Effects of egg of origin and chick post-hatch nutrition on broiler live performance and meat yields

S.L. VIEIRA¹ and E.T. MORAN Jr.²

¹Departamento de Zootecnia, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 7712, C.P. 776, Porto Alegre 91501-970, Brazil
²Department of Poultry Science, Auburn University, Auburn, Alabama 36849-5416, USA

The weight of hatching eggs can influence broiler live performance regardless of hen age. Egg composition is altered with egg weight, but such alterations do not seem to have major effects on broiler growth and processing yields. The chick hatches with a yolk sac which provides nutrients for the transition to independent feeding. Alterations in egg weight and composition do not affect the proportion of yolk sac to body weight as much as its composition, particularly with eggs from very young hens. The contents of the yolk sac are high in fat and protein but very low in carbohydrate, which could lead to ketosis with prolonged fasting. Enhancing the first feed with either carbohydrate or gluconeogenics such as propionic acid may alleviate this ketosis and help early development. The digestive system of the chick is physically complete at hatching but is not fully competent at nutrient retrieval as many enterocytes are orientated to immunoglobulin uptake. Villi length and enzymatic activity increases with feeding, reaching maturity within a few weeks. Access to food and water after hatching varies, and long delays until placement are common. These delays cause losses in live performance. Loss in body weight due to late placement or undernutrition may also affect early muscle development. These adverse effects extend to marketing age and reduced meat yield. Factors that affect early chick development are gaining interest as the length of time to market progressively decreases and the chick's first days represent an increasing proportion of the total time for production.

Keywords: Broiler chick; egg and chick composition; post-hatch nutrition; yolk sac
Introduction
The rate of weight gain by broilers has substantially increased during the last few decades. Consequently, slaughter age has been decreasing such that the final carcass weight, attained at 12 weeks of age in the early 1960s, now occurs by 6 weeks. The first few days of “adjustment” after hatching now therefore represent a much greater proportion of the broiler’s life span.

Early chick development can be affected by many factors. Several of these, such as age of the breeder hen and egg weight, are established before incubation. The environment prevailing at hatch is also important, and the first exposure of chicks to the hatchery and farm presents a host of microbial threats. Passive immunity is essential but only conveys protection from those microbes previously encountered by the hen.

The nutrients provided by the first food given during the transition from the yolk sac represents another major early influence. The current broiler nutrient recommendations of the National Research Council (1994) encompass the needs from placement to 21 days and assume that the utilisation of these nutrients by the post-hatched chick are as efficient as at 21 days of age. However, differences in feed utilisation are likely, given the changes which occur in the gastrointestinal system during the transition from embryo to juvenile and the variation in the reserves conveyed by the egg.

Egg and chick composition
Before incubation the egg provides all the factors necessary for successful embryonic development with the exception of oxygen which enters the egg through its porous shell (Romanoff and Romanoff, 1949). The fertile egg progresses through several changes en route to becoming a chick ready to cope with the external environment 3 weeks later. Before incubation, although the blastoderm has already divided into 60 000 cells (Burley and Vadehra, 1989), its diameter approximates only 3.0 mm and it represents an insignificant part of the whole egg (Dehnel, 1929). At this point a large amount of nutrients are available from the yolk, albumen and shell to support subsequent growth.

The average hen’s egg is composed of 58.5% albumen, 31.0% yolk and 10.5% shell (Shenstone, 1968). These proportions are not fixed but are affected by the hen’s age and its genetic background. Egg weight increases with the age of the hen, and this increase is accompanied by a greater proportion of yolk at the expense of albumen; however, heavier eggs within any one age of flock respond differently with a reduced proportion of yolk and a higher proportion of albumen than small eggs (Wiley, 1950; Marion et al., 1964, 1966; Varadarajulu and Cunningham, 1972). Different genetic sources of hens have also been shown to produce eggs varying in their proportions of yolk, albumen and shells (Cunningham et al., 1960; Marion et al., 1964; Kline et al., 1965).

Water is the dominant constituent of eggs. Albumen (88.8%) has the greatest concentration followed by the yolk (47.5%); the shell only has 1%. Total egg solids are dominated by proteins in the albumen, whereas lipids are almost exclusively found in the yolk. A huge reserve of calcium carbonate is found in the shell (Romanoff and Romanoff, 1949). Albumen contains several different proteins which represent more than 90% of its dry matter. These consist of simple proteins (54% ovalbumin and 12% ovotransferrin) and glycoproteins (11% ovomucoid and 1.5% ovomucin) (Osuga and Feeney, 1977). Ovoglobulins and lysozyme, which
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also have carbohydrates in their molecules, are other major constituents at 8% and 3.5%, respectively (Nakamura et al., 1980).

Yolk dry matter consists primarily of protein and lipid in a ratio of 2:1 (Chung and Stadelman, 1965). Most of the dry matter is present as very low density lipoproteins (VLDL) suspended within the yolk's aqueous system (Bellairs et al., 1972). These VLDLs overwhelmingly originate from the liver with a small proportion coming directly from the small intestine (Moran, 1987). Phosvitin is the second most abundant lipoprotein with 11% of its weight being phosphorus (Burley and Vadehra, 1989). Yolk lipid comprises 72.5% triglycerides, 24.4% phospholipids and 3.9% cholesterol (Schneider and Tatrie, 1968). Oxidation of the associated fatty acids provides the bulk of energy needed by the embryo, but much of the phospholipid, particularly lecithin, may be directly incorporated unchanged into the membranes of the embryo during development (Burley and Vadehra, 1989).

The egg contains very little free carbohydrate. Tunmann and Silberzahn (1961) found 0.5% in the albumen and 0.2% in the yolk, of which 98% was glucose. Carbohydrates present in the yolk and albumen taken together account for approximately 1% of the whole egg (Romanoff and Romanoff, 1949).

The chemical composition of the egg varies to a small extent with the age of the hen and between genetic sources. Data have been mostly gathered from hens providing table eggs. The moisture and protein contents of whole eggs increase as the hens age, while eggs from various strains can differ in their composition (May and Stadelman, 1960); however, these alterations are not consistent for albumen and yolk. With increasing hen age the content of protein in the yolk increases, whereas a reduction (to a lesser degree) takes place in the albumen (Ambrosen and Rotenberg, 1981). The fat content of egg yolk also increases as broiler breeder hens age (McNaughton et al., 1978). The fatty acid composition of the whole egg may be altered by genetic selection (Edwards, 1964), particularly in lines selected for reduced fatness (Cahaner et al., 1986).

Changes in the amount of albumen in the egg appear to have a greater impact on embryo development than changes in the yolk. Removal of up to 20% of the yolk from fertilised eggs before incubation did not influence the metabolic rate in the embryo nor the size of the chick at hatching, but did reduce the amount of yolk sac available at hatch (Finkler et al., 1998). Although a decrease in the amount of egg yolk therefore does not alter the body mass of the embryo, it may compromise subsequent post-hatch performance because of the reduction in yolk sac reserve. Removal of the albumen, however, results in a decrease in both body and yolk sac masses. The albumen in the egg provides considerable water and protein and any reduction in its content is likely to cause a shortage of critical material for embryo development.

The increase in egg weight that occurs as breeder hens age is known to be accompanied by comparatively small alterations in the proportions of yolk, albumen and their dry matter contents (Table 1). Vieira and Moran (1998a) conducted analyses of eggs and chicks originating from breeders representing commercial extremes in age. Similar amino acid profiles were observed in the proteins from both eggs and chicks taken from breeders at 27 and 62 weeks of age; similar proportions of minerals were also noted. An exception to this was the phosphorus concentration in the yolk sac of chicks derived from 27-week-old breeders which was lower than that from 62-week-old hens, whereas there was little difference in the phosphorus contents of their respective carcasses. Given that the phosphorus concentrations in the egg yolks were similar at the two
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Table 1 Eggs, chicks, and yolk sacs originating from breeder hens at extremes in age (27 versus 62 weeks of age). Reproduced from Vieira and Moran (1998a) with permission.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Breeder age (weeks)</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>27</td>
</tr>
<tr>
<td>Egg</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight (g)</td>
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<td>55.5</td>
</tr>
<tr>
<td>Yolk (%)</td>
<td>***</td>
<td>30.6</td>
</tr>
<tr>
<td>Albumen (%)</td>
<td>***</td>
<td>55.8</td>
</tr>
<tr>
<td>Shell (%)</td>
<td>***</td>
<td>12.9</td>
</tr>
<tr>
<td>Chick carcass without yolk sac</td>
<td>NA</td>
<td>43.4</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>*</td>
<td>49.2</td>
</tr>
<tr>
<td>CP (% DM)</td>
<td>NA</td>
<td>13.5</td>
</tr>
<tr>
<td>EE (% DM)</td>
<td>NA</td>
<td>5.1</td>
</tr>
<tr>
<td>Ash (% DM)</td>
<td>NA</td>
<td>5.1</td>
</tr>
<tr>
<td>Yolk sac with contents</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight (g)</td>
<td>*</td>
<td>4.4</td>
</tr>
<tr>
<td>% of body weight</td>
<td>NS</td>
<td>11.1</td>
</tr>
<tr>
<td>CP (% DM)</td>
<td>NA</td>
<td>58.0</td>
</tr>
<tr>
<td>EE (% DM)</td>
<td>NA</td>
<td>19.2</td>
</tr>
<tr>
<td>Ash (% DM)</td>
<td>NA</td>
<td>4.0</td>
</tr>
<tr>
<td>Phosphorus (% Ash)</td>
<td>NA</td>
<td>6.6</td>
</tr>
</tbody>
</table>

***p < 0.0001; *p < 0.05.
NA, not statistically analysed; NS, not significant; CP, crude protein; EE, ether extract; DM, dry matter.

Extremes in breeder age before incubation, this difference in the phosphorus concentrations of the yolk sacs may mean that a greater phosphorus allowance needs to be provided in the first diet, particularly since phosphorus is a common limiting nutrient.

Within breeds, the proportions of yolk and albumen in eggs from broiler breeders can also differ at any one age (Vieira and Moran, 1998b; Table 2). “Large” and “small” eggs representing the top and bottom thirds of the population from breeder flocks of similar age but represented by different strains also had comparatively small differences in their proportions of yolk and albumen and proximate compositions. After these eggs were hatched, the resulting chick weights reflected egg weight irrespective of the strain, but the carcasses were of similar composition. The percentage of yolk sac did not change with egg weight but its composition was altered.

Performance and egg of origin

Egg weight and chick weight at hatching are known to be highly correlated (Halbersleben and Mussehl, 1922). Within each avian species the size of the embryo before and at hatching can be altered by the weight of the egg and the incubation environment (Wilson, 1991). The ratios between the weights of the chick at hatching and the egg range between 0.615 and 0.760 (Shanawany, 1987). This ratio is higher the greater the egg weight because of progressive decreases in the water loss during incubation and the effect of the residual shell, the surface area of which decreases relative to the total egg mass (Washburn and Guill, 1974; Whiting and Pesti, 1983).
Table 2. Eggs, chicks, and yolk sacs originating from breeder hens of diverse strain crosses of similar age. Reproduced from Vieira and Moran (1998b) with permission.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Egg weight</th>
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<th>Strain cross</th>
<th></th>
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<tr>
<td></td>
<td>p value</td>
<td>Heavy</td>
<td>Light</td>
<td>A</td>
</tr>
<tr>
<td>Egg weight (g)</td>
<td>***</td>
<td>65.3</td>
<td>57.1</td>
<td>***</td>
</tr>
<tr>
<td>Yolk (%)</td>
<td>***</td>
<td>31.7</td>
<td>32.8</td>
<td>***</td>
</tr>
<tr>
<td>Albumen (%)</td>
<td>***</td>
<td>56.6</td>
<td>55.4</td>
<td>***</td>
</tr>
<tr>
<td>Shell (%)</td>
<td>NS</td>
<td>11.4</td>
<td>11.4</td>
<td>***</td>
</tr>
<tr>
<td>Chick carcass without yolk sac</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight (g)</td>
<td>***</td>
<td>44.5</td>
<td>39.6</td>
<td>***</td>
</tr>
<tr>
<td>CP (% DM)</td>
<td>*</td>
<td>60.5</td>
<td>61.5</td>
<td>NS</td>
</tr>
<tr>
<td>EE (% DM)</td>
<td>NS</td>
<td>24.7</td>
<td>25.2</td>
<td>NS</td>
</tr>
<tr>
<td>Ash (% DM)</td>
<td>NS</td>
<td>6.9</td>
<td>7.0</td>
<td>NS</td>
</tr>
<tr>
<td>Yolk sac with contents</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight (g)</td>
<td>***</td>
<td>5.6</td>
<td>4.0</td>
<td>NS</td>
</tr>
<tr>
<td>% of body weight</td>
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<td>9.4</td>
<td>NS</td>
</tr>
<tr>
<td>CP (% DM)</td>
<td>NS</td>
<td>51.4</td>
<td>49.4</td>
<td>NS</td>
</tr>
<tr>
<td>EE (% DM)</td>
<td>***</td>
<td>32.7</td>
<td>36.9</td>
<td>***</td>
</tr>
<tr>
<td>Ash (% DM)</td>
<td>***</td>
<td>4.3</td>
<td>4.9</td>
<td>***</td>
</tr>
<tr>
<td>Phosphorus (% Ash)</td>
<td>NA</td>
<td>9.5</td>
<td>8.9</td>
<td>NA</td>
</tr>
</tbody>
</table>

In the absence of significant interactions (p > 0.05), data on egg weight and strain crosses are given as contrasts.

***p < 0.0001; **p < 0.05, *p < 0.05.

NA, not statistically analysed; NS, not significant; CP, crude protein; EE, ether extract; DM, dry matter.

Means followed by different letters in the same row are statistically different by the Tukey test, p < 0.05.

The correlation existing between egg and chick weights decreases with age of the progeny after hatching (Upp, 1928; Wiley, 1950; O’Neil, 1955). However, the influence of egg weight remains until marketing when each gramme advantage at hatch translates into a 2–13 g improvement in the body weight at 6 weeks of age (Wilson, 1991). Because the growth of females is less than that of males, it follows that the response of females to egg weight is not as great (Joubert et al., 1981).

Selection for rapid growth has led to a progressive reduction in the age at which market weight is attained. Given the high correlation between egg weight and final body weight, the economic importance of egg weight is apparent (Wilson, 1991). McNaughton et al. (1978) and Tufft and Jensen (1991) demonstrated that the effect of the egg weight on body weight at market age is independent of the age of the breeders from which the eggs originated. Mortality is usually greater among chicks hatched from small eggs than those from large eggs (McClung and Smith, 1949; Wiley, 1950; McNaughton et al., 1978; Wyatt et al., 1985; Hearn, 1986). The effect of breeder age in this case seems to be largely associated with egg weight. Use of very young parents influences hatchability as well as early chick survival and egg weight per se does not seem to be involved. High mortality of embryos originating from very young hens has been correlated with the reduced mobilisation of lipid from the yolk to the embryo at day 19 of incubation. This decreases development during the last week of incubation (Noble et al., 1986). Egg yolks from 41-week-old breeder hens have been shown to have lower concentrations of phospholipids and...
free cholesterol than those from 25-week-old hens because triglyceride concentrations were higher.

Conversion of food into body weight by growing broilers does not seem to be directly related to their egg weight of origin. Results are mixed, with some reports showing an improvement in food conversion with egg weight (Wiley, 1950; Proudfoot et al., 1982) while others indicate an impairment or no effect (O’Neil, 1955; Morris et al., 1968; Proudfoot and Hulan, 1981; Wyatt et al., 1985; Hearn, 1986). A portion of the body weight advantage attributable to birds from heavy eggs may be related to their associated increased food intake (Pinchasov, 1991).

In studies conducted by Vieira and Moran (1998c, d), weight gains of broilers were greater among chicks originating from “heavy” eggs irrespective of the age of the breeder hen (Table 3). Food conversion efficiency was not affected, but higher mortality occurred among broilers from “light” eggs when they originated from young hens. However, when eggs were classified by weight within each flock age, overall mortality was generally greater with broilers from “heavy” eggs. Upon processing, broilers from “heavy” eggs generally provided a greater proportion of carcass yield than those from “light” eggs.

Yolk sac utilisation

The chick hatches with an attached yolk sac which represents around 10% of its total body weight (Romanoff, 1960). Yolk sac contents enable nutritional adaptation of the newly hatched chick from the embryonic environment to independent life. A direct relationship exists between the amount of nutrients provided by the yolk sac and the subsequent performance of the broilers. Deutectomised chicks have poorer early performance than sham operated controls (Edwards et al., 1962). Genetic selection for body weight at 8 weeks has been shown to increase the proportion of yolk sac at hatch and is probably an important factor in the improved weight gain observed among these birds (Nitsan et al., 1991a).

Yolk sac contents are high in fat and protein to provide an important part of the chick’s nutritional needs during the first few days after hatching. Chicks receiving food ad libitum have 50% of the energy and 43% of their protein needs provided by the yolk sac during the first day after hatching (Murakami et al., 1988). Yolk sac nutrients rapidly diminish and are almost depleted by the third day. Nutrients in the yolk sac may be differentially utilised with time. Although 80% of the fat has

Table 3 Effects of hatching egg weight on live performance of broiler males. Reproduced from Vieira and Moran (1998c, d) with permission

<table>
<thead>
<tr>
<th>Breeder Age</th>
<th>Weight gain (1–49 days) (g)</th>
<th>Food conversion (1–49 days)</th>
<th>Mortality (1–49 days) (%)</th>
<th>Carcass yield (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Different breeder age</td>
<td>***</td>
<td>NS</td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td>62 weeks (heavy)</td>
<td>2692</td>
<td>1.90</td>
<td>9.0</td>
<td>66.5</td>
</tr>
<tr>
<td>27 weeks (light)</td>
<td>2595</td>
<td>1.93</td>
<td>14.8</td>
<td>65.6</td>
</tr>
<tr>
<td>Similar breeder age</td>
<td>***</td>
<td>NS</td>
<td>**</td>
<td>NS</td>
</tr>
<tr>
<td>Heavy</td>
<td>2827</td>
<td>1.90</td>
<td>5.0</td>
<td>66.3</td>
</tr>
<tr>
<td>Light</td>
<td>2750</td>
<td>1.89</td>
<td>1.3</td>
<td>65.9</td>
</tr>
</tbody>
</table>

*p < 0.05; **p < 0.01; ***p < 0.001.
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disappeared by the end of the first day after hatching, protein may be provided
for up to 4 days (Nitsan et al., 1991b).

The age of breeder hens can influence the proportion of the yolk sac in the
hatched chick and its composition at that time. McNaughton et al. (1978) and Tuft
and Jensen (1991) observed an increase in the proportion of fat and reductions in
the moisture and protein in the carcasses of chicks from breeder hens of
advancing age. Chicks from progressively older breeder flocks have increased
energy reserves. Latour et al. (1996) observed that newly hatched chicks from
young breeder stock have less circulating cholesterol from lipoproteins than
chicks from older breeders. Such a difference supports the view that fat
metabolism and lipoprotein transfer are reduced in newly hatched chicks from
young hens, thereby threatening their viability (Latour et al., 1998).

The yolk sac is also an important means of providing passive immunity until
the juvenile immune system becomes mature. Passive immunity present in the
egg represents defences that are determined from maternal experiences. Albu-
men has IgA that is largely transferred to the embryo by the end of the second
week of incubation, when the sero-amniotic connection ruptures and oral
consumption is enabled. IgA can be detected in the digestive tract and yolk sac
of embryos at pipping (Rose et al., 1974). IgG provided by the hen is transferred
across the follicular epithelium of the ovary and accumulates in the yolk during
oogenesis (Rose and Orlans, 1981). Generally, the heavier the yolk the greater
the amount of IgG available to the chick. Yolk sac IgG is continuously absorbed
by the embryo during incubation until 2 days after hatching when its source
depletes (Li et al., 1998).

Assimilation of the yolk by the yolk sac membrane is multifaceted. Most occurs
by direct absorption through the yolk sac membrane (Murakami et al., 1992).
Evidence suggests that lipid uptake occurs through non-specific phagocytosis
(Noble and Cocchi, 1990). A portion of the yolk sac contents appears to be
transferred into the gut through the yolk stalk whereupon normal digestion
ensues (Sulaiman et al., 1996). Yolk utilisation is more rapid in fed than in fasted
chicks, suggesting that the transfer of yolk into the intestine may be facilitated by
the intestinal motility of fed chicks (Noy and Sklan, 1996). Such entry of yolk sac
contents into the small intestine is also thought to stimulate the development of
the digestive-absorptive functions at this time (Noy and Sklan, 1997).

Nutrient metabolism in the newly hatched chick

Yolk is the primary energy source for the embryo during its development,
whereas albumen is the dominant source of protein. Albumen remaining at the
end of the second week of incubation flows into the amniotic cavity when the
sero-amniotic connection is ruptured; the amniotic cavity mixture is then
progressively swallowed by the embryo (Romanoff, 1967). The albumen so
transferred is partly absorbed as it passes through the intestine with the
remainder entering the yolk sac. Presumably, a portion of the albumen entering
the yolk sac provides for gluconeogenesis upon absorption at the yolk sac
membrane (Kusuhara and Ishida, 1974; Pons et al., 1986). Because the amount of
carbohydrate in the egg is very low (Shenstone, 1968), gluconeogenesis from
protein metabolism is very likely to be the inane source of glucose for the
accumulation of glycogen that eventually fuels hatching (John et al., 1988).
Glycolysis rather than fatty acid oxidation is needed at hatching to provide
energy because oxygen is limited (Bakhuis, 1974; John et al., 1987) during the
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transition from chorioallantois to pulmonary respiration (White, 1974; Wittman and Weiss, 1981; Hoiby et al., 1987). Glycogen stores decrease to a very low level after hatching when the newly hatched chick has full access to oxygen and can fully use the fat stored in its carcass and remaining in its yolk sac (Roseborough et al., 1978). Increasing the dependence on fat for energy when combined with inaccessibility of glucose leads to a progressive ketosis in the newly hatched chick (Best, 1966). Furthermore, incomplete fatty acid catabolism also reduces the production of the metabolic water that is crucial for tissue hydration (Hammond, 1944). Dependence on gluconeogenesis from protein at this time is presumed to divert its use from growth that would otherwise have occurred.

The predominant energy source for the chick ordinarily changes from yolk-based lipid to dietary carbohydrate within 2–3 days of hatching. Diets high in carbohydrate and fed soon after hatching increase the blood glucose concentration and lower hepatic glucose-6-phosphatase activity which indicates reduced gluconeogenesis (Donaldson and Christensen, 1991). Under commercial conditions, chicks may be delayed access to carbohydrate for a considerable time after hatch and this increases the likelihood of ketosis and dehydration. Early access to glucose for newly hatched chicks can be made possible by oral dosing of sugars after hatching (Kienholz and Ackerman, 1970; Waldroup et al., 1974), but if the glucose provided in this manner is excessively concentrated it may cause diarrhoea (Moran, 1988). Subcutaneous injections are easier to perform than oral gavage but are of limited value because only small doses are possible. Improvement in early body weight gain was greater in chicks receiving glucose administered by subcutaneous injection than by crop incubation, but exploiting this advantage depends on subsequent early access to food and water (Moran, 1990). Feeding a diet containing 20% glucose improved body weight gain and food intake in naive birds but not in 55 inoculated chicks.

Propionic acid is gluconeogenic and is rapidly absorbed by the chick after oral administration (Hume et al., 1993). High doses, administered in the first diet, have been shown to reduce early mortality in poults hatched from small eggs (Phelps et al., 1992). Propionic acid has been suggested to be an anorectic (Donaldson et al., 1994; Pinchasov and Elmaliah, 1994) which could complicate the initiation of food intake; however, limiting its use in chicks to that period before yolk sac depletion is expected to relieve ketosis from fat oxidation. Propionic acid also has bacteriocidal properties, particularly for Salmonella and other consumed pathogens (Westerfeld et al., 1970). Studies were conducted by Vieira and Moran (1998c, 1999a) with a view to improving glucose access to post-hatched chicks. Calcium propionate was added to the starter diet which was given to chicks up to 3 days of age. Ground maize, as a high carbohydrate diet, was also fed at placement for 3 days. These dietary treatments failed to improve the early growth of broiler chicks as had previously occurred when propionic acid was fed from placement to 7 days. However, reductions in mortality were observed following access to the maize (Table 4).

Embryonic transition to the independent chick

Progression from embryonic to independent life is aided by the chick’s ability to digest and absorb nutrients from its food. The pancreas, liver and small intestine develop rapidly after hatching, emphasising the importance of these organs to the newly hatched chick (Katanbaf et al., 1988). This rapid growth of the intestine reaches a maximum between 3 and 7 days and declines thereafter.
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Table 4 Weight gain and mortality of broilers fed on ground corn or standard starter feeds and the effect of supplementation with 2.4% calcium propionate to 3 days of age (Experiment 1) compared with propionic acid supplementation in the starter given to chicks originated from young breeders to 7 days of age (Experiment 2). Reproduced from Vieira and Moran (1998c, 1999a) with permission

<table>
<thead>
<tr>
<th></th>
<th>Weight gain (1-21 days) (g)</th>
<th>Weight gain (1-49 days) (g)</th>
<th>% mortality (1-21 days)</th>
<th>% mortality (1-49 days)</th>
</tr>
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<tbody>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
<td></td>
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<tr>
<td>Feed</td>
<td></td>
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</tr>
<tr>
<td>Standard</td>
<td>706</td>
<td>2980</td>
<td>2.7</td>
<td>13.6</td>
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<tr>
<td>Ground corn</td>
<td>644</td>
<td>2873</td>
<td>1.3</td>
<td>8.7</td>
</tr>
<tr>
<td>Ca propionate</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>0</td>
<td>674</td>
<td>2927</td>
<td>2.9</td>
<td>12.7</td>
</tr>
<tr>
<td>2.4% (0–3 days)</td>
<td>685</td>
<td>2926</td>
<td>1.6</td>
<td>9.5</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Propionic acid</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>672</td>
<td>2630</td>
<td>4.3</td>
<td>17.6</td>
</tr>
<tr>
<td>3% (0–7 days)</td>
<td>659</td>
<td>2609</td>
<td>7.6</td>
<td>12.1</td>
</tr>
</tbody>
</table>

*p < 0.05; ***p < 0.001.

(Murakami et al., 1992). The length of the small intestine increases during the first week after hatching even when the bird is fasted, but for villus development initiation of feed intake is essential (Baranyiová, 1972; Baranyiová and Holman, 1976).

Generally, the intestines are not fully competent at digestive and absorptive activities until 2 weeks after hatching. Enterocytes covering the villi at the second week of incubation are orientated to immunoglobulin uptake and have no associated carbohydrases nor the means for active transport (Moran, 1985). The height of the microvilli 10 days before hatching remains the same until 5 days before hatching when there is a gradual increase over the next 10 days with food intake leading to their rapid extension (Overton and Shoup, 1964). Broiler strains selected for rapid weight gain show additional villus volume after hatching, but the rate of change thereafter is not different from slow growing strains (Uni et al., 1995). Early access to food stimulates the growth of the intestines and their absorptive capacity as new enterocytes with digestive-absorptive capacity are generated from the crypts of Lieberkühn (Moran, 1985). Absence of stimulation from food intake causes shortening and thinning of the villi, even in 6-week-old chickens (Michael and Hodges, 1973).

Nutrients accessible to the newly hatched chick change from the maternal source provided by the yolk to consumed food. Although the ability to utilise dietary carbohydrates can be detected in the embryo by 18 days of incubation, a meaningful capacity does not become established until a few days after hatching (Siddons, 1969). Marchaim and Kulka (1967) detected pancreatic α-amylase at 18 days of incubation, but maximum specific activity was not attained until 4 days after hatch. The ability to digest starch can be 85% complete by 4 days after hatch with no obvious improvements thereafter (Noy and Sklan, 1995).

Lipase activity has been detected in the yolk sac membrane of turkey poultts as early as 7 days of incubation. It increases further to the point of hatch and thereafter decreases to zero by 4 days (Escribano et al., 1988). In contrast,
pancreatic lipase increases linearly until 16 days after hatching when it reaches a plateau. Liver and intestinal phospholipases also increase embryo and early chick development, suggesting involvement with the pre- and post-absorption of yolk phospholipids (Prasad, 1977). Generally, the ability to absorb dietary lipids is not well developed in the newly hatched chick. Part of the problem appears to result from an impaired enterohepatic circulation of bile salts because of an accumulation of taurocholate in the ileum (Jeanson and Kellogg, 1992) leading to an inability to respond fully with emulsification when the addition of dietary fat increases the demand (Serafin and Nesheim, 1970). Fat digestion improves with age as pancreatic lipase increases; however, lipase does not seem to be as limiting to fat digestion as does access to bile (Krogdahl and Sell, 1989). Fat digestion by the chick is improved when bile salts are added to the diet (Polin and Hussein, 1982) and when the extent of fatty acid unsaturation increases (Renner and Hill, 1960; Carew et al., 1972). Accordingly, long chain saturated fatty acids should be avoided in the diet of the young chick (Blanch et al., 1995) whereas unsaturated fat is to be favoured (Noy and Sklan, 1995).

The embryonic pancreas provides the enzyme capacity to digest protein before hatching. The specific activities of carboxypeptidase A and chymotrypsin progressively increase from 16 days of incubation and reach their maxima 2 days after hatching (Kulka and Duskin, 1964; Marchaim and Kulka, 1967). A trypsin inhibitor has been identified in the ovomucoid fraction of the albumen (Lineweaver and Murray, 1947). This inhibitor passes orally after the rupture of the sero-amniotic membrane at the end of the second week of incubation, thereby inhibiting trypsin activity and preventing activation of most other pancreatic enzymes that may be released into the intestinal lumen. Inhibition of protein digestion at this time presumably acts to protect IgA immunoglobulins intended for passive protection. Although trypsin and chymotrypsin have reduced activities after hatching, they rapidly increase to reach maxima 10 days later (Nitsan et al., 1991a; Nir et al., 1993). Protein digestive efficiency improves from 78% to 90% during the period from 4 to 21 days after hatching, indicating that digestion of protein is more limited than that of either carbohydrate or fat in the newly hatched chick (Bielorai et al., 1973; Noy and Sklan, 1995). Secretion of active pancreatic proteases after hatching, together with the development of peptide hydrolysis at the enterocyte luminal surface, not only depends on the age of the chick but also on the initiation of the food intake (Austic, 1985; Tarvid, 1992).

The increase in digestive efficiency that occurs with age develops in parallel with an adjustment in the food passage rate (Sibbald, 1979). The threefold increase in food consumption that takes place between 4 and 10 days after hatching is accompanied by a 30% reduction in the rate at which it progresses through the gastrointestinal tract (Noy and Sklan, 1995).

**Post-hatch variables**

Any effects resulting from delays in emergence to access to food and water depend on the nutrient reserves provided by the yolk sac. These delays result from the time spent in the hatchery and transportation to the farm. Variability in the time spent at the hatchery can be extensive because of asynchrony of chick emergence from the egg. Chicks hatching early may be held 36 hours longer than those hatching late (Hager and Beane, 1983). Eggs from old breeders hatch earlier than those from younger flocks, and chicks from smaller eggs tend to hatch earlier than those from larger eggs (Shanawany, 1984).
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Delaying access to food and water increases the danger of performance being adversely affected. During their first 24 hours of life broiler chicks lose body weight even when food and water is immediately provided (Pinchasov, 1991). This initial loss increases with time (Misra and Fanguy, 1978; Hager and Beane, 1983). Removing chicks that emerge early from the hatcher and immediately providing them with food and water increases subsequent growth compared with that achieved by similar birds placed with those that emerge later (Williams et al., 1951). Loss in body weight associated with holding chicks in the hatchery is perpetuated through to their marketing (Kingston, 1979; Fanguy et al., 1980; Hager and Beane, 1983; Wyatt et al., 1985). Weight losses incurred by chicks held for 24 and 48 hours were equivalent to lengthening the time taken to reach market weight by 1 and 2 days, respectively (Nir and Levanon, 1993).

Reduced growth and increased early mortality that occurs among chicks held without access to food and water is associated with dehydration and a shortage of available energy. Reduction in yolk sac weight is linear during the first 48 hours after hatching and is more rapid than the reduction in the weight of the associated carcass. During their depletion the lipid in both the yolk sac and carcass decreases, whereas a reduction in protein only occurs in the yolk sac with the proportion in the carcass remaining constant. These alterations in composition are particularly important when birds are under heat stress, when mortality is accentuated (Kingston, 1979; Nir and Levanon, 1993; Pinchasov and Noy, 1993). Xin and Lee (1997) have demonstrated that inadequate nutrition plays a more important role than dehydration in causing chick morbidity resulting from prolonged delays in placement. Prolonged fasting, as with delayed placement, results in a reduction in the rate of absorption of amino acids and other nutrients from the intestine (Newey et al., 1970; Baranyiová and Holman, 1976). Stress associated with holding can also decrease the chick's ability to produce antibodies against disease (Wyatt et al., 1986). Casteel et al. (1994) reported a lower antibody titre in chicks held in the hatcher for 24 hours compared with that in birds placed immediately after hatching.

In a recent experiment conducted by Vieira and Moran (1999a), broiler chicks were placed immediately after hatching or after a 24 hour delay in floor pens with litter used for a previous broiler flock or new pine shavings. The diet was not supplemented with any antimicrobial compound. Birds delayed 24 hours before placement had a reduced weight gain after hatching that was perpetuated until market, whereas birds placed on used litter that also experienced an early reduction in weight gain were able to recover (Table 5). Mortality was significantly increased among birds of delayed placement, but was not influenced by used litter.

Early undernutrition and muscle growth

Birds with restricted nutrition early after hatching never attain the weight of those that are fed early (Misra, 1978; Hager and Beane, 1983; Wyatt et al., 1985; Nir and Levanon, 1993). This failure is likely to involve depressed development of muscle (Elliot et al., 1943). Muscle growth after hatching in the chicken is considered to result from the hypertrophy of a fixed number of fibres (Smith, 1963). Chicks experiencing delayed access to food have reduced subsequent overall food consumption. This has been used as a partial explanation for their reduced weight gain (Nir and Levanon, 1993). However, this live weight reduction may also be partly caused by a decreased potential for protein deposition. Early nutrient
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Table 5 Weight gain and mortality of broilers given feed and water immediately after hatching compared with those with a 24 h delay when grown in pens having new pine shavings or used litter. Reproduced from Vieira and Moran (1998d, 1999a) with permission

<table>
<thead>
<tr>
<th>Placement</th>
<th>Weight gain (1-21 days) (g)</th>
<th>Weight gain (1-49 days) (g)</th>
<th>% mortality (1-21 days)</th>
<th>% mortality (1-49 days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immediate</td>
<td>647</td>
<td>2654</td>
<td>2.0</td>
<td>6.3</td>
</tr>
<tr>
<td>24 h delay</td>
<td>598</td>
<td>2568</td>
<td>1.5</td>
<td>10.5</td>
</tr>
<tr>
<td>Litter</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>New</td>
<td>633</td>
<td>2801</td>
<td>1.5</td>
<td>8.3</td>
</tr>
<tr>
<td>Used</td>
<td>613</td>
<td>2621</td>
<td>2.0</td>
<td>8.5</td>
</tr>
</tbody>
</table>

*p < 0.05; **p < 0.01; ***p < 0.001.

Inadequacies have also been shown to decrease skeletal muscle growth, and animals may subsequently either have to compensate or never overcome this deficit. Lack of growth compensation by rats suffering from nutrient restriction very early in life led Winick and Noble (1966) to speculate that such animals have a reduced number of cells that permanently restricts the capacity for subsequent growth, regardless of later food intake. Pitts (1986) speculated that the number of DNA units added to myofibres may be reduced in young rapidly growing animals as a consequence of nutrient restriction. However, it is now considered that nutritional inadequacies reduce DNA unit size without affecting their number and "catch up" to their previous position on the growth curve can be achieved once nutritional adequacy is established.

Myoblasts grown in vitro are unable to divide once they develop into myotubes and become muscle fibres (Bintliff and Walker, 1960); however, in vivo studies demonstrated that muscle nuclei number increases as growth ensues in rats (Eonesco and Puddy, 1964) and chickens (Moss, 1968). These increased nuclei originated from satellite cells (Moss and Leblond, 1971) which are located between the basement membrane and plasmalemma of each fibre and consist of a single nucleus surrounded by scanty cytoplasm (Mauro, 1961). Even though satellite cells are needed during early posthatch muscle growth to increase myonuclei that provide for myofibre growth (Allbrook et al., 1971), they become quiescent once the muscle matures (Schultz et al., 1978).

Alteration in the rate of satellite cell mitotic activity during early development may be the basis whereby differences exist in the number of myofibre nuclei during subsequent growth. Moss and Leblond (1971), using autoradiographic and electron microscopic techniques, calculated the actual and relative incidence of labelled satellite cell nuclei and myofibre nuclei over a 72 hour period in rats from 14 to 21 days of age. They concluded that mitotic activity and incorporation rate were consistent with the hypothesis that satellite cells account for all nuclei incorporated into normally growing myofibres.

It is presumed that each DNA in multinucleated myofibres controls its surrounding volume of cytoplasm (Cheek, 1985) because mRNA produced by a single myonucleus is restricted to the immediately surrounding area (Ralston and Hall, 1992). Given that satellite cells fuse with enlarging myofibres at a rate sufficient to maintain a constant DNA unit size during posthatch muscle growth
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(Moss, 1968), then the rate of muscle growth depends on myonuclear accretion. In turn, myofibre size would also be controlled by the number of DNA units (myonuclei) added from satellite cell mitotic activity. Mozdziak et al. (1997) suggested that muscle size can be permanently reduced by the inhibition of nuclear accretion during early development, because turkey poult breast muscle did not compensate in weight after irradiation and did not achieve the growth of non-irradiated muscle. Mozdziak et al. (1997) observed no difference in DNA unit size between selected muscles from turkeys at any time, but an age-related increase was detected. Inhibition of satellite cell mitotic activity by irradiation of turkey breast muscle reduced muscle growth by decreasing the number of satellite cell nuclei available for fusion with myofibres at a critical time (3–6 weeks of age) to prevent permanently a full expression of growth. In fact, Halevy et al. (1998) found a high correlation between the weight of chicken breast muscle and the number of satellite cells per gramme of breast muscle at 5 days of age.

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