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Relationship of the Eggshell Conductance Constant to Intestinal Physiology[1]

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Abstract: The hypothesis was proposed that eggshell conductance constants (k) alter embryonic intestinal development and affect growth post hatching. Egg weight (EW), eggshell conductance (G) and length of the incubation period (IP), the three components of the conductance constant were changed to determine their effect on intestinal physiology. Eggs were selected based on EW and G properties. Half of the selected eggs were incubated using a single stage temperature profile to shorten IP in each of two experiments. EW, G and IP interacted in the first experiment to affect intestinal growth and metabolism. In Experiment 2, k reduced intestinal weight in embryos as well as poults. EW and IP affected the size and maturity of intestinal tissue at the time of hatching. Differences in EW, G and IP observed at hatching were shown to affect the growth of poults for the first week following hatching. Thus, k may act to reduce growth in poults by affecting intestinal maturation. It is suggested that large eggs with low permeability may be at risk for weak poults. This may be especially true when they are exposed to shorter IP.

Key words: Eggshell conductance, weak poults, intestinal physiology

Introduction

Eggshell conductance (G) determines the characteristic length of the incubation period for each species (Rahn, 1981). The conductance constant (k) varies directly with G and the length of the incubation period (IP) but inversely with egg weight (EW) (Ar and Rahn, 1978). Thus, these three egg measurements may be interdependent. The G determines the timing of the plateau stage in oxygen consumption by limiting oxygen diffusion to a growing embryo (Rahn, 1981). The plateau stage in oxygen consumption and intestinal maturation occur simultaneously, but little is known of the effect of the plateau on the maturation of intestinal tissue. Intestinal maturation is one of the most energy demanding processes during late development (Fan *et al*., 1997). Excess energy required to survive the hypoxia of the plateau and the demands of pipping and hatching results in less energy for growth or maturation of the intestine. Intestinal dissacharidases must function immediately following hatching because of a critical need for available carbohydrate (Donaldson and Christensen, 1991). Therefore, the hypothesis tested in the current experiments was that k or the factors that affect the timing and length of the plateau stage, also influence intestinal physiology of embryonic and neonatal turkeys. If this hypothesis is true, egg characteristics may be identified that would predispose embryos to hatch as weak poults.

Materials and Methods

Experiment 1: The experimental methods for the first experiment investigated the effect of k on maturation of intestine tissue in Large or Small eggs (EW) produced by hens of the same age with High or Low G. An additional treatment was imposed as each of the EW and G treatments was exposed to a higher (High) temperature (T) to shorten the incubation period (IP) compared to a constant T (Control). Fertilized eggs were incubated as described (Christensen *et al*., 2002) then following 25 d of incubation and computation of G (Tullett, 1981), selected eggs were categorized into EW and G treatments. The High T shortened the IP by nearly 6 h. Ten poults were selected randomly and sampled at hatching from each of the treatment combinations. Poult (nearest 0.01 g) and intestinal (nearest 0.1 mg) weights and function were measured. Because of difficulty in dissecting intestine without the yolk stalk, the BW also included residual yolk. The poults were decapitated and the intestine was exposed and dissected using the following protocol. The duodenum was excised from the attachment to the stomach to the point of the attachment of the pancreas. The jejunum was dissected from the pancreas to Meckel's diverticulum and the ileum was taken from Meckel's diverticulum to the outcropping of the cecal pouches. Each segment of the intestine was weighed; the unstretched length was measured (nearest 0.1 cm) and immediately frozen in physiological

[1]The mention of trade names in this publication does not imply endorsement of the products mentioned nor criticism of similar products not mentioned.

Abbreviation Key: G = Eggshell conductance (mg of water/d/mm Hg). EW = Egg weight. T = Incubation temperature ALP = alkaline phosphatase. k = conductance constant

Table 1: Intestinal segment lengths of poults from heavy and light eggs with high and low eggshell conductance values given two developmental periods

EW[1]	G[2]	Temperature[3]	Jejunum	Duodenum	Ileum
Large	High	Control	12.4	6.6	13.5
		High	13.7	6.5	13.7
		√		6.6[b]	
	Low	Control	12.1	7.5	14.6
		High	13.7	7.1	12.7
		√		7.5[a]	
Small	High	Control	13.3	7.5	13.6
		High	13.1	6.4	11.0
		√		6.9[ab]	
	Low	Control	13.8	6.7	13.2
		High	13.2	6.6	12.0
		√		6.7[b]	
		Control√		7.2[a]	13.7[a]
		High√		6.7[b]	12.3[b]
	Overall √ ± SEM		13.2 ± 0.4	6.9 ± 0.1	13.0 ± 0.5
		Factor	Probabilities		
			---	---	---
		EW	NS	NS	NS
		G	NS	NS	NS
		Temperature (T)	NS	0.05	0.05
		EW x G	NS	0.04	NS
		EW x IP	NS	NS	NS
		G x IP	NS	NS	NS
		EW x G x IP	NS	NS	NS

[a,b]Columnar means with different superscripts differ significantly ($P < 0.05$). [1]EW = Egg weight (g); Large = weight greater than 2 SD above the mean. Small = weight less than 2 SD below the mean. [2]G = Eggshell conductance (mg H_2O/d/torr)[2]; High = eggshell conductance greater than 2 SD above the mean. Low = eggshell conductance 2 SD below the mean. [3]Temperature = Control = eggs were incubated using standard conditions at 37.5 C; Short = eggs were incubated using single stage profile to shorten the developmental period (37.8 C for 14 d followed by 37.5 C for remainder of incubation period).

saline (-22 °C). Each tissue segment was assayed for maltase and alkaline phosphatase (ALP) activity using the procedure of Black (1978). The entire length of each segment was used in the assay. Intestinal function was assayed by measuring maltase activity, a disaccharidase whose activity increases at hatching and ALP activity. ALP is a ubiquitous enzyme associated with increased phosphorus metabolism. Both intestinal enzymes were examined for total and specific activities.

Experiment 2: It was not possible to select sample eggs with different k prior to hatching because hatching time is one of the determinants of k and k cannot be computed prior to hatching. Thus, testing the embryonic effects of k on intestinal physiology required a second experiment utilizing flocks of hens of two ages. Fertilized eggs were obtained from flocks at the initial 2 wk of lay or from a flock 16 wk of lay because hen age increases both EW and G (Christensen *et al.*, 1996). Both flocks were from the same strain as Experiment 1. Approximately 200 fertilized eggs from each flock were numbered and weighed individually (nearest 0.01g) to determine EW and G. Half of the eggs from each flock by hen age category were incubated to shorten the incubation period (High) compared to Controls as in Experiment 1. Thus, the interdependent components of k (EW, G and IP) were treatments in the experiment to create different values for k. Intestinal tissues from each treatment combination (n = 9) in Experiment 2 were sampled from embryos and hatchlings as described in Experiment 1.

Poults hatching from the treatments (N = 264) were placed randomly into two battery brooders and grown to 7 d of age. Body weights were recorded and feed consumption was measured (nearest 0.1 g) at 0, 3 and 7 d post hatching.

Statistical Analysis: Data from Experiment 1 were analyzed as a completely random design and a 2 x 2 x 2 factorial arrangement. The main factors were EW (Large and Small), G (High and Low) and T (High and Control). All possible main effects and interactions were tested for significance and means determined to differ significantly were separated by the least square means procedure of

Table 2: Total intestinal specific maltase activity (µmol of glucose/h/intestine) of poults from heavy and light eggs with high and low eggshell conductance values given two developmental periods

EW[1]	G[2]	Temperature (T)[3]	Specific activity
Large	High	Control	16.9[d]
		High	24.2[a]
	Low	Control	16.1[d]
		High	18.7[cd]
Small	High	Control	20.6[bc]
		High	20.9[bc]
	Low	Control	20.3[bc]
		High	23.4[ab]
	Overall √ ± SEM		20.2 ± 0.5
		Factor	Probability

		EW	0.03
		G	NS
		T	0.003
		EW x G	0.04
		EW x T	NS
		G x T	NS
		EW x G x T	0.05

[a,b,c,d]Columnar means with different superscripts differ significantly ($P < 0.05$). [1]EW = Egg weight (g); Large = weight greater than 2 SD above the mean. Small = weight less than 2 SD below the mean. [2]G = Eggshell conductance (mg H_2O/d/torr)[2]; High = eggshell conductance greater than 2 SD above the mean. Low = eggshell conductance 2 SD below the mean. [3]Temperature = Control = eggs were incubated using standard conditions (37.5 C); High = Incubated using single stage profile to create short developmental period (37.8 C for the initial 14 d followed by 37.5 C for the remainder of incubation).

SAS (SAS Inst., 1998). The statistical analysis for Experiment 2 was a 2 x 2 factorial arrangement of treatments. The main factors tested were EW (Large and Small) and T (High or Control). All possible main effects and interactions were again tested for significance and means were separated as described in Experiment 1. Probability of a Type I error was based on $P \leq 0.05$ in both experiments.

Results

Experiment 1: Large eggs hatched into significantly heavier poults (64.5 g) than did Small (59.6 g), but no other factor or interaction affected poult weight. Neither EW, G, T nor their interactions affected intestinal weights (Weight means for jejunum = 452 mg ± 20; duodenum = 305 mg ± 16; ileum = 358 mg ± 17), but intestinal lengths were (Table 1). High T resulted in shorter duodena than controls. The EW and G interacted to affect duodenum length as Large eggs with Low G yielded significantly longer duodena than Large EW with High G. Small eggs displayed no such differences. Liver and skeletal muscle weights were observed, but no differences were seen in either tissue (data not shown). An EW by G by T interaction affected specific intestinal maltase activity of intestines (Table 2). Among Large eggs with High G at High T, poults displayed elevated maltase activity compared to those from Large eggs in the remaining treatments. Among Small eggs total intestinal maltase activity did not differ. When each segment was examined individually, maltase specific activity affected only the duodenum (data not shown).

Table 3: Total intestinal alkaline phosphatase activity (µmol of phosphorus/h/intestine) of poults from heavy and light eggs with high and low eggshell conductance values given two developmental periods

EW[1]	Temperature (T)[2]	Specific activity
Large	Control	0.84[b]
	High	1.12[b]
Small	Control	1.52[a]
	High	1.14[b]
	Overall √ ± SEM	1.15 ± 0.08
	Factor	Probability

	EW	0.05
	G[3]	NS
	T	NS
	EW x G	NS
	EW x T	0.05
	G x T	NS
	EW x G x T	NS

[a,b]Columnar interaction means with different superscripts differ significantly ($P < 0.05$). [1]EW = Egg weight (g); Heavy = weight greater than 2 SD above the mean. Small = weight less than 2 SD below the mean. [2]Temperature = Control = eggs were incubated using standard conditions (37.5 C); High = Incubated using single stage profile to create short developmental period (37.8 C for the initial 14 d followed by 37.5 C for the remainder of incubation). [3]G = Eggshell conductance (mg H_2O/d/torr)[2]; High = eggshell conductance greater than 2 SD above the mean. Low = eggshell conductance 2 SD below the mean.

An EW by T interaction affected total intestine ALP activity across all intestinal segments (Table 3). Small eggs at the Control T produced poults with elevated levels of ALP compared to the other interaction means. As with maltase, changes in ALP activity occurred principally in duodenal tissue with little or no effect on jejunum or ileum (data not shown).

Experiment 2: Using eggs from hens of different ages as well as changing incubation periods resulted in different k (Table 4). The embryos compensated for the changes in EW and T by shortening or lengthening the

Table 4: Eggshell conductance (G) of eggs of two weights when exposed to two incubation temperatures

Hen age[1]	Temperature[2]	EW[3](g)	G (mg/d/mm Hg)	IP (h)	k[4]
16	Control	90.2	19.9	652[a]	5.98
	High	87.4	20.9	641[c]	6.29
	√	88.8[a]	20.4[a]		6.13[a]
1	Control	80.1	17.6	649[b]	5.90
	High	78.5	17.3	642[c]	5.94
	√	79.3[b]	17.4[b]		5.92[b]
	Control √	85.2	18.8		5.94[b]
	High √	83.0	19.1		6.11[a]
	√ ± SEM	84.0 ± 0.1	18.9 ± 0.1	644 ± 0.1	6.02 ± 0.01
	Probabilities				
	Egg weight (EW)	0.0001	0.0001	NS	0.04
	Temperature (T)	NS	NS	0.0001	0.05
	EW x T	NS	NS	0.01	NS

[a,b,c,d]Columnar means with different superscripts differ significantly ($P < 0.05$). [1]Hen age; 16 = eggs from flock at 49 wk of age (16 wk of lay). 1 = eggs from flock at 33 and 34 wk of age (1 and 2 wk of lay). [2]Temperature = Control eggs were incubated using standard conditions (37.5 C); High eggs were incubated using single stage profile to create short developmental period (37.8 C for the initial 14 d followed by 37.5 C for the remainder of incubation). [3]EW = Egg weight (g). [4]k = Conductance constant computed by dividing the product of G and the incubation period divided by EW.

Table 5: Body weights (g) of poults hatched from eggs of two weights when exposed to two incubation temperatures

EW[1]	Temperature[2]	e27	0 d	3 d	7 d
Large	Control	62.0	63.3[a]	93.8[a]	135.2
	High	60.5	56.8[b]	90.0[b]	132.5
	√	61.3[a]			133.8[a]
Small	Control	54.7	54.1[c]	80.3[c]	120.3
	High	58.2	50.9[d]	81.5[c]	119.6
	√	56.4[b]			120.0[b]
	Control √	58.4			127.7
	High √	59.3			126.1
	√ ± SEM	58.9 ± 0.1	56.2 ± 0.1	85.9 ± 0.1	127.0 ± 1.8
	Probabilities				
	Egg weight (EW)	0.05	0.0001	0.0001	0.0001
	Temperature (T)	NS	0.0001	NS	NS
	EW x T	NS	0.02	0.02	NS

[a,b,c,d]Columnar means with different superscripts differ significantly ($P < 0.05$). [1]EW = Egg weight (g); Heavy = eggs from flock in wk 1 and 2 of lay. Light = eggs from flock at least 16 wk in lay. [2]Temperature = Control eggs were incubated using standard conditions (37.5 C); High eggs were incubated using single stage profile to create short developmental period (37.8 C for the initial 14 d followed by 37.5 C for the remainder of incubation).

IP in each case. Large eggs had greater G and reduced IP by 11 h when exposed to High whereas Small eggs had smaller G and reduced IP by only 7 h when exposed to High.

The EW x T interacted at 0 and 3 d to affect BW, but only EW effects were seen at 7 d (Table 5). At 0 d High poults weighed less than controls regardless of EW, but Control poults from Large eggs were significantly heavier than those from Small. At 3 and 7 d the poults from Large eggs were heavier than those from Small.

For simplicity, total intestinal measurements are presented because they did not differ from that seen in the segments. The EW and T interacted to affect intestinal weights at 27 d of embryonic development (Table 6). High increased intestinal weight compared to all other treatment combinations and Large EW increased weight compared to Small EW only and the Control IP. At hatching Large EW increased intestinal weights compared to Small and High T depressed intestinal weights compared to the controls. At 3 d posthatching, Large EW again increased intestinal weights compared to Small, but no other differences were noted. Intestinal lengths differed only at hatching (data not shown). High produced shorter intestines (31.3 cm) than Control (34.3 cm).

Intestinal specific maltase activity displayed a significant

Table 6: Intestinal weights (mg) of poults hatched from eggs of two weights when exposed to two different incubation periods

EW[1]	Temperature[2]	e27	0 d	3 d
Large	Control	539[b]	1.312	5.182
	High	519[bc]	1.157	5.231
	√		1.234[a]	5.207[a]
Small	Control	500[c]	1.225	4.906
	High	598[a]	836	4.858
	√		1.030[b]	4.882[b]
	Control √		1.269[a]	5.044
	High √		997[b]	5.045
	√ ± SEM	539 ± 17	1.133 ± 45	5.045 ± 168
	Probabilities			
	Egg weight (EW)	NS	0.04	0.02
	Temperature (T)	NS	0.01	NS
	EW x T	0.05	NS	NS

[a,b] Columnar means with different superscripts differ significantly (P < 0.05). [1]EW = Egg weight (g); Heavy = eggs from flock in wk 1 and 2 of lay. Light = eggs from flock at least 16 wk in lay. [2]Temperature = Control eggs were incubated using standard conditions (37.5 C); High eggs were incubated using single stage profile to create short developmental period (37.8 C for the initial 14 d followed by 37.5 C for the remainder of incubation).

Table 7: Intestinal specific maltase activity (µmol of glucose/min/µg of protein) of poults hatched from eggs of two weights when exposed to two different incubation periods

EW[1]	Temperature[2]	e27	0 d	3 d
Large	Control	53.8[b]	54.1	77.0
	High	45.8[b]	52.7	21.1
	√		53.4[a]	49.0
Small	Control	56.0[b]	51.9	97.3
	High	79.3[a]	38.3	15.8
	√		45.1[b]	56.6
	Control √		53.0[a]	87.2[a]
	High √		45.5[b]	18.5[b]
	√ ± SEM	59.2 ± 4.2	49.2 ± 2.3	52.8 ± 18.0
	Probabilities			
	Egg weight (EW)	0.05	0.05	NS
	Temperature (T)	NS	0.03	0.05
	EW x T	0.05	NS	NS

[a,b] Columnar means with different superscripts differ significantly (P < 0.05). [1]EW = Egg weight (g); Heavy = eggs from flock in wk 1 and 2 of lay. Light = eggs from flock at least 16 wk in lay. [2]Temperature = Control eggs were incubated using standard conditions (37.5 C); High eggs were incubated using single stage profile to create short developmental period (37.8 C for the initial 14 d followed by 37.5 C for the remainder of incubation).

EW by T interaction at 27 d of incubation (Table 7). Small EW embryos had elevated maltase activity compared to all other treatment combinations. At hatching, Both EW and T had significant effects but did not interact. Large EW had greater maltase activity than Small and High depressed maltase activity compared to Controls. High also depressed maltase activity at 3 d compared to Controls.

An EW by T interaction affected specific intestinal ALP activity at 27 d of embryo development and 0 d or hatching (Table 8). At 27 d of incubation, embryos in Small eggs exposed to High elevated ALP compared to all other treatments. At 0 d the opposite effect was seen as hatchlings from Small eggs with High depressed ALP activity compared to all other groups. Additionally at hatching, poults from Large eggs at High depressed ALP compared to controls. High depressed ALP at 3 d compared to controls.

Discussion

The hypothesis proposed in the current study was that k might affect hatchling intestinal weight and physiology. Evidence from the current study supports the hypothesized interdependence of the three determinants

Table 8: Intestinal specific alkaline phosphatase activity (µmol of phosphorus/min/µg of protein) of poults hatched from eggs of two weights when exposed to two different incubation periods

EW[1]	Temperature[2]	e27	0 d	3 d
Large	Control	0.15[b]	1.66[a]	1.35
	High	0.21[b]	1.02[b]	0.65
	√			1.00
Small	Control	0.24[b]	1.19[b]	1.19
	High	0.37[a]	0.65[c]	0.94
	√			1.06
	Control √			1.27[a]
	High √			0.80[b]
	√ ± SEM	0.25 ± 0.02	1.13 ± 0.07	1.03 ± 0.05
	Probabilities			
	Egg weight (EW)	0.01	0.01	NS
	Temperature (T)	0.03	0.001	0.008
	EW x T	0.05	0.001	NS

[a,b]Columnar means with different superscripts differ significantly ($P < 0.05$). [1]EW = Egg weight (g); Heavy = eggs from flock in wk 1 and 2 of lay. Light = eggs from flock at least 16 wk in lay. [2]Temperature = Control eggs were incubated using standard conditions (37.5 C); High eggs were incubated using single stage profile to create short developmental period (37.8 C for the initial 14 d followed by 37.5 C for the remainder of incubation).

of k and their effect on intestinal maturation. Eggshell G, EW and IP interacted in numerous ways to affect intestinal growth or function. Depressed embryonic intestinal weight was similarly followed by depressed BW and growth efficiency for 7 d post hatching.

Intestinal function is essential to postembryonic development in avian species and exhibits straight-line growth with the body (Konarzewski *et al.*, 1990). Intestines grew and matured rapidly posthatching in the current study and were affected by k. Greater k, due primarily to longer IP, increased BW and feed efficiency. Thus, it may be inferred that for optimal intestinal development and posthatching growth, k should be increased.

Intestinal maturation post hatching is well understood (Sell *et al.*, 1991; Fan *et al.*, 1997; Uni *et al.*, 1995ab; 1999; Suvarna, 1999). Lipid digestion and assimilation develop during the first week posthatching (Sell *et al.*, 1991) and intestinal disacchridases and glucose transport mechanisms are functional at about 48 h post hatching and can adjust rapidly to different types of food even at 72 h post hatching (Suvarna, 1999). Intestinal mass increases in parallel to nutrient intake as opposed to an up regulation of function (Noy and Sklan, 1996; Uni *et al.*, 1999). A similar pattern was seen in the current study as greater intestinal mass corresponded to greater BW and feed efficiency, but increased maltase and ALP activity did not.

Embryonic yolk digestion and absorption act primarily on lipids (Donaldson and Christensen, 1991). The yolk sac membrane has the lipid digestive enzymes and absorption mechanisms necessary for sustaining life in the shell and the sac maintains these capabilities following yolk retraction in the first few days following hatching (Romanoff, 1960; Noy and Sklan, 1998; Denbow, 2000). After hatching, the neonate must begin life on a carbohydrate-based diet (48% of the diet) that requires different digestive processes (Donaldson and Christensen, 1991). Thus, many intestinal functions (e.g., disaccharidases and glucose transport mechanisms) intended for carbohydrate digestion and absorption must activate quickly following hatching (ca. 24 h) when the initial feed is consumed. Some estimates (Fan *et al.*, 1997) indicate that 60% of the total energy of a neonate may be devoted to maturation and growth of intestinal tissue in the first few days following hatching. It may be inferred from the results of the current study that k may diminish energy availability and delay intestinal maturation post hatching. Thus, gluconeogenesis (Donaldson and Christensen, 1991) may sustain life and support growth of such poults in preparation for the initial few days of life outside the shell.

The relationship between delayed intestine maturity at hatching and weak poults is not clear. In the current study, shorter incubation periods associated with G or EW reduced intestinal growth and function, but it is the hatchlings that emerge later rather than earlier in incubation that survive poorly (Kingston, 1979). Early hatching corresponded with k less than 5.13 (Ar and Rahn, 1978) and hatching earlier also reduced intestinal weight and function. Thus, based on data from the current study, the relationship would suggest that early hatching poults might be at risk.

In summary, the G, EW qualities of the egg and the resulting IP may be determinants of hatchling intestinal

maturity. Embryonic intestinal growth and maturation in Large, Low G eggs was depressed. If the IP was shortened, the condition was worse. For improved poult livability, it is recommended that extremes in egg size and functional characteristics be avoided and that incubation temperatures be moderated to provide longer incubation periods.

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