Relationship between the stage of digestive tract development in chicks and the effect of viscosity reducing enzymes on fat digestion

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ABSTRACT

Different fats are added to low energy cereal diets for broiler chickens so as to satisfy the energy requirements of the chickens. However, the viscous soluble dietary fibre present in some cereals negatively affects fat digestion and absorption by chickens. Lowering the viscosity of digesta by feed enzyme supplementation of cereal diets enhances fat digestion and absorption. The effect of chicken age and the degree of saturation of the added fat on these processes are discussed.

KEY WORDS: viscosity, fat digestion, feed enzymes, chicken

INTRODUCTION

The successful utilization of microbial enzymes in poultry rations depends upon an understanding of their modes of action and the role they are to perform. Up to now, the most effective enzymes used to improve the nutritional value of cereals containing highly viscous non-starch polysaccharides (NSP) are those with pentosanase and β-glucanase activity. The beneficial action of these enzymes has been associated with freeing nutrients masked by insoluble cell wall material (Hesselman and Åman, 1986) and with reducing digesta viscosity (Bedford and Classen, 1992). Under practical conditions these enzymes are most effective in the first weeks of life of chickens, with little or no effects seen in adult birds (Brenes et al., 1993) because adult birds digest diets rich in viscous NSPs better than young ones (Smulikowska, 1995).
The energy density of diets used in the first weeks of life of broiler chickens is very high and reaches 13.4 MJ of metabolizable energy (ME) per kg of diet. The ME value of cereals containing soluble, viscous non-starch polysaccharides (NSP) is low, so it is necessary to add fat to broiler chicken diets based on such cereals. The lower the ME of the cereal used, the more fat is needed to optimize the energy level of diets. The energy density of laying hen diets reaches only 11.3 MJ ME/kg and they rarely need to be supplemented with fat. The relationship between the stage of digestive tract development and the effect of viscosity reducing enzymes on fat digestion is discussed in this paper.

THE ANATOMY AND MOTILITY OF THE DIGESTIVE TRACT OF THE CHICKEN

The digestive tract of the chicken is relatively shorter and anatomically different from that of mammals. It consist of the beak, the oesophagus which widens into the crop, the lower oesophagus, proventriculus, gizzard, duodenum, jejunum and ileum. The gizzard connects with the proventriculus by a narrow and short isthmus, and with the duodenum via a narrow pylorus. Pancreatic and bile ducts open into the distal end of the duodenal loop. Regardless of age, the largest parts of the GIT (gastrointestinal tract) involved in digestion are the gizzard and ileum (Table 1), which corresponds with their importance in the digestive process. The feed which enters the gizzard is degraded mechanically by grinding and vigorously mixing. The gizzard movements are pendular; contractions are rapid, of the order of 2 to 3 per min, followed by contractions of the proventriculus. Due to

<table>
<thead>
<tr>
<th>Item</th>
<th>Male broilers 9-days-old</th>
<th>Male broilers 24-days-old</th>
<th>Laying hens 48-week-old</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live body weight, g</td>
<td>200.7</td>
<td>1017.0</td>
<td>1886.7</td>
</tr>
<tr>
<td>Digestive tract, g</td>
<td>19.8</td>
<td>61.6</td>
<td>93.0</td>
</tr>
<tr>
<td>Parts of DT</td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>g</td>
<td>% DT</td>
<td>g</td>
</tr>
<tr>
<td>crop</td>
<td>1.2</td>
<td>6.2</td>
<td>4.2</td>
</tr>
<tr>
<td>proventriculus</td>
<td>2.1</td>
<td>10.7</td>
<td>6.3</td>
</tr>
<tr>
<td>gizzard</td>
<td>7.3</td>
<td>36.6</td>
<td>16.6</td>
</tr>
<tr>
<td>duodenum</td>
<td>2.1</td>
<td>10.6</td>
<td>8.3</td>
</tr>
<tr>
<td>ileum</td>
<td>7.1</td>
<td>35.9</td>
<td>26.2</td>
</tr>
</tbody>
</table>

* sum of empty crop, proventriculus, gizzard, duodenum, ileum
these contractions, the digesta is shuttled between the proventriculus and gizzard, and liquid digesta is pushed through the pylorus into the duodenum. In the duodenum, peristalsis is followed by antiperistalsis. In the turkey, intestinal reflexes occur 2 or 3 times per h, involving the entire duodenum and the upper ileum in one or two antiperistaltic contractions (Duke, 1982, 1992). In the chick this process is continuous, enabling penetration of the gizzard by duodenal contents during the contractile period of the gizzard. This motility pattern is unique to birds and enables reverse passage of intestinal digesta containing pancreatic and intestinal juice, and bile into the gizzard and proventriculus (Sklan et al., 1978). The presence of bile salts in the gizzard enables fat emulsification, which is necessary for the further stages of digestion and absorption in the duodenum and jejunum. The shuttling of digesta between the gizzard and duodenum increases the time the feed is exposed to digestive enzymes and favours its absorption in the upper parts of the small intestine.

DIGESTION OF FAT IN POULTRY

Fat digestion in chicks is a complex process. Ingested lipids must first be emulsified in the presence of conjugated bile salts. Fairly large (5000 Å) droplets of emulsion are subjected to the hydrolytic action of pancreatic lipase in the presence of colipase and pancreatic phospholipase A2. The products of lipolysis – unsaturated long chain fatty acids, medium chain free fatty acids, monoglycerides and phospholipids, spontaneously form mixed micelles with conjugated bile salts (30 to 100 Å). The hydrophobic cores of these micelles are able to solubilize long chain saturated fatty acids, fat soluble vitamins and cholesteryl esters. Micelles, dispersed in the aqueous medium of the intestinal lumen, are transported to the mucosal surface and pass through the brush border membrane, leaving bile salts in the gut lumen (Scott et al., 1982; Krogdahl, 1985). The effectiveness of utilization of dietary fat by chickens depends on its degree of saturation. Fats rich in unsaturated fatty acids are better digested and absorbed than saturated fats. Tallow, due to the specific arrangement of saturated and unsaturated fatty acid on the glycerol moiety of the triglyceride molecule (a high proportion of palmitic and stearic acid is distributed throughout positions 1- and 3- of the triglyceride) is poorly digested and absorbed by poultry. Both palmitic and stearic fatty acids are nonpolar and cannot form mixed micelles spontaneously, but can be solubilized by such micelles formed from unsaturated fatty acids and conjugated bile salts. Tallow is better absorbed in the presence of vegetable oil as there are more mixed micelles in the digesta (Wiseman, 1990). The main site of lipid absorption in fowls is the duodenum and jejunum, while the bile salts are absorbed in the jejunum and ileum (Scott et al., 1982; Johnson, 1992).
In newly hatched chicks the intestinal system is anatomically complete and its capacity to digest starch and fats is essentially complete by day 4, whereas N digestion increases from 70-80% on day 4 to 90% on day 10-14 (Noy and Sklan, 1995; Uni et al., 1995). The broiler chick has a reserve of bile acids in the yolk sac after hatching, however, the concentration of bile acids in the gastrointestinal tract is relatively low in the first weeks of life (Inarrea et al., 1989).

PHYSIOLOGICAL EFFECTS OF THE VISCOSITY OF WATER SOLUBLE NSPs ON FAT DIGESTION IN BIRDS

The viscosity of digesta depends on the structure and size of soluble NSP molecules ingested by birds, as well as on their concentration (Bedford and Classen, 1992; Annison, 1995). From among the cereals the most viscous are arabinoxylans and β-glucans present in rye, barley, oats and some varieties of wheat. Increasing substitution of rye by wheat (Table 2) caused a substantial decrease in fat digestibility both in the experiments of Antoniou and Marquardt (1982) and Ward and Marquardt (1983).

Knowledge about how the physicochemical properties of NSPs might affect fat digestion in poultry is limited. It has been suggested that high digesta viscosity

<table>
<thead>
<tr>
<th>Rye level, %</th>
<th>Enzyme</th>
<th>AFD</th>
<th>AME&lt;sub&gt;N&lt;/sub&gt; MJ/kg</th>
<th>AME&lt;sub&gt;N&lt;/sub&gt;/GE %</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td>91.5</td>
<td>14.58</td>
<td>74.8</td>
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<td>0</td>
<td>+</td>
<td>90.6</td>
<td>14.56</td>
<td>74.7</td>
</tr>
<tr>
<td>15</td>
<td>-</td>
<td>83.6</td>
<td>13.73</td>
<td>70.6</td>
</tr>
<tr>
<td>15</td>
<td>+</td>
<td>91.5</td>
<td>14.00</td>
<td>72.9</td>
</tr>
<tr>
<td>30</td>
<td>-</td>
<td>82.8</td>
<td>13.26</td>
<td>69.0</td>
</tr>
<tr>
<td>30</td>
<td>+</td>
<td>87.5</td>
<td>13.93</td>
<td>72.6</td>
</tr>
<tr>
<td>45</td>
<td>-</td>
<td>74.7</td>
<td>12.24</td>
<td>63.6</td>
</tr>
<tr>
<td>45</td>
<td>+</td>
<td>83.3</td>
<td>13.54</td>
<td>70.9</td>
</tr>
<tr>
<td>Pooled SEM</td>
<td></td>
<td>1.10</td>
<td>0.12</td>
<td>0.63</td>
</tr>
</tbody>
</table>

Source of variation Probability
rye 0.001 0.001 0.001
enzyme 0.001 0.001 0.001
rye x enzyme 0.001 0.001 0.001

- diet containing 8.5% added mixed fat (soya oil + lard 1:1)
associated with ingestion of soluble viscous NSP slows proper reflux of digesta and makes diffusion and convective transport of droplets of emulsion, fatty acids, mixed micelles, bile salts and lipase within the gastrointestinal contents more difficult, reducing transport of micelles to the mucosal surface. Molecules of NSP in solution can present charged, weakly hydrophobic and weakly hydrophilic surfaces. They may associate with surfaces of food particles, lipid micelles or the glyco­calyx surface of the gut (Johnson, 1992; Annison, 1995). Viscous polysaccharides might also directly complex with digestive enzymes and reduce their activity (Ike­da and Kusano, 1983). It has been shown that gel-forming gums and pectins give rise to an increase in the thickness of the unstirred water layer, which is adjacent to the intestinal mucosa (Johnson and Gee, 1981, 1986 after Johnson, 1992), which in turn may increase its resistance to the transport of nutrients. The absorption of fatty acids may be impaired by gelling agents if the effective surface of the micro­villi or the function of the fatty acid binding protein in the mucosal membrane are diminished (Smits and Annison, 1996).

It was demonstrated (Rakowska et al., 1993) that in very young chicks fed a diet based on rye, with a very high content of soluble dietary fibre, resulted in severe damage of intestinal villi and the mucous layer of the duodenum and small intestine. This was due to the proliferation of detrimental microflora, since the addition of an antibiotic protected the intestinal walls. Changes in the morphology of the villi and microvilli may also affect fatty acid absorption. With a rise in the concentration of soluble, viscous NSP in digesta, more undigested organic matter reaches the ileum, which in turn promotes the proliferation of detrimental microflora, which can deconjugate bile acids (Campbell et al., 1983a, b). Binding of bile acids by gel-forming soluble dietary fibres, as well as excessive bacterial bile acid deconjugation, may lead in turn to poor fat solubilization, as free bile acids are not active in micelle formation (Nagengast, 1992). Campbell et al. (1983a, b) demonstrated that the addition of sodium taurocholate to the rye-based diet substantially improved the digestibility of lipids.

Finally it is possible that endogenous lipid losses may increase due to binding of bile by viscous NSPs. Contrary to that of mammals, the bile of broiler chickens contains a large amount of triacylglycerols and cholesteryl esters (Noble and Con­ner, 1984; Noble et al., 1988, after Smits and Annison, 1996). In our own experi­ment (Smulikowska, 1998) the apparent fat digestibility of 10-day old broiler chi­ckens fed rye averaged only 0.6%, and in a few birds negative values were obtained, which points to endogenous lipid losses (Table 3).

Under experimental (Tables 3 and 4) and practical (Table 5) conditions, supple­mentation of broiler chicken diets containing cereals rich in soluble viscous NSP with feed enzymes lowers digesta viscosity and increases digestion and absorption of nutrients, which improves the performance of the birds.
TABLE 3

Effect of age of the chicks on AFD, organic matter retention (OMR) and AME<sub>N</sub> of rye, triticale and wheat (after Smulikowska, 1998)

<table>
<thead>
<tr>
<th>Cereal</th>
<th>Age of birds*</th>
<th>AFD</th>
<th>OMR</th>
<th>AME&lt;sub&gt;N&lt;/sub&gt; MJ/kg DM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rye</td>
<td>young</td>
<td>0.6</td>
<td>61.7</td>
<td>11.0</td>
</tr>
<tr>
<td></td>
<td>adult</td>
<td>74.8</td>
<td>76.4</td>
<td>14.9</td>
</tr>
<tr>
<td>Triticale</td>
<td>young</td>
<td>46.8</td>
<td>75.5</td>
<td>14.4</td>
</tr>
<tr>
<td></td>
<td>adult</td>
<td>78.3</td>
<td>78.7</td>
<td>14.3</td>
</tr>
<tr>
<td>Wheat</td>
<td>young</td>
<td>60.3</td>
<td>73.2</td>
<td>13.7</td>
</tr>
<tr>
<td></td>
<td>adult</td>
<td>78.9</td>
<td>80.4</td>
<td>15.1</td>
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<tr>
<td>Pooled SEM</td>
<td></td>
<td>2.4</td>
<td>1.4</td>
<td>0.2</td>
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</table>

Source of variation

<table>
<thead>
<tr>
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<th>Probability</th>
</tr>
</thead>
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<tr>
<td>cereal</td>
<td>0.01</td>
</tr>
<tr>
<td>age of bird</td>
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</tr>
<tr>
<td>cereal x age</td>
<td>0.01</td>
</tr>
</tbody>
</table>

* young 10-day-old broiler cockerels; adult 45-week-old White Leghorn cockerels

TABLE 4

Effect of fat source and enzyme supplementation on AFD, AME<sub>N</sub>, metabolizability of energy, and viscosity of excreta and digesta (in cP) (after Smulikowska and Mieczkowska, 1996)

<table>
<thead>
<tr>
<th>Fat source</th>
<th>Enzyme</th>
<th>AFD</th>
<th>AME&lt;sub&gt;N&lt;/sub&gt; MJ/kg DM</th>
<th>AME&lt;sub&gt;N&lt;/sub&gt;/GE %</th>
<th>Viscosity, cP excreta</th>
<th>Viscosity, cP ileal digesta</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soya oil</td>
<td>-</td>
<td>75.9</td>
<td>13.53</td>
<td>64.9</td>
<td>50.3</td>
<td>49.8</td>
</tr>
<tr>
<td>Lard</td>
<td>-</td>
<td>66.4</td>
<td>12.86</td>
<td>64.0</td>
<td>130.4</td>
<td>46.2</td>
</tr>
<tr>
<td>Tallow</td>
<td>-</td>
<td>45.5</td>
<td>12.25</td>
<td>58.8</td>
<td>287.7</td>
<td>30.7</td>
</tr>
<tr>
<td>Mixed fat*</td>
<td>-</td>
<td>61.7</td>
<td>13.02</td>
<td>64.3</td>
<td>92.6</td>
<td>41.1</td>
</tr>
<tr>
<td>Soya oil</td>
<td>+</td>
<td>84.8</td>
<td>14.69</td>
<td>71.3</td>
<td>29.0</td>
<td>16.8</td>
</tr>
<tr>
<td>Lard</td>
<td>+</td>
<td>77.7</td>
<td>13.80</td>
<td>68.3</td>
<td>30.8</td>
<td>17.9</td>
</tr>
<tr>
<td>Tallow</td>
<td>+</td>
<td>63.1</td>
<td>13.90</td>
<td>67.6</td>
<td>27.4</td>
<td>20.5</td>
</tr>
<tr>
<td>Mixed fat*</td>
<td>+</td>
<td>73.9</td>
<td>14.76</td>
<td>70.6</td>
<td>23.1</td>
<td>16.4</td>
</tr>
<tr>
<td>Pooled SEM</td>
<td>+</td>
<td>1.8</td>
<td>0.20</td>
<td>1.0</td>
<td>27.7</td>
<td>2.7</td>
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Source of variation

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Probability</th>
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<tr>
<td>fat</td>
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</tr>
<tr>
<td>enzyme</td>
<td>0.001</td>
</tr>
<tr>
<td>fat x enzyme</td>
<td>NS</td>
</tr>
</tbody>
</table>

* soya oil and tallow in proportion 1:1
TABLE 5

Effect of rape seed oil (RO) and feed enzyme supplementation on body weight (BW, g) and feed conversion ratio (FCR, g/g) of 6-week-old broiler chickens fed cereal-based isoprotein diets (after Rutkowski, 1996)

<table>
<thead>
<tr>
<th>Cereal in diet</th>
<th>Unsupplemented</th>
<th>+ RO (up to 13 MJ EM/kg diet)</th>
<th>+RO + feed enzyme</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BW</td>
<td>FCR</td>
<td>BW</td>
</tr>
<tr>
<td>Maize</td>
<td>1447</td>
<td>2.07</td>
<td>1604</td>
</tr>
<tr>
<td>Wheat</td>
<td>1261</td>
<td>2.33</td>
<td>1555</td>
</tr>
<tr>
<td>Triticale</td>
<td>1352</td>
<td>2.37</td>
<td>1562</td>
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<tr>
<td>Barley</td>
<td>968</td>
<td>2.72</td>
<td>1443</td>
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<tr>
<td>Oat</td>
<td>839</td>
<td>2.80</td>
<td>1169</td>
</tr>
<tr>
<td>Rye</td>
<td>867</td>
<td>2.85</td>
<td>1072</td>
</tr>
</tbody>
</table>

INTERACTION BETWEEN VISCOSITY AND DEGREE OF FAT SATURATION

Tallow-fortified diets have often been used to prove a beneficial action of enzyme supplementation on the AME$_N$ value of rye-based diets (Fengler and Marquardt, 1988; Friesen et al., 1992; Marquardt et al., 1994). Choct and Annison (1992 a,b) reported that the depression of lipid digestibility was proportional to the content of wheat pentosans in the diet, – digestibility of saturated was more affected than of unsaturated fatty acids. Supplementation of rye-containing diets with saturated fats causes a substantial elevation in the viscosity of ileal digesta and excreta. Dänicke et al. (1995) reported that in 28-day-old birds fed a rye-tallow diet the viscosity in the jejunum was 100%, but in the ileum it was 240% higher than in birds fed a rye-soya oil diet. The effect of fat saturation on ileal viscosity was not confirmed in our experiment (Smulikowska and Mieczkowska, 1996) but the droppings of chicks fed a rye-tallow diet were 470% more viscous than of birds fed a rye-soya oil diet (Table 4). The presence of substantial amounts of undigested fats, connected with viscous NSP could have delayed the movement of digesta. Under these conditions, more insoluble NSP may have become solubilized in the last parts of digestive tract due to the action of microflora, adding to the viscosity and stickiness of excreta. The viscosity of digesta and excreta after enzyme supplementation diminished significantly and did not depend on the source of added fat.

The difference between the digestibility of soya oil and lard, tallow and mixed fat in unsupplemented wheat-rye diets reached 10, 30 and 14 percent, respectively. Reduction of digesta viscosity due to supplementation of diets with feed enzyme improved fat digestibility by 21% on average, and the difference between the digestibility of soya oil and other fats diminished to 7, 22 and 11 percent (Table 4).
The increase in fat digestibility was correlated with better metabolizability of energy and higher $\text{AME}_N$ value of the diets, as found in the experiments of Dänicke et al. (1995) and Schutte et al. (1995).

THE RELATIONSHIP BETWEEN THE AGE OF THE BIRDS AND THE EFFECT OF VISCOSITY ON FAT DIGESTION

The effect of viscosity on fat digestion is not so detrimental in adult birds, as diets containing 65% of wheat, barley, oats or rye supplemented with tallow did not negatively affect the laying rate, and enzyme supplementation did not have a positive effect on laying performance (Brenes et al., 1993). The absolute mass of GIT tissues increases when birds mature, even if it decreases relative to live body weight (Table 1). However, in the very young chick, the weight, hence the thickness of muscular walls and the diameter of the GIT, is smaller than in adult birds. Increases in the thickness of the unstirred water layer due to NSP action may further diminish the diameter of the intestines. It is obvious that the strength needed to push digesta through the intestinal tract increases with rising viscosity, and decreases with increasing GIT diameter. The muscular walls of the GIT in young birds are relatively thin, and not strong enough to effectively relocate viscous digesta. The high viscosity of intestinal contents, due to feeding rye or low quality wheat, disturbs the proper flow of digesta to and from the gizzard and often results in dilation of the proventriculus and gizzard in broiler chicks and atrophy of the isthmus, with the dilation reaching the crop in severe cases (Scott, 1993; Smulikowska, 1998). A dilated gizzard does not work effectively, which may disturb the fat emulsification necessary for digestion to proceed. A decrease in digesta viscosity enabling proper flow of digesta may have a positive effect on fat digestion. This is not so important in adult birds, as their small intestine is wider and the muscular layer of the GIT is sufficiently strong for even viscous digesta to be properly mixed and relocated. Also, the bacterial flora of adult birds is established and does not change as dramatically in the presence of viscous NSPs. Due to this, apparent fat digestion in adult birds is not as dependant on the presence of soluble viscous NSP as in young birds (Table 3) and the effect of enzyme supplementation is less pronounced.

CONCLUSIONS

It may be concluded that the presence of viscous NSP, the degree of saturation of added fat, and the age of the birds greatly affect utilization of fat in poultry. Supplementation with enzyme preparations containing xylanase and $\beta$-glucanase
is particularly advisable if diets prepared for very young chickens contain viscous NSP and are fortified with animal fat, since it may greatly enhance the retention of fat and metabolizability of energy. The effect is associated with a reduction in the viscosity of digesta and excreta. The effect of enzyme supplementation on fat digestion is negligible in adult birds.

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VISCOSITY REDUCING ENZYMES AND FAT DIGESTION


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