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308 Lasani Town, Sargodha Road, Faisalabad - Pakistan
Mob: +92 300 3008585, Fax: +92 41 8815544
E-mail: editorijps@gmail.com

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Incubator Temperature and Oxygen Concentration at the Plateau Stage Affects Intestinal Maturation of Turkey Embryos[3]

V.L. Christensen[1], M.J. Wineland[1], I. Yildirum[2], D.T. Ort[1] and K.M. Mann[1]
[1]Department of Poultry Science, College of Agriculture and Life Sciences,
North Carolina State University, Raleigh, North Carolina 27695-7608, USA
[2]The University of Selcuk, Agriculture Faculty, Department of Animal Science,
42031 Campus Konya, Turkey
E-mail: vern_christensen@ncsu.edu

Abstract: The plateau stage in oxygen consumption of turkey embryos occurs at 25 and 26 days of incubation when many embryos die. The plateau stage creates hypoxia, hypercapnia and presents a paradox for growth and embryo metabolism. Prior to the plateau, vital tissues accumulate glycogen to ensure embryonic survival through anaerobic metabolism during the plateau. Intestinal maturation at the plateau demands great amounts of energy. Therefore, the objective of the study was to define the temperature and oxygen concentrations at the plateau that affect intestinal maturation. Three experiments were conducted to test incubator conditions during the plateau stage and their affect on intestinal maturation. In Experiment 1, turkey embryos at the plateau stage were exposed to 36, 37, 38 or 39°C. In Experiment 2, embryos at the plateau stage were exposed to 17, 19, 21 or 23% oxygen concentrations, and in Experiment 3, the extreme levels of temperature and oxygen treatments were combined to test interaction effects on intestinal maturation. Elevating temperature depressed intestinal weight but not length. The elevated temperature also depressed intestinal maltase and alkaline phosphatase activities indicating inhibited function. Increasing oxygen had little effect on intestinal weight or length, but hypoxia increased maltase and decreased alkaline phosphatase activities in hatchlings. When examined in a factorial arrangement, temperature and oxygen displayed independent effects on growth and function and did not interact. Thus, incubator temperature greater than 37°C and oxygen concentrations less than 19% during the plateau stage delay intestinal maturation.

Key words: intestine, plateau stage, oxygen, temperature, and turkey embryo

Introduction

Turkey embryos at 25 and 26 d of development consume more oxygen and expel more carbon dioxide than the eggshell functional properties provide thus constraining oxygen flux (Dietz *et al*., 1998). The constraint creates a plateau effect in oxygen consumption (Rahn, 1981). A consequence of the plateau may be an insufficiency of anaerobic energy that delays intestinal maturation. In a prior study low eggshell conductance constant (ratio of the product of incubation periods and eggshell conductance divided by egg weight) delayed maturation of intestinal tissue (Christensen *et al*., 2003a). Major maturation of intestine occurs at the plateau stage in oxygen consumption (Black, 1978; Rahn, 1981) and is an energy-demanding process (Fan *et al*., 1997). Additionally, glycogen for cardiac and skeletal muscle glycolysis is required to hatch, and energy is required for other vital tissue maturation (Dietz *et al*., 1998). If stress arises during the plateau, growth and function become antagonistic and additional energy would be required to adapt (Schmalhausen, 1930). Following hatching, the poult has a critical need for readily available carbohydrate (Donaldson and Christensen, 1991) so a functional intestine is vital at that stage as well. Therefore, the hypothesis was proposed that temperature and oxygen concentration during the plateau stage in oxygen consumption might affect the growth and maturation of turkey embryo intestine.

Materials and Methods

Experimental incubation cabinets simulating commercial incubators were manufactured[3] and used to control ambient temperature and oxygen concentrations. Each cabinet contained one incubator tray with capacity for 100 eggs. Digitized thermostats, connected to microprocessors with temperature sensitivity of + 0.1 C, controlled the set and dry bulb temperatures. Digital thermometers[5] were used in each cabinet to verify set point temperatures, and ports were used to infuse desired gaseous concentrations.

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

Temperature: Fertilized turkey eggs from a commercial strain were obtained on the day of oviposition and incubated until the 25th day when they were candled to determine embryo viability. The 25th day of incubation for turkeys is the beginning of the plateau stage for that species (Rahn, 1981). Following candling and removal of nonviable embryos, randomly selected viable embryos were transferred to one of the four experimental cabinets. Each cabinet operated at one of the treatment temperatures (36, 37, 38 or 39°C).

Ten embryos or poults were selected randomly from each incubator at 27 d of incubation (external pipping) and at 28 d of incubation (hatching) to represent each temperature. Poult (nearest 0.1 g) and intestinal (nearest 0.01 mg) weights were recorded and intestinal function was measured for maltase and alkaline phosphatase (ALP) activities. Maltase digests readily available carbohydrate (maltose) to glucose during the initial few days of life, and ALP is a ubiquitous enzyme found in nearly every tissue of the body that indicates overall growth and maturation of the body. The poults were decapitated and the intestine was exposed and dissected using the following protocol. The jejunum was dissected from the pancreas to Meckel's diverticulum. Each segment of the intestine was weighed; the unstretched length was measured and immediately frozen in physiological saline (-22°C). Each segment was assayed for both specific and total maltase and ALP activity using the procedures of Black (1978). The entire length of each jejunum was used in the assay. Intestinal activity was expressed per unit of protein and per jejunum, but because of differences between weights and lengths, only total enzyme activity will be presented.

Oxygen: Four oxygen concentrations were the treatments in the second experiment. The concentrations were 17, 19, 21 or 23% of the atmosphere within the cabinets. Each fractional concentration at sea level (Raleigh, NC) corresponded to oxygen partial pressures of 129, 144, 160 and 175 mm Hg, respectively. Concentrations lower than ambient oxygen concentrations (20.9%) were maintained by infusing nitrogen gas into the cabinet at a rate that resulted in the desired concentration of 17 or 19% oxygen. Concentrations were measured with an oxygen meter and flow rates from oxygen or nitrogen storage tanks were adjusted hourly to maintain the desired oxygen level.

Eggs were incubated together until the beginning of the 25th day of development, candled to determine viability and selected as described in Experiment 1. Embryo intestines were collected and analyzed identically as in

Experimental 1

Temperature and Oxygen: The most extreme temperatures (36 and 39°C) and oxygen (17 and 23%) levels in the previous experiments were combined in a factorial arrangement for Experiment 3. The incubator temperatures and oxygen concentrations were arranged as a 2 x 2 factorial. All treatments were maintained identically as described in the previous experiments. Fertilized eggs were again incubated 25 days in an incubator when viable embryos were assigned randomly to one of the four cabinets. The conditions were 36 C with 17 or 23% oxygen or 39°C with 17 or 23% oxygen. Embryos or hatchlings were sampled identically as described in the previous experiments.

Statistical Analysis: Data for all three experiments were analyzed using the general linear models procedure (SAS Inst., 1998). Experiments 1 and 2 were analyzed as four levels of oxygen or temperature treatment. In Experiment 3, the data were analyzed as two temperatures by two oxygen concentrations factorial arrangement. Means determined to differ significantly were separated by the least square means procedure. All means given in tables are least square means. All possible main and interaction effects were tested for significance. All probabilities were based on $P < 0.05$ unless otherwise noted.

Results

Temperature: Temperature had no effect on BW (Table 1), but temperatures above 37.0 C depressed the embryonic jejunum weight (Table 2). Temperature did not affect the length of the jejunum. Significant increases in jejunum weight and length but not BW were seen between 27 and 28 d of incubation.

Total maltase activity declined as temperatures increased (Table 3). At 36 or 37°C maltase activity was greater than at 38 or 39°C at both days of incubation. Total ALP activity displayed a temperature by day interaction. Activity at 27 d of incubation was similar at all temperatures, but in hatchlings ALP was greater among poults at 39°C than in those at 36, 37 or 38°C. Relative to ALP activity, maltase increased as the temperature reached 38°C but declined at 39°C.

Oxygen: Significant oxygen by day interaction was seen for BW (Table 4). The BW at 27 d was heavier in 23% oxygen than in all other oxygen concentrations. At 28 d the 17% oxygen concentration depressed BW compared to the 19%, but no other treatments differed. Increased oxygen also increased the utilization of yolk (data not shown)

Oxygen concentrations of 17% depressed jejunal weight at 27 d compared to 23% but not any other treatment (Table 5). At 28 d, 19% oxygen resulted in heavier jejuna than all other treatments, and 17% resulted in heavier jejuna than either 21 or 23%.

Total jejunum maltase activity indicated significant oxygen by day interactions (Table 6). At 27 d, 23% oxygen

Table 1: Body weights (g) of turkey embryos incubated at four temperatures during the plateau stage in oxygen consumption

	Day of incubation		
Temperature (°C)	27	28	√
	Body weight without yolk sac (g)		
36.0	52.9	54.2	53.5
37.0	53.6	53.3	53.5
38.0	54.0	51.5	52.8
39.0	56.1	53.8	54.9
√	54.1	53.2	
√ ± SEM	53.7 ± 0.5		
Probabilities	Temperature (T)	NS	
	Day (D)	NS	
	T x D	NS	

Table 2: Jejunal weight (mg) and length (cm) of turkey embryos incubated in four temperatures during the plateau stage in oxygen consumption

	Day of incubation		
Temperature (°C)	27	28	√
	Jejunal weight		
36.0	225	318	272^{ab}
37.0	236	334	285^{a}
38.0	207	284	246^{c}
39.0	195	325	260^{bc}
√	216^{b}	315^{a}	
√ ± SEM	266 ± 4		
Probabilities	Temperature (T)	0.01	
	Day (D)	0.0001	
	Tx D	NS	
	Jejunal length		
36.0	10.6	11.9	11.3
37.0	11.2	11.8	11.5
38.0	10.4	11.5	10.9
39.0	10.2	12.3	11.2
√	10.6^{b}	11.9a	
√ ± SEM	11.2 ± 0.1		
Probabilities	Temperature (T)	NS	
	Day (D)	0.0001	
	T x D	NS	

elevated maltase activity compared to all other treatments, but at 28 d, 19% oxygen showed greater maltase activity than all other treatments. Total ALP activity displayed a similar interaction of oxygen by day as 21 and 23% oxygen elevated total ALP compared to 17 or 19%, and at 28 d 19% produced significantly greater total ALP activity that all other oxygen treatments. Relative to ALP activity, maltase declined as oxygen concentrations increased.

Table 3: Total jejunal maltase (µmol glucose/h/jejunum) and alkaline phosphatase activity (µmol P/h/jejunum) in turkey embryos incubated in four temperatures during the plateau stage in oxygen consumption

	Day of incubation		
Temperature (°C)	27	28	√
	Total maltase activity		
36.0	104^{e}	318^{b}	
37.0	158^{d}	399^{a}	
38.0	97^{e}	217^{c}	
39.0	111de	237^{c}	
√			
√ ± SEM	205 ± 8		
Probabilities	Temperature (T)	0.0001	
	Day (D)	0.0001	
	T x D	0.02	
	Total alkaline phosphatase activity		
36.0	1,970^{d}	9,070^{b}	
37.0	2,967^{d}	10,042^{b}	
38.0	1,480^{d}	5,642^{c}	
39.0	1,926^{d}	12,516^{a}	
√			
√ ± SEM	5,702 ± 341		
Probabilities	Temperature (T)	0.002	
	Day (D)	0.0001	
	T x D	0.01	
	Ratio of specific maltase to alkaline phosphatase activities		
36.0	60.5	32.5	46.5^{b}
37.0	72.7	43.2	57.0^{ab}
38.0	83.3	51.2	67.2^{a}
39.0	64.5	32.1	48.3^{b}
√	70.2^{a}	39.7^{b}	
√ ± SEM	55.0 ± 3.6		
Probabilities	Temperature (T)	0.05	
	Day (D)	0.0001	
	T x D	NS	

Temperature and Oxygen: Temperature and oxygen concentration treatments were tested simultaneously in Experiment 3, and a temperature by day interaction affected BW (Table 7). At 27 d, BW was depressed at 39°C compared to 36°C, but by 28 d no difference was noted. The 23% oxygen increased BW of embryos at both sampling days compared to 17%.

Jejunum weight was increased by 44 mg at 36°C compared to 39°C (Table 8), and oxygen and stage of incubation interacted for intestine weight. The 23% oxygen increased jejunum weight at 27 but not at 28 d. Jejunum length was affected similarly by oxygen and days interacting when the 17% treated jejuna were

Table 4: Body weight (g) of turkey embryos incubated in four oxygen concentrations during the plateau stage in oxygen consumption

	Day of incubation		
Oxygen (%)	27	28	√
	Body weight without yolk sac		
17	49.0[bc]	47.8[c]	
19	49.9[b]	50.9[b]	
21	49.6[b]	49.6[bc]	
23	54.2[a]	48.5[bc]	
√			
√ ± SEM	49.9±0.4		
Probabilities	Oxygen (O)	0.06	
	Day (D)	0.06	
	O x D	0.01	

Table 5: Jejunal weight (mg) and length (cm) of turkey embryos incubated in four oxygen concentrations during the plateau stage in oxygen consumption

	Day of incubation		
Oxygen (%)	27	28	√
	Jejunal weight		
17	198[e]	328[b]	
19	215[de]	372[a]	
21	209[de]	304[c]	
23	237[d]	301[c]	
√			
√ ± SEM	269 ± 6		
Probabilities	Oxygen	NS	
	Day (D)	0.0001	
	O x D	0.04	
	Jejunal length		
17	9.8	11.9	10.9
19	10.0	12.6	11.3
21	11.0	11.7	11.4
23	10.2	11.1	10.7
Ö	10.3[b]	11.8[a]	
√ ± SEM	11.0 ± 0.2		
Probabilities	Oxygen (O)	NS	
	Day (D)	0.0001	
	O x D	NS	

shorter than 23% at 27 but did not differ in length at 28 d. Oxygen and day of incubation interacted to affect the total maltase activity (Table 9). The 23% oxygen increased total maltase activity at 27 d compared to 17%, but at 28 d the opposite was noted as 17% oxygen increased total maltase to a greater extent than did 23%. Temperature and day of incubation interacted at 28 d similarly to affect total ALP activity when 39°C elevated ALP compared to

Table 6: Total jejunal maltase (µmol glucose/h/jejunum) and alkaline phosphatase activity (µmol P/h/jejunum) in turkey embryos incubated in four oxygen concentrations at the plateau stage in oxygen consumption

	Day of incubation		
Oxygen (%)	27	28	√
	Total maltase activity		
17	107[d]	315[b]	
19	114[d]	486[a]	
21	140[d]	273[bc]	
23	232[c]	259[bc]	
√			
√ ± SEM	239 ± 10		
Probabilities	Oxygen (O)	0.003	
	Day (D)	0.0001	
	O x D	0.0001	
	Total alkaline phosphatase activity ()		
17	1,976[e]	5,245[c]	
19	1,855[e]	9,867[a]	
21	4,096[d]	6,703[b]	
23	4,402[d]	6,297[b]	
√			
√ ± SEM	5,028 ± 298		
Probabilities	Oxygen (O)	0.05	
	Day (D)	0.0001	
	O x D	0.002	
	Ratio of specific maltase to alkaline phosphatase activities		
17	61.0	64.5	62.8[a]
19	72.7	57.4	60.9[a]
21	49.5	42.8	46.2[b]
23	60.7	43.2	51.9[b]
√			
√ ± SEM	55.5 ± 2.9		
Probabilities	Oxygen (O)	0.05	
	Day (D)	NS	
	O x D	NS	

36°C at hatching following no differences at 27 d. Relative to ALP activity, maltase increased in response to elevated temperature at 27 but not at 28 d, and oxygen did not affect the activity of maltase relative to ALP.

Discussion

Dietz *et al.* (1998) have described the plateau stage as a paradox because embryonic growth and function must continue without the full provision of oxygen. When confronted with life threatening situations, embryonic growth and function are antagonistic (Schmalhausen, 1930). Increased plasma thyroid and adrenal hormone concentrations facilitate survival and are predetermined developmentally by eggshell conductance (Rahn, 1981;

Table 7: Poult weight (g) when exposed to different temperature and oxygen treatments during the plateau stage in oxygen consumption

Temperature (°C)	Oxygen (%)	Day of incubation		
		27	28	√
		Body weight		
36	17	51.6	52.3	
	23	54.2	51.1	
√	52.9[a]	51.7[ab]		
39	17	48.8	54.2	
	23	51.0	54.2	
	√	49.9[b]	52.2[a]	
	Oxygen √	17% = 50.7[b]		
		23% = 52.6[a]		
	√ ± SEM	51.7 ± 0.5		
Probabilities	Temp. (T)	NS		
	Oxygen (O)	0.05		
	Day (D)	NS		
	T x O	NS		
	T x D	0.05		
	O x D	NS		
	T x O x D	NS		
	O x D	NS		
	T x O x D	NS		

Christensen and Biellier, 1982; Wentworth and Hussein, 1982; Christensen *et al*., 2002). Low eggshell conductance prolongs development and reduces thyroid hormone concentrations (Christensen *et al*., 2002), intestinal weight and function (Christensen *et al*., 2003a). The current study shows clearly that elevated temperature and depressed oxygen in the incubator during the plateau stage deter the process of intestinal maturation and preparation for life outside the shell as well.

Thyroid and adrenal hormones play major roles during the plateau in maturation of intestines (Black, 1978) and improved neonate survival (Davis and Siopes, 1989; Christensen *et al*., 2003b). In a prior study we showed that conditions similar to those in the current study affected plasma concentrations of thyroid hormones (Christensen *et al*., 2003c). The current data indicate that the same conditions affect intestinal tissue.

Temperature: In the current experiment, temperatures greater than 37°C slowed yolk utilization, but had no affect on yolk-free embryonic body mass. Thus, although hatchling poults appeared heavy at high temperatures, more residual yolk was responsible for the difference and not tissue mass. Temperatures above 37°C depressed jejunum weight without affecting jejunum length. Elevated temperatures also suppressed plasma thyroid hormone concentrations at these stages of development (Christensen, unpublished data). Thus, we conclude that incubator temperatures greater than 37°C during the plateau depress intestinal weight and yolk utilization. The actions of temperature on thyroid hormones and intestinal maturation seem to parallel one another.

Temperature effects on intestinal function were more obscure. In Experiment 1, more maltase activity was noted at lower temperatures at both EP and hatching but no differences were seen at 36°C. When the 36 and 39°C treatments were repeated in Experiment 3 there were no effects so we conclude the results are indeterminate for temperature effects on maltase activity in turkey embryos. Temperature had pronounced effects on ALP activity in both experiments. High temperature elevated jejunum ALP activity at hatching. Therefore, the data suggest a relationship of elevated ALP and intestinal metabolism associated with temperature stress. The maltase and ALP activities ratio indicated that maltase was increasing faster than was ALP activity in both experiments in response to elevated temperatures.

Oxygen: Increasing concentrations of oxygen in the incubators increased BW and yolk utilization in contrast to temperature. Thus, additional oxygen enhances both growth and yolk nutrient utilization during the plateau stage. The data infer that hypoxia suppresses BW to a greater extent than elevated temperature.

Hypoxia at 17% depressed jejunum weight compared to 23% while the embryo was pipping the shell. This observation was further substantiated by similar results

Table 8: Jejunal weight (mg) and length (cm) of poults exposed to different temperature and oxygen treatments during the plateau stage in oxygen consumption

Temperature (°C)	Oxygen (%)	Day of incubation 27	28	√
		Jejuna weight		
36	17	242	370	313[a]
	23	280	361	
	√			
39	17	173	345	269[b]
	23	229	332	
	√			
	O x D √ 17%	207[c]	357[a]	
	23%	255[b]	347[a]	
	√ ± SEM	292 ± 6		
Probabilities	Temperature (T)	0.001		
	Oxygen (O)	NS		
	Day (D)	0.0001		
	T x O	NS		
	T x D	NS		
	O x D	0.01		
	T x O x D	NS		
		Jejuna length		
36	17	9.6	12.2	
	23	10.8	12.3	
	√			
39	17	9.6	12.6	
	23	10.4	11.3	
	√			
	Day √	10.1[b]	12.1[a]	
	O x D √ 17%	9.6[c]	12.4[a]	
	23%	10.6[b]	11.8[ab]	
	√ ± SEM	11.1 ± 0.1		
Probabilities	Temperature (T)	NS		
	Oxygen (O)	NS		
	Day (D)	0.0001		
	T x O	NS		
	T x D	NS		
	O x D	0.01		
	T x O x D	NS		

at EP from Experiment 3. In both experiments, 17% oxygen also increased jejuna weights at hatching faster than 23%. Thus, the concentration of oxygen in an incubator has both suppressing and stimulating effects on jejunum tissue depending upon embryonic age. From these data it can be concluded that oxygen concentrations above 19% during EP increase jejunum weight, but jejunum weight is greater in hatchlings when oxygen concentrations are maintained below 19%. The effects of low oxygen concentration seemed to parallel circulating thyroid hormone concentrations as well (Christensen *et al.*, 2003b). We speculate that this may be a physiological mechanism preparing the bird for life outside the shell. If the embryo is stressed through hatching, one of its greatest needs at hatching is readily available carbohydrate (Donaldson and Christensen, 1991). A functional intestine would be required to supply glucose for metabolism.

Hypoxia delayed maturation of maltase activity until hatching similarly as it slowed growth. At EP, maltase activity in embryos incubating was greater at 23% than 17% oxygen. However, at hatching, the values at 17% were much greater perhaps indicating similar preparation by the hatchling poult in jejunum function as well as the growth noted above for readily available carbohydrate following the hypoxia of the plateau (Donaldson and Christensen, 1991). Thus, we conclude that optimal oxygen concentration for maltase activity is

Table 9: Total jejunal maltase (µmol of glucose/h/jejunum) and alkaline phosphatase activity (µmol phosphorus/h/jejunum) in poults exposed to different temperature or oxygen treatments during the plateau stage in oxygen consumption

			Day of incubation		
Temperature (°C)	Oxygen (%)		27	28	√
			Maltase		
36	17		98	393	
	23		157	352	
	√				
39	17		104	440	
	23		100	291	
	√				
	O x D √	17	69[c]	417[a]	
		23	130[b]	321[b]	
	√ ± SEM		232 ± 12		
Probabilities	Temperature (T)		NS		
	Oxygen (O)		NS		
	Day (D)		0.0001		
	T x O		NS		
	T x D		NS		
	O x D		0.003		
	T x O x D		NS		
			Alkaline phosphatase		
36	17		1,641	10,068	
	23		2,248	11,872	
	√		1,945[c]	10,970[b]	
39	17		614	18,734	
	23		1,884	16,375	
	√		1,249[c]	17,550[a]	
	√ ± SEM		7,792 ± 454		
Probabilities	Temperature (T)		0.004		
	Oxygen (O)		NS		
	Day (D)		0.0001		
	T x O		NS		
	T x D		0.0001		
	O x D		NS		
	T x O x D		NS		
			Ratio of specific maltase to alkaline phosphatase activities		
36	17		68.5	43.0	
	23		71.8	30.5	
	√		70.2[b]	36.7[c]	
39	17		105.9	24.0	
	23		96.1	20.0	
	√		101.0[a]	22.0[c]	
	√ ± SEM		57.9 ± 4.4		
	Temperature (T)		NS		
	Oxygen (O)		NS		
	Day (D)		0.0001		
	T x O		NS		
	T x D		0.01		
	O x D		NS		
	T x O x D		NS		

also dependent upon embryo age. Some evidence in the current study suggested depressed ALP activity at EP at less than 21% oxygen, but the effects of hypoxia on ALP were not repeated in Experiment 3.

Maltase and ALP activities indicate contrasting responses. Temperature was the major influence on ALP activity in embryonic intestine, and oxygen played only a minor role. In contrast, increased oxygen concentration elevated maltase activity with little influence on ALP activity. Because the enzyme ALP is ubiquitous and involved with more tissues than is maltase, it may be that temperature spares ALP to allow metabolism to cope with the stress of high temperature while delaying intestinal maturation as described by Schmalhausen (1930).

Temperature and Oxygen: When temperature and oxygen treatments were tested together, no interactions were noted. Lower incubator temperature increased the jejuna weights and greater concentrations of oxygen increased both jejuna weight and length as had been seen in the previous experiments. Therefore, it is clear that the primary influence on embryonic jejunum growth during the plateau is from oxygen, but as the poults hatched jejunum weights were equivalent regardless of oxygen treatment. Although the depressing effects of temperature as compared to oxygen at EP were not as great in magnitude. High temperature depressed jejunum weight throughout the hatching process, but hypoxia depressed weights initially followed by increased weights at hatching.

In a prior study, egg weight, eggshell conductance and the length of the incubation period interacted to affect intestinal growth and function (Christensen *et al.*, 2003a). The three egg characteristics interact in precocial species to determine the time that an embryo attains the plateau stage in oxygen consumption (Rahn, 1981). In the current study, we show that not only does the time of the plateau stage affect turkey embryo intestinal maturation, but environmental temperature and oxygen concentrations during the plateau are determinants as well.

Thus, the data from the current study indicate separate actions of incubator temperature and oxygen concentration on intestinal maturation during the plateau. The plateau stage in oxygen consumption can delay intestinal development of turkey embryos if temperatures exceed 38°C or oxygen concentrations fall below 19%. Thus, at 25 to 27 d of incubation, temperatures greater than 38°C and oxygen concentrations of 19% or less should be avoided.

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