Digestion and Absorption in the Young Chick

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ABSTRACT Digestion, enzyme secretion, and intestinal rate of passage were determined in broiler chicks from hatch until 21 d using ^{141}Ce as a nonabsorbed reference substance. Body weight and feed intake increased more rapidly after 10 d posthatch, and, in parallel, time of passage of feed through the intestines decreased by approximately 33%. Net duodenal secretion of amylase, trypsin, and lipase was low at 4 d and increased 100-, 50-, and 20-fold, respectively, by 21 d. Enzyme activity decreased distally in the small intestine. This change was greater with age. The contribution of the ileum to fatty acid absorption decreased after 7 d. Small intestine digestion of nitrogen increased from 78% at 4 d to 92% at 21 d, whereas fatty acid and starch digestion ranged from 82 to 89% in this period. It appears that digestibilities of starch and lipids are not limiting factors in the growth of young chicks.

(*Key words*: chick, digestion, enzyme secretion, absorption, passage time)

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INTRODUCTION

In the newly hatched chick, energy metabolism changes from yolk-based lipid supply to a predominantly exogenous carbohydrate feed source as early as 1 d posthatch (Kuenzel and Kuenzel, 1977). Feed intake increases many fold during the growing period and changes occur in the gastrointestinal tract (GIT) and its secretions to match these developments. Different studies have reported on increases in pancreatic enzyme concentrations during the early posthatch period. Amylase and trypsin concentrations in the pancreas increase considerably during the first 21 d in poults (Krogdahl and Sell, 1989), and Moran (1982) concluded that starch digestion was not limiting in young chicks. Pancreatic lipase concentrations increased somewhat less posthatch and may be limiting in some diets (Krogdahl and Sell, 1989). Several studies have indicated that fat digestion increases during the initial weeks after hatching (Carew *et al.*, 1972; Whitehead and Fisher, 1975; Krogdahl and Sell, 1989). This may be due to low lipase activity (Krogdahl and Sell, 1989) or to lack of bile secretions. Polin and Hussein (1982) found that supplemental bile salts enhanced fat digestion in 7-d-old chicks.

Studies on the effect of diet on intestinal passage time indicated that fibrous diets have a longer transit time (Hurwitz and Bar, 1966). Slower rate of passage improves nutrient absorption by increased time of contact with absorptive cells and increases digestibility of dietary fiber by allowing more time for microbial fermentation (Washburn, 1991). Vergara *et al.* (1989) reported that rate of feed passage increases with growth posthatch.

In the first days posthatch the weight of GIT segments increases faster than does body weight (Sell *et al.*, 1991). However, after 4 d GIT weight relative to body weight remains constant (Pinchasov and Noy, 1994). Changes in the size of the GIT and the intestinal mucosa (Cook and Bird, 1973) would affect the rate of passage and efficiency of absorption. As no single study has reported on changes with age in intestinal enzyme activities, passage time, and digestion in the young chick, this study was designed to determine changes in these variables from hatching to 21 d of age.

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MATERIALS AND METHODS

Day old Arbor Acres chicks were obtained from a commercial hatchery and transferred to a battery brooder. Chicks were fed the experimental diet shown in Table 1, which was formulated according to requirements of NRC (1984). Two hundred μCi/kg ^{141}Ce was added as a nonabsorbed reference substance (Sklan *et al.*, 1975a) to the chick diet for 4 d before slaughter. Five chicks were killed with an intracardiac overdose of sodium pentobarbital on Days 4, 7, 10, 14, and 21 after hatching.

Digesta were obtained by gentle manipulation from segments of the small intestine as follows: the duodenum was defined as the segment from the pylorus to the distal point of entry of the bile ducts, Meckel's diverticulum marked the end of the jejunum, and the entry of the ceca marked the end of the ileum. Jejunum and ileum were divided into two equal parts by length. Digesta were weighed, homogenized with cold .9% NaCl, and aliquots of the homogenate taken for lipase (Sklan *et al.*, 1982), trypsin (Sklan and Halevy, 1985), and amylase activity (Pinchasov and Noy, 1994). Enzyme activities were defined as the amount of enzyme hydrolyzing 1 μmol of substrate/min under the specified conditions. Cerium-141 was determined by scintillation, nitrogen by the Kjeldahl method, starch as described by Rose *et al.* (1991), fatty acids after methylation by gas chromatography using an internal standard, and bile acids colorimetrically (Sklan *et al.*, 1975b).

TABLE 1. Composition of the experimental diets

Ingredients and composition	Percentage
Corn	51.0
Soybean meal	37.6
Soybean oil	6.0
$CaCO_3$	1.6
Dicalcium phosphate	1.6
NaCl	.4
Methionine	.3
Vitamins and minerals[1]	1.5
Analyzed nutrient composition	
Protein	22.5
Fat	7.8
Fiber	2.5
Ca	1.06
P	.70

[1]The vitamin and mineral mix contained (in milligrams per kilogram of diet): $FeSO_4$, 2.5; $CoCO_3$, .64; KI, 3.8; $MnSO_4$, 208; Na_2MoSO_4, 3.5; $CuSO_4$, 20; $ZnSO_4$, 220; thiamin, 5; riboflavin, 3.5; nicotinic acid, 60; pantothenic acid, 15; pyridoxine, 5; folic acid, .5; biotin, .2; menaquinone, .5; cyclocobalamine, .02; α-tocopherol acetate, 30; cholecalciferol, .125; retinol acetate, 35.

Calculations

When a nonabsorbed reference substance such as ^{141}Ce is fed until a steady state is obtained with respect to input-output of the isotope, assuming no chemical changes occur, a decrease in ratio of any component (A) to ^{141}Ce between two points in the intestine can be defined as absorption and any increase as secretion (Sklan *et al.*, 1975a). Overall net absorption between feed and lower ileum can be calculated as follows:

$$100\ [(A/^{141}Ce)_f - (A/^{141}Ce)_i]/(A/^{141}Ce)_f$$

where $(A/^{141}Ce)_f$ is the ratio of A to ^{141}Ce in the feed; and $(A/^{141}Ce)_i$ is the ratio in the ileum. Net secretion to the duodenum can be calculated by:

$$(\text{daily } ^{141}Ce \text{ intake}) \times [(A/^{141}Ce)_d - (A/^{141}Ce)_f]$$

where $(A/^{141}Ce)_d$ is the ratio of A to ^{141}Ce in the duodenum. Passage time through any segment can be calculated by dividing the mean amount of isotope recovered from the segment by the daily intake of ^{141}Ce. Least squares means of results are presented after analysis of variance using the General Linear Models procedures of SAS® (SAS Institute, 1986). Differences between means were tested using *t* tests.

RESULTS

Body weight increased from 45 g at hatching to close to 400 g at 21 d (Figure 1, upper panel). Feed intake rose from 7 g/d at d 4 to 45 g/d at 21 d (Figure 1, upper panel). In the same period, passage time (Figure 1, lower panel) through the small intestines decreased from 161 min on Day

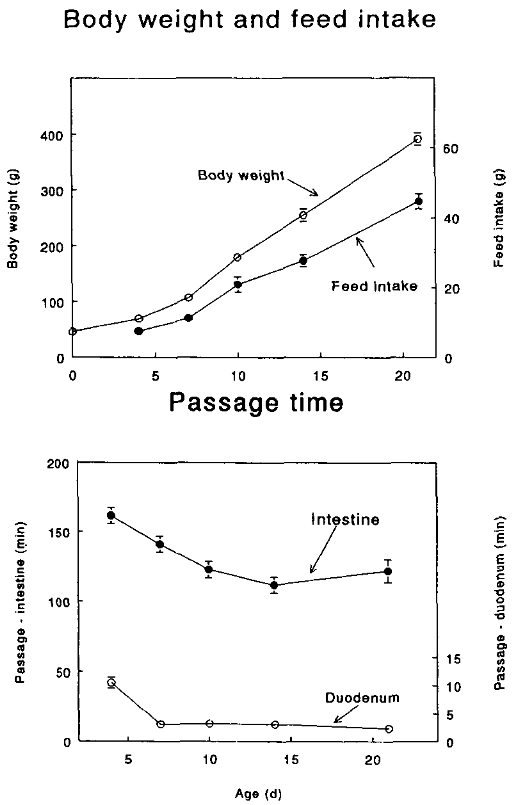

FIGURE 1. Body weight (open circles) and feed intake (filled circles) in chicks from 4 to 21 d after hatching (upper panel) and passage time (low panel) through the small intestines (filled circles) and duodenum (open circles). Results are means and bars are SD from five chicks at each age. Duodenal passage time was longer at Day 4 than all other days ($P < .001$), and small intestine passage time was significantly longer at Day 4 than Day 7 and at Day 7 than Days 10 to 21.

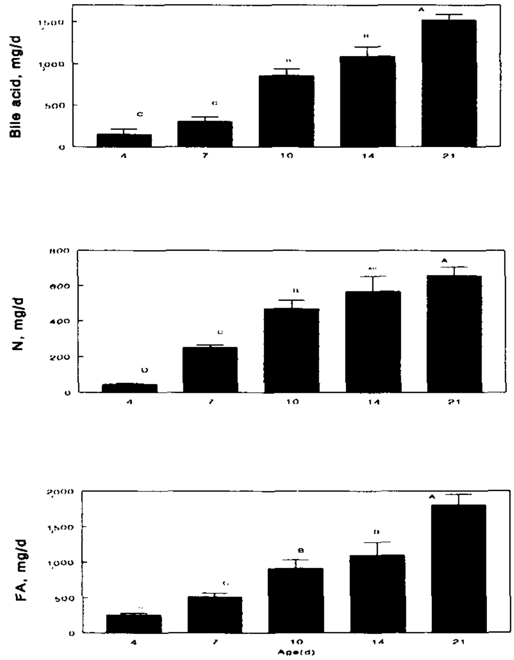

FIGURE 2. Net daily secretion of bile acids (upper panel), nitrogen (middle panel), and fatty acids (lower panel) to the duodenum of chicks at different ages. Bars are means ± SD from five chicks and bars marked with different letters differ significantly ($P < .01$).

4 to 110 min on Day 14, remaining constant up to 21 d. Duodenal passage time was 10 min on Day 4 and decreased to 3 min by Day 10 with no significant change until Day 21 (Figure 1, lower panel).

Net daily secretion to the duodenum was calculated from the 24-h ^{141}Ce intake. Duodenal bile acid secretion increased more than twofold between 4 and 7 d and between 7 and 10 d (Figure 2, upper panel). Thereafter the rate of secretion increased by 80% between 10 and 21 d. Nitrogen secretion to the duodenum increased by 15-fold from 4 to 21 d, with the major increase between 4 and 10 d (Figure 2, middle panel). The pattern of fatty acid secretion was similar to the bile salt secretion, increasing 8- to 10-fold during 4 to 21 d posthatch (Figure 2, lower panel). Daily secretions of bile acids, fatty acids, and nitrogen calculated per body weight or per feed intake was maximal at 10 to 14 d and decreased from then until 21 d (not shown).

The duodenal enzyme activity to ^{141}Ce ratio multiplied by the daily ^{141}Ce intake yields the net enzyme secretion, which is shown in Figure 3 for amylase, trypsin, and lipase. Net daily secretion increased by 100-, 50-, and 20-fold, respectively, between 4 and 21 d. The relative increases in enzyme secretion between 4 and 21 d was lowest for lipase and highest for amylase.

Enzymatic activities relative to ^{141}Ce through the different segments of the small intestine in chicks at the different

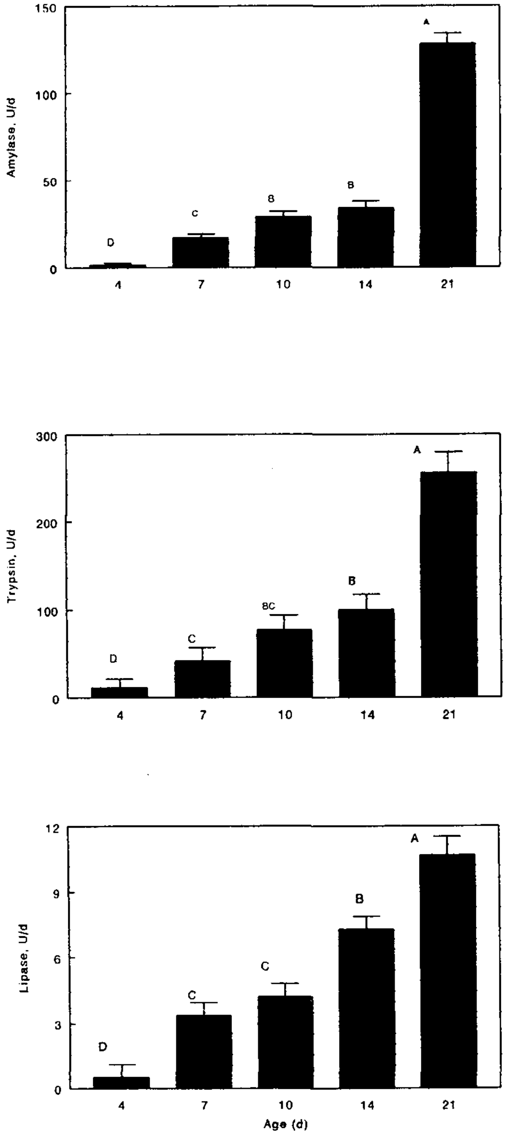

FIGURE 3. Net daily secretion of amylase (upper panel), trypsin (middle panel) and lipase (lower panel) to the duodenum of chicks at different ages. Enzyme activities were defined as the amount of enzyme hydrolyzing 1 μmol of substrate/min under the specified conditions. Bars are means ± SD from five chicks and bars marked with different letters differ significantly ($P < .01$).

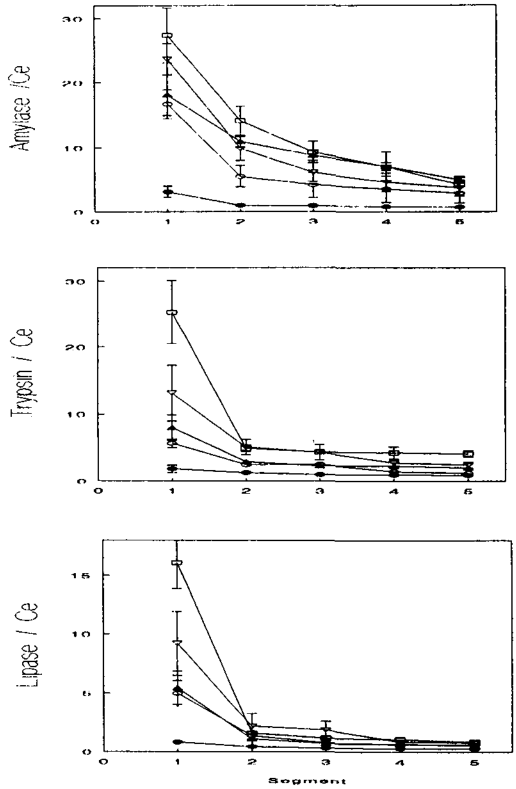

FIGURE 4. Ratios of amylase (upper panel), trypsin (middle panel) and lipase (lower panel) to ^{141}Ce in the segments of the small intestine from 4 to 21 d posthatch. The intestinal segments were defined as follows: the duodenum was the segment from the pylorus to the distal point of entry of the bile ducts, Meckel's diverticulum marked the end of the jejunum, and the entry of the ceca marked the end of the ileum. Jejunum and ileum were divided into two equal parts by length. Segments are designated by numbers 1 to 5 with segment 1 the duodenum. Values are means from five chicks and bars are SD. Results are represented at 4 d by filled circles, at 7 d by open circles, at 10 d by filled triangles, at 14 d by open triangles, and at 21 d by squares.

ages are shown in Figure 4. Ratios of enzymes to ^{141}Ce in the duodenum increased with age, reflecting the increasing secretion. The pattern of enzyme disappearance through the small intestine is similar for amylase, trypsin, and lipase. All had the highest net flux through the duodenum and activity decreased rapidly between duodenum and jejunum and less rapidly thereafter. These changes were less pronounced on Day 4, with a smaller decrease in enzyme activities occurring as digesta moved distally. Amylase activity decreased somewhat less along the intestine than the other enzymes examined.

The ratios of nitrogen and fatty acids to ^{141}Ce in feed and the various segments of

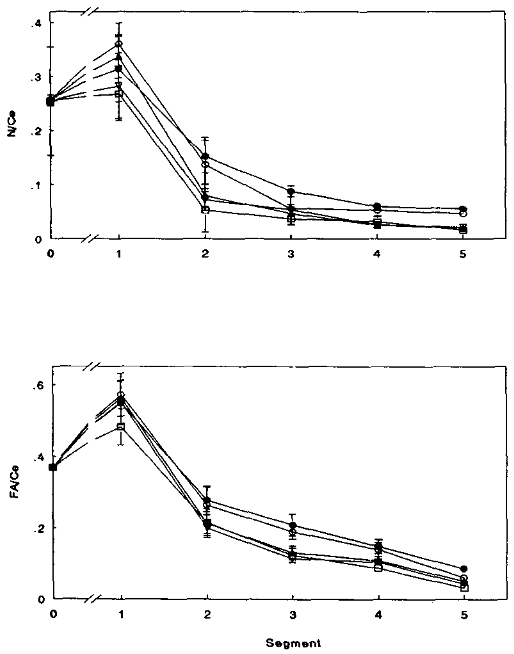

FIGURE 5. Ratios of nitrogen (top) and fatty acids (bottom) to ^{141}Ce in the segments of the small intestine from 4 to 21 d posthatch. The intestinal segments were defined as follows: the duodenum was the segment from the pylorus to the distal point of entry of the bile ducts, Meckel's diverticulum marked the end of the jejunum, and the entry of the ceca marked the end of the ileum. Jejunum and ileum were divided into two equal parts by length. Segments are designated by numbers 1 to 5 with segment 1 the duodenum. Values are means from five chicks and the bars are SD. Results are represented at 4 d by filled circles, at 7 d by open circles, at 10 d by filled triangles, at 14 d by open triangles, and at 21 d by squares.

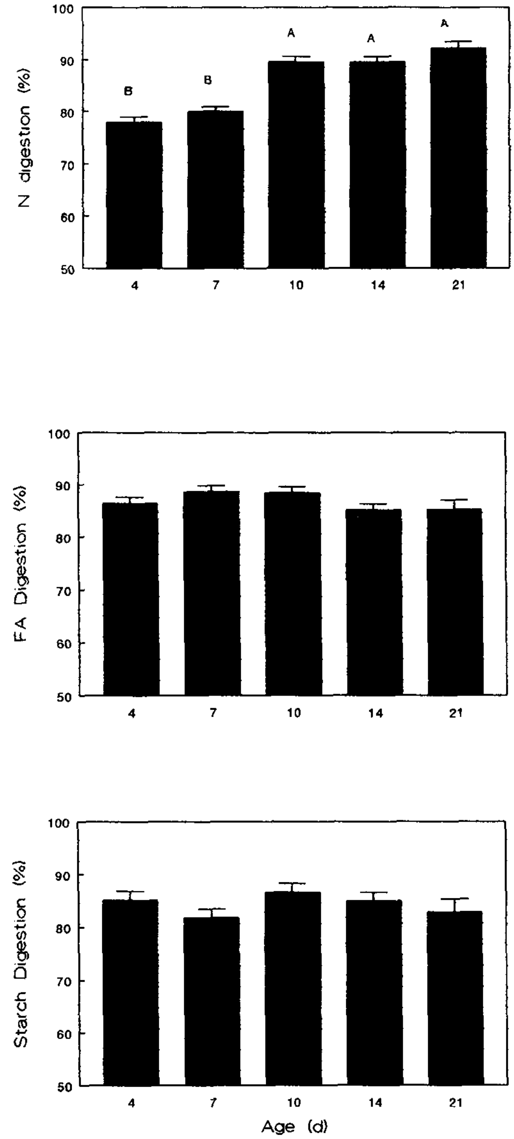

FIGURE 6. Apparent digestion between feed and lower ileum of nitrogen (upper panel), fatty acids (middle panel), and starch (lower panel) from 4 to 21 d posthatch. Bars are means ± SD from five chicks and bars marked with different letters differ significantly ($P < .01$).

the small intestine are shown in Figure 5. Net secretion of both nitrogen and fatty acids was observed in the duodenum and major absorption occurred between duodenum and upper jejunum with less change in the ileum, particularly for nitrogen absorption. The nitrogen:^{141}Ce ratios at 4 d were higher in the distal intestine than in older chicks. In young chicks the contribution of the ileum to fatty acid absorption was 33% of the duodenal flux as compared with 20% in 21-d-old chicks.

Digestion between feed and ileum is shown in Figure 6 for nitrogen, fatty acids, and starch. Small intestine nitrogen digestion increased from 78% at 4 d to 92% at 21 d ($P < .01$, Figure 6, upper panel). Starch and fatty acid digestion did not change significantly between 4 and 21 d and ranged from 82 to 89% (Figure 6, middle and lower panels).

DISCUSSION

Uptake of nutrients is dependent on their digestion and absorption from the GIT. Digestion and absorption of macromolecules requires sufficient enzymatic hydrolysis at, or before, the sites of uptake. When feed intake increases, as in the posthatch chick, greater enzyme activity or longer retention time may be necessary for hydrolysis in the small intestine.

Changes in Passage Rate with Age

Feed consumption increases with age, and Sibbald (1979) suggested that as increases in feed intake shortened transit time, intake thus outstrips GIT development rate in young chicks. Previous studies have indicated the segments of the GIT and pancreas increase in size and weight more rapidly than body weight and other organs posthatch; relative weights of GIT segments peak at 4 d with a gradual decrease thereafter (Katanbaf *et al.*, 1988; Sell *et al.*, 1991; Pinchasov and Noy, 1994). In the present study, feed consumption increased threefold between 4 to 10 d posthatch and in parallel the rate of passage decreased by 30%. However, after 10 d no changes in passage rate were observed, although feed intake continued to increase. The decrease in transit time observed here was especially marked in the duodenum, the major site of activity of digestive enzymes and of uptake (Sklan *et al.*, 1975b; Sklan and Hurwitz, 1980). In previous studies, using the same method with 7- to 8-wk-old chickens, small intestinal passage times were 63 to 80 min, which may indicate that further decreases in passage time occur between 3 and 7 wk of age (Sklan *et al.*, 1975a).

Duodenal Secretions

In young chicks, pancreatic enzyme concentrations have been examined, and these increase with age, although proteolytic, amylolytic, and lipolytic enzyme concentrations change at different rates (Marchaim and Kulka, 1967). Krogdahl and Sell (1984) found increases in pancreatic trypsin and amylase activities during the 21 d posthatch and suggested that pancreatic lipase activity may be a limiting factor in lipid digestion in young poults (Krogdahl and Sell, 1989).

In our study we have determined actual net secretion of some representative enzymes and biliary components in the duodenum and followed their disappearance along the GIT. Total enzyme secretion can also be estimated from the nitrogen secretion to the duodenum. Daily secretion of all enzymes determined in this study increased rapidly with age. Lipase, trypsin, and amylase secretion to the duodenum increased 20- to 100-fold from 4 to 21 d. Lipase activity increased less and somewhat more slowly than the other enzymes and this parallels the findings in the pancreas (Krogdahl and Sell, 1984). Amylase secretion was relatively low at 4 d, possibly as no carbohydrates are present in the yolk, and then showed a relatively rapid increase in secretion with age.

Biliary secretions are low posthatch, increase with age, and may limit fat absorption, because dietary additions of cholic acid improve fat digestion in some circumstances in young chicks (Serafin and Nesheim, 1967; Gomez and Polin, 1976; Polin *et al.*, 1980). Krogdahl and Sell (1985) found that bile salt secretion increased until 21 d and then decreased. In this study, secretion of bile components, including bile salts and fatty acids, to the duodenum increased 8- to 10-fold between 4 and 21 d posthatch. As the major source of fatty acid secretions in the duodenum was bile phospholipids (Sklan *et al.*, 1975b), it may be assumed that phospholipid and bile salt ratios in bile secretions were constant over this period. Nitrogen secretion to the duodenum increased 15-fold between 4 and 21 d, and this is consistent with larger increase in enzyme secretion in this period. Feed consumption increased approximately sevenfold in this period. Biliary and nitrogen secretions per feed intake or body weight peaked at 10 to 14 d, possibly representing a regulatory overshoot to the increase in feed intake.

Changes in Digestion with Age

Apparent absorption of over 90% dietary fatty acids has been reported in 12- to 15-d-old chicks fed diets with up to 10%

unsaturated fats (Renner and Hill, 1960; Sklan *et al.*, 1973; Whitehead and Fisher, 1975). Others have indicated that digestion is lower posthatch when saturated fats or high-fat diets are fed, and increases with age (Katongole and March, 1980; Polin and Hussein, 1982). In this study with 6% added unsaturated fat, digestion of fatty acids at 4 d was over 85% and increased little thereafter. Thus, it appears that sufficient lipase and bile salts were available for almost complete fatty acid uptake already at 4 d on these diets.

In this study, from 4 to 21 d digestion of starch was above 85%; previously it has been shown that starch digestion in 12-d-old birds was over 95% in the jejunum (Reisenfeld *et al.*, 1980). This indicates that the increases in pancreatic amylase concentrations (Sell *et al.*, 1989) result in adequate intestinal amylolytic activity for starch breakdown early posthatch.

Nitrogen digestion by the ileum increased from 78 to 80% at 4 and 7 d to close to 90% at 21 d, this is similar to results reported by Bielorai *et al.* (1973), who found 86% nitrogen absorption between feed and ileum in 19-d-old chicks. Proteolysis may not have been sufficient in the early posthatch period to hydrolyze exogenous and endogenous proteins. Decreased proteolysis may also explain the slower decrease in enzyme activity along the small intestine in young chicks.

The results of this study indicate that at 4 d posthatch digestion was over 85% for starch and fatty acids and 78% for nitrogen with the diets and feed intakes observed. Digestion of starch and fatty acids hardly changed between 4 and 21 d, and digestion of nitrogen increased to 92% at 21 d, although both pancreatic and biliary secretions increased. In fact, enzymes may well be secreted at excess levels, as considerable activity was observed in the lower small intestine distal to the major sites of absorption. The changes occurring with age were that soon after hatching increased feed intake decreased time of intestinal passage with sufficient enzymatic activity for hydrolysis and uptake of sugars and lipids, whereas proteolysis was more limiting. From 10 d of age, increased feed intake was compensated for by enhanced intestinal capacity and enzyme secretion. Feed intake may be regulated so as not to exceed the digestive capability.

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