases with the age of the embryo until hatching (Macpherson and Deamer, 1964; Bagley, 1987). This occurs by both erythropoiesis and reticulocyte recruitment and maturation (Bagley, 1987). The processes for haemoglobin maturation and synthesis undergo similar patterns (Isaacks *et al.*, 1976). Post-hatching, erythrocyte numbers have been reported to increase initially for 3–4 days then decline to 10 days of age (Phelps *et al.*, 1987a). Sexual dimorphism affects erythrocyte numbers because in males numbers of cells declined more rapidly than in females, and erythrocyte changes were accompanied by declines in packed cell volumes, cell sizes and haemoglobin concentrations (Phelps *et al.*, 1987a).

Heart growth has been reported to be more variable than other organs during the first two weeks post-

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hatching (Phelps *et al.*, 1987a). Rates of heart growth peak at about five to six days post-hatching then plateau to a rate similar to body growth at about 10 days. Spontaneous turkey cardiomyopathy (round heart disease, cardiohepatic syndrome; Magwood and Bray, 1962) and ascites in broiler chicks are manifestations of conflicts between organ growth and function. These syndromes are characterised by an enlarged heart due to extensive dilation of the ventricles (primarily the right ventricle initially), congestive heart failure and mortality. Julian *et al.* (1992) and Breeding *et al.* (1994) showed that rapid growth rates in connection with high protein diets contribute to the problem. Lilja and Olsson (1987) hypothesised that rapidly growing poultry will develop supply tissues before demand tissues.

Hearts in avian species are demand tissues because they can neither recycle lactate nor can they create glucose from gluconeogenic amino acids. Thus, heart growth, heart energy metabolism and blood cell maturation may be greatly influenced by the overall growth of the animal. These problems have been shown to occur during embryogenesis and manifest themselves throughout the life of the bird (Buyse *et al.*, 1998).

KIDNEY AND BODY FLUIDS SYSTEM

Embryos create urea as nitrogenous waste that is partitioned from the embryo and stored in liquid form in the allantoic fluid (Watterson and Sweeney, 1973). Approximately half way through incubation, the system begins creating insoluble uric acid, as a nitrogenous waste product. Water serving as the solvent for urea is recycled from the allantoic sac into the embryo via the chorio-allantoic circulation or the hindgut (Romanoff, 1960; Baggott, 2001). This makes it very difficult to dehydrate the embryo itself during incubation (Ar, 1991). However, egg weight losses of greater than 20% can result in physiological problems for embryos (Davis and Ackerman, 1987; Ar, 1991). The embryo relies on this system to filter nitrogenous waste until it hatches. After hatching a "new" renal system develops to maintain body fluid balances. Water is an essential nutrient for neonates while the system maintaining water balance matures (Doneen and Smith, 1982). Maturation of the renal clearance system requires a few days post-hatching whereas establishment and maintenance of acid-base balance is completed during the final stages of embryonic development (Goldstein and Skadhauge, 2000).

In birds, the renal system performs the additional functions of gluconeogenesis and maintenance of blood glucose concentrations (Fasenko, 1996). As stress and difficulties in food acquisition are encountered, the kidney becomes essential to neonatal survival (Donaldson and Christensen, 1994). Maturation of the kidney in the gluconeogenic sense occurs whilst still in the egg but can be affected by the length of the incubation period (Fasenko, 1996). Glucose in hatchlings increases significantly from hatching until day five or six then may decrease achieving constant values by about day nine (Phelps, 1985).

DIGESTIVE SYSTEM

The yolk sac contains all of the enzymes and absorption mechanisms necessary for sustaining life in the shell and following yolk sac retraction into the body before hatching, it maintains these capabilities for the first few days following hatching (Romanoff, 1960; Denbow, 2000). The yolk digestive system is based primarily on lipids (Donaldson and Christensen, 1994; Donaldson *et al.*, 1994) but after hatching, the neonate must begin life on diet rich in carbohydrate (48%) and this basically requires a new metabolic process. Many intestinal mechanisms are required to be established and mature during a very short time from hatching (*circa* 24 hours) until food is consumed. The yolk sac system is drawn into the body prior to hatching to continue yolk digestion after hatching. Some estimates indicate as much as 60% of the total energy of a neonate (Fan *et al.*, 1997) is devoted to maturation and growth of intestinal tissue in the first few days after hatching.

Yolk assimilation in neonates is altered by feeding, temperature extremes and type of feed but not water (Phelps, 1985). Gender also has no effect (Moran and Reinhart, 1980). Yolk absorption is reported to be complete after five to six days post-hatching. Yolk is utilised post-hatching by two mechanisms: (1) transfer of yolk into blood in embryos and (2) anti-peristaltic movement of yolk from the distal end towards the proximal small intestine where it is absorbed by the intestine (Noy and Sklan, 1998).

Intestinal maturation post-hatching has been studied extensively (Sell *et al.*, 1989; Fan *et al.*, 1997; Uni *et al.*, 1995a, 1995b, 1999; Suvarna, 1999) because of its economic importance to commercial poultry. Intestinal dissacharidases and glucose transport mechanisms are fully functional at about 48 hours post-hatching and can adjust rapidly to different types of food even at 72 hours post-hatching (Suvarna, 1999). In most domestic species of poultry, intestinal mass increases in parallel to nutrient intake (Noy and Sklan, 1996; Uni *et al.*, 1999). Therefore, starvation or lack of intake of various food types slows maturation of the intestine

(Noy *et al.*, 1996). In genetic lines of domestic fowl (O'Sullivan *et al.*, 1992; Uni *et al.*, 1995a) and turkeys (Christensen, unpublished) selected for rapid growth, hatchlings used increased growth of the intestine, rather than improved intestinal function, to increase nutrient uptake for more rapid growth.

One of the fastest growing organs during the first 10 days of the neonatal life is the pancreas (Phelps *et al.*, 1987b). The exocrine pancreas is the source of many digestive enzymes. Little is known about the function of the pancreas at these stages although glucagon and insulin from the endocrine pancreas are readily available in the embryo and neonate (Christensen *et al.*, 2001a).

Appetite is controlled neurologically in precocial species at hatchling (Noble *et al.*, 1999). The principal neurochemicals involved are norepinephrine and epinephrine (noradrenalin and adrenalin respectively). Both neurotransmitters are functional at hatching in poultry species (Denbow and Sheppard, 1993). Manipulations of neurotransmitters by dietary tyrosine or tryptophan did not improve livability or growth of hatchlings but dietary carbohydrate did (Nicholson, 1992).

BODY TEMPERATURE REGULATION

The zone of thermoneutrality for newly hatched avian species is very narrow. Birds vary enormously in their thermoregulatory capacities immediately after hatching, and they have been classified according to these and other capabilities (Nice, 1962). Precocial species are covered with down and are able to respond effectively to heat and to cold. By contrast, altricial birds are naked when hatched and have little ability to regulate their body temperature at air temperatures below 35°C or above 40°C. Other species are intermediate between precocial and altricial types (Dawson and Whittow, 2000). Most are not comfortable until they are provided an environment within this very narrow temperature range. During the last half of the incubation period the fowl egg maintains a temperature above that of the ambient air temperature of 37–38°C. When hatchlings are exposed to room air at 28°C, a new equilibrium state is reached in 5 hours (Tazawa and Rahn, 1987; Tazawa and Whittow, 2000). The difference between body temperature and ambient temperature increases from 6°C immediately after hatching to 10°C at five days post-hatching. Most altricial species require up to 10 days post-hatching to develop thermoregulatory abilities (Dawson and Whittow, 2000).

There are two types of thermoregulation available to the neonate. The first is thermoregulation by behavioural means (Dawson and Whittow, 2000). Thermoregulatory behaviour involves movement of the entire bird, or part of the bird, such as a limb, in response to a change of either environmental or body temperatures, and it often requires conscious effort. This is demonstrated in cold temperatures when the neonate will reduce its surface area by "hunching" or "huddling". Behavioural thermoregulation is available to most avian species at hatching.

Both peripheral temperature receptors and temperature-sensitive neurones in the central nervous system are involved in neural thermoregulation, the second mechanism in birds. Shivering is usually the response in neurological thermoregulation. Neural thermoregulation is available to birds at differing times following hatching. Some species, such as the domestic turkey, may require as long as four weeks to become fully mature and thermoregulate without supplemental heat (Dawson and Whittow, 2000). Brooding, the process of providing supplemental heat in domestic poultry, simulates a similar response by the mother under natural conditions.

Thyroid function is associated with thermoregulation because of its involvement with feather growth and basal metabolism and has been used as a basis to discriminate between precocial and altricial neonates (McNichols and McNabb, 1988). Thyroid hormone levels in precocial species peak prior to hatching and remain elevated during the first week after hatching whereas in altricial species they peak following hatching. Weytjens *et al.* (1999) related plasma tri-iodothyronine concentrations to the onset of thermoregulation in high and low body weight lines of fowl. Greater tri-iodothyronine levels indicated earlier thermoregulatory abilities.

RESPIRATORY SYSTEM

The final days of embryonic life for avian species are a time of respiratory transition. Respiration evolves from a system totally dependent upon diffusion of gases through the eggshell pores to one that is fully dependent upon convective forces for gas exchange in the lungs. Eggs are created with a functional property that allows respiration to occur by simple diffusion through pores created in the shell by the hen. Amazingly, these pores determine precisely the developmental time for the embryo (Ar and Rahn, 1978) as well as the time of lung inflation. The timing of the "plateau stage" in oxygen consumption determines the characteristic maturity of the respiratory system at hatching. The functional properties of the shell are thought to initiate convective mechanisms that will sustain the animal throughout the remainder of its life. The fluids must be evacuated from the lungs, which can then become functional. Fluid evacuation and aeration are gradual process and occur over several days both within the egg and post-hatching (Vince and Tolhurst, 1975; Bagley, 1987).

At the beginning of the last third of embryonic development in the fowl, the parabronchi have reached their final number and position (Duncker, 1977). Two to three days before hatching, blood capillary connections between arterioles and venules rapidly increase and air-filled capillaries sprout from the infundibula to surround the developing blood capillaries, forming a three-dimensional network of gas-exchange tissue. At this time the lung is aerated (Powell, 2000). Thus, the lung gradually becomes used as an organ of gas exchange between the time of internal pipping and hatching (the parafoetal period). The lung therefore does not suddenly expand at the time of hatching, as is the case with mammals at birth, but gradually grows to an air-filled structure during the parafoetal period.

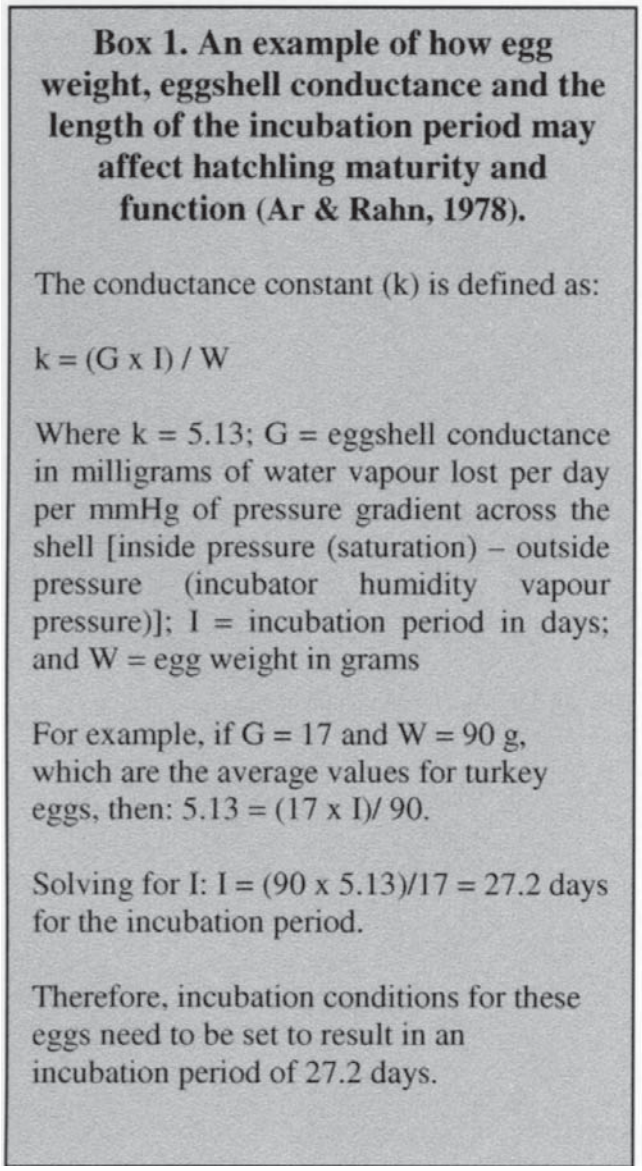
During post-hatching growth, the number of parabronchi in the lung does not increase; only their diameter and length increase. However, pneumatisation of the skeleton only occurs post-hatching (Duncker, 1977).

IMMUNE SYSTEM

The avian immune system is nearly non-existent in the embryo and is very weak at hatching (Zander, 1978). Lymphocytes are present in small numbers in the embryonic circulation during the final week of incubation and increase during the first two weeks of life (Bagley, 1987). The development of the subsystems that comprise the immune system also occur very slowly during the first two weeks post-hatching (Glick, 2000). Early studies revealed that the bursa of Fabricius grew most rapidly during the first three weeks after hatching, pleateaued, and then regressed as early as eight weeks of age (Glick, 1956, 1960). The spleen and bursa also grow very slowly during the first ten days of age in turkey poults and were classified as late maturing organs (Phelps *et al.*, 1987b). Similar results were obtained for thymus maturation (McCorkle *et al.*, 1983). Detectable graft-versus-host responses were first observed at 6 days post-hatching. After 6 days post-hatching, detectable responses were noted in their xenobiologic condition but appreciable responses were noted only in the 6 to 21 day old birds (McCorkle *et al.*, 1983).

EFFECT OF INCUBATION CONDITIONS ON MATURATION PROCESSES POST-HATCHING

One of the discriminating features of altricial and precocial species is the existence of a plateau phase in oxygen consumption (Ar and Rahn, 1978). Thus, it has been inferred that the existence of such a phase may play a major role in the characteristic maturity of the species at hatching. The factors determining the characteristic maturity have been summarised in what is called the conductance constant. Three variables seem to be interdependent in determining the maturity of a hatchling, and these three may be interrelated. The variables are eggshell conductance, the incubation period and the egg weight (Ar and Rahn, 1978). An example of how these measurements may be used in incubation is given in Box 1. Incubation conditions must be adjusted to account for these variables to allow optimal maturation of hatchlings (Christensen *et al.*, 2001b).



Box 1. An example of how egg weight, eggshell conductance and the length of the incubation period may affect hatchling maturity and function (Ar & Rahn, 1978).

The conductance constant (k) is defined as:

$k = (G \times I) / W$

Where k = 5.13; G = eggshell conductance in milligrams of water vapour lost per day per mmHg of pressure gradient across the shell [inside pressure (saturation) – outside pressure (incubator humidity vapour pressure)]; I = incubation period in days; and W = egg weight in grams

For example, if G = 17 and W = 90 g, which are the average values for turkey eggs, then: $5.13 = (17 \times I)/ 90$.

Solving for I: $I = (90 \times 5.13)/17 = 27.2$ days for the incubation period.

Therefore, incubation conditions for these eggs need to be set to result in an incubation period of 27.2 days.

Box 1 An example of how egg weight, eggshell conductance and the length of the incubation period may affect hatchling maturity and function (Ar and Rahn, 1978).

Table 1 Developmental rates of different physiological systems during the first seven days post-hatching in broilers and turkeys

System	Growth	Function
Circulatory system	Rapid and early in embryogenesis	Rapid and early
Kidney and body fluids system	Rapid and early following hatching	Slow until midway through embryogenesis to hatching
Digestive system	Rapid at hatching	Rapid at hatching
Body temperature control system	Slow	Depends upon species
Respiratory system	Slow	Slow
Immune system	Slow	Slow

If the timing of the plateau phase in oxygen consumption is accelerated or decelerated by incubation conditions or physical egg properties, then the embryo makes adjustments and may delay maturation and function. Examples of incubation conditions that may affect the plateau stage in oxygen consumption are the incubation temperature or the ventilation rates of the machines. When these conditions are imposed upon embryos in late development, the results can be long term (Buys *et al.*, 1998; Weytjens *et al.*, 1999). At high altitude, eggs are produced that naturally have longer incubation periods because hens at high altitude create eggs with decreased eggshell conductance values (Rahn *et al.*, 1977). Thus, conditions for high altitude incubation must be adjusted to preserve optimal plateau phase conditions to result in a mature hatchling.

CONCLUSIONS

The most striking feature of the initial days of life outside the shell is the rate at which different physiological systems mature (Table 1). Some systems become totally functional within a 24 hour period but others take considerably longer. As during the continued commercial development of different strains of poultry additional emphasis is placed on rapid growth, the ontogeny of some systems may be compromised (Lilja and Olsson, 1987). Management strategies need to be formulated to deal with such systems and simultaneously maintain the overall health of the neonate. Examples of tissue systems that need to mature rapidly in both size and function post-hatching are the heart, intestines and lungs.

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