The Relevance of Starch and Protein Digestive Dynamics in Poultry

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Primary Audience: Nutritionists, Researchers, Students

SUMMARY

The fundamental premise of starch and protein digestive dynamics is that an ideal balance of glucose and amino acids is made available at sites of skeletal muscle protein synthesis to promote efficient growth. Digestive dynamics involve the digestion of protein and starch in the gut lumen, absorption of glucose and amino acids along the small intestine and their transition across the gut mucosa into the portal circulation. However, the post-enteral, bilateral bioavailability of glucose and amino acids is ultimately dependent on their metabolic fates in enterocytes as both may be catabolized in avian enterocytes for energy to drive digestive processes. Importantly, digestive dynamics consider rates and sites of glucose and amino acid absorption along the small intestine in addition to their extents of digestion as determined by static digestibility coefficients. There is considerable interest in the development of low-protein/high-supplemental amino acid diets but the digestive dynamics of supplemental and protein-bound amino acids are inherently different. Therefore, the relevance of starch and protein digestive dynamics in poultry will become increasingly evident if low-protein diets are to be developed successfully in the future.

Key words: amino acids, broiler chickens, digestive dynamics, glucose, protein, starch

DESCRIPTION OF PROBLEM

That an ideal balance of glucose and amino acids is made available at sites of protein synthesis to optimize broiler performance is the principal theory of starch and protein digestive dynamics. Thus, the problem declares itself as how best to identify the factors influencing digestive dynamics in order to harness and take advantage of them in chicken-meat production.

Intestinal uptakes of glucose and amino acids are almost certainly critical to broiler performance [1]; thus, the absorption of glucose and amino acids is pivotal pursuant to the digestion of starch and protein. However, glucose and amino acids may compete for intestinal uptakes [2], possibly for co-absorption with sodium via their respective Na⁺-dependent transport systems, where SGLT-1 holds relevance for glucose. However, the post-enteral bioavailability of glucose and amino acids is ultimately dependent on their metabolic fates in enterocytes during their transition across the gut mucosa to enter the portal circulation. Amino acids may enter anabolic pathways and be incorporated into protein, including mucin and digestive enzymes, and not gain entry to the portal circulation. In addition, both glucose and amino acids, especially glutamate and glutamine, are catabolized in avian enterocytes [3] to meet the

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copious energy requirements of the digestive tract [4]. In essence, these anabolic and catabolic “losses” in the gut mucosa disrupt the post-epithelial bilateral bioavailability of glucose and amino acids.

Digestive dynamics may be defined as a 3-tiered process: digestion of starch and protein in the gut lumen, absorption of glucose and amino acids along the small intestine, and their transition across the gut mucosa into the portal circulation. The digestibilities of starch and protein/amino acids are usually expressed as apparent digestibility coefficients determined at the terminal ileum. Although ileal digestibility coefficients avoid the confounding effects of hind-gut fermentation, the majority of glucose and amino acids are absorbed along the jejunum. Also, ileal digestibility coefficients are static measurements and disregard the kinetics of digestion and absorption. Therefore, digestive dynamics take the rates and sites of digestion and absorption into consideration in addition to the extent of starch and protein digestion.

One researcher [5] opined that feed intakes of single-stomached animals are discontinuous and vary in amount and composition. These feed intake variations may influence digestive processes that are related to food transit and enzyme hydrolysis, especially the extent and kinetics of nutrient absorption. Although digestibility coefficients are used to evaluate the disappearance of ingested nutrients, these digestibility coefficients are static and do not account for the different absorption rates that vary for different nutrients. Studies of kinetics associated with differences in relative absorption rates across the various nutrients are necessary for a more complete understanding of variations in the nutritive value of feedstuffs. For example, this researcher found that amino acids from wheat and fishmeal were absorbed more rapidly than from barley in pigs [6]. Also, 60- to 120-min post-prandial concentrations of α-amino N in portal blood were substantially higher from a blend of synthetic amino acids than from fishmeal.

The purpose of this review is to consider the relevance of starch and protein digestive dynamics in relation to the performance of broiler chickens. The likelihood is that starch and protein digestive dynamics will be increasingly taken into consideration in the formulation of broiler diets in the future to the advantage of chicken-meat production.

BACKGROUND

The genesis of our interest in digestive dynamics was the series of studies completed by Ted Batterham, who demonstrated that the utilization of lysine monohydrochloride (HCl) was compromised in pigs when their access to feed was restricted [7–9]. It was concluded [10] that the utilization of lysine HCl with once daily feeding was 0.53 for weight gain and 0.56 for feed conversion efficiency on the basis of carcass weight relative to frequent feeding. This shortfall was attributed to the delay of protein-bound amino acids arriving at sites of protein synthesis relative to lysine HCl. Similar findings were reported earlier [11] where decreasing time intervals at which tryptophan was provided separately to fortify tryptophan-deficient diets linearly increased weight gains in young rats. Modern broiler chickens have their feed access restricted in that they are subject to varying periods of up to 6 or 8 h/d without illumination. On the basis of Batterham’s outcomes in pigs, this “lights-off” period could be expected to compromise the utilization of lysine HCl, and other supplemental amino acids, in poultry. However, this assumption is not supported by findings in poultry [12]. These researchers reported that feeding frequency did not impact on lysine HCl utilization although the growth performance between the unrestricted and restricted fed birds was very different. This prompted the suggestion that lysine is retained in tissue pools in lysine-deprived birds rather than being deaminated. More recently, it was contended that lysine is unique among indispensable amino acids in that it can be conserved and there are several reports, albeit in rats, that support this position [13].

A Box–Behnken study in which broiler chicks were given feed access of 6, 15, and 24 h duration is of interest [14]. Accurate comparisons are not possible due to differences in diets; however, birds given unlimited feed access appeared to perform better (weight gain of 1265 g/bird, FCR of 1.354) than birds given 15 h feed access (weight gain of 1194 g/bird, FCR of 1.360) from 15 to 28 d post-hatch. Not
surprisingly, feed access of only 6 h duration compromised growth performance. However, it is interesting that the percentage supplemental lysine represented of total dietary lysine was negatively correlated to weight gain and positively correlated to FCR to similar and highly significant extents in birds given both 6 and 24 h feed access. Thus, the tentative indication is that lysine HCl was not utilized as well as protein-bound lysine in this feeding study but efficiency of utilization was essentially independent of feed access duration.

Clearly, the extent to which the feeding patterns of broiler chickens impact on digestive dynamics requires clarification. Arguably, even under “lights-on” illumination, broilers chicks are intermittent rather than continuous feeders. Broiler chickens exhibit diurnal feeding patterns and consume most of their ration either at the start or end of the day rather than the middle of the day [15]. In chickens offered pelleted diets, 4.7% of illuminated time was spent eating under a “12-h-on” lighting regime [16]. Under a “14-h-on” lighting regime, chickens spent 10.8% of illuminated time eating [17]. Modern genotype broiler chickens have substantially higher feed intakes now than was the case decades ago but due to improvements in feed conversion efficiency their feed intakes have not increased relative to their body weights.

Given that broilers are intermittent feeders, it is pertinent that there are tangible differences between avian and porcine digestive tracts. Retention of digesta in the crop and also the gizzard coupled with episodes of reverse peristalsis are unique to poultry and may increase the uniformity with which supplemental and protein-bound amino acids are absorbed. This is possibly an alternative explanation for the reported differences between pigs [10] and poultry [12] in respect of lysine HCl utilization.

Our curiosity in digestive dynamics is not confined to the utilization of supplemental amino acids although, given the interest in developing low-protein diets, this issue is of increasing relevance [18]. The feeding patterns of broiler chickens may well impact on starch and protein digestive dynamics; however, the probability is that there are additional contributing factors that are influential quite irrespective of feeding patterns.

EXTENTS, RATES, AND SITES OF STARCH AND PROTEIN DIGESTION

The apparent ileal digestibility coefficient of starch in broilers offered maize-based diets is in the order of 0.950, which is superior to sorghum- and wheat-based diets [19]. An apparent ileal digestibility coefficient of 0.858 for starch was reported in broilers offered a sorghum-based diet in comparison to 0.719 for protein (N) and a mean of 0.785 for 16 amino acids [20, 21]. Also, the digestion rate constant of starch was 67% higher (3.44 vs. $2.06 \times 10^{-2} \text{ min}^{-1}$) than the protein (N) digestion rate constant [20]. Apparent ileal digestibility coefficients of protein and amino acids are lower than starch principally because of endogenous amino acid flows. Endogenous amino acids are derived largely from secretions of digestive enzymes, mucin, and desquamated epithelial cells from the gut wall. The most abundant amino acids in endogenous flows in the ileum are glycine, cysteine, threonine, alanine, and aspartic acid, whereas the least abundant endogenous amino acids include methionine, lysine, leucine, phenylalanine, and histidine [22]. This is reflected in the apparent amino acid ileal digestibility coefficients from many poultry studies where methionine is frequently the most digestible, and threonine the least digestible, across the essential amino acids.

Extents of Starch and Protein Digestion

The apparent digestibility coefficients of starch, protein (N), and amino acids in 4 small intestinal segments (proximal jejunum, distal jejunum, proximal ileum, distal ileum) of broiler chicks offered a red sorghum-based diet are show in Table 1. In respect of starch, 54.3% was digested in the proximal jejunum (rapidly-digestible starch), 31.5% was digested in the 3 posterior small intestinal segments (slowly digestible starch), 31.5% was digested in the 3 posterior small intestinal segments (slowly digestible starch) leaving a balance of 14.2% that remained undigested (resistant starch) to enter the large intestine. The 600 g/kg grain sorghum diet was supplemented with 4.8 g/kg lysine HCl, 3.4 g/kg methionine and 1.3 g/kg threonine. The proportions of lysine (87.4%) and methionine (89.3%), especially, digested in the jejunum are noticeably higher than the
Table 1. Apparent digestibility coefficients of starch, protein (N), and amino acids in 4 small intestinal segments of broiler chicks offered a red sorghum-based diet steam-pelleted at a conditioning temperature of 80°C [20, 21].

<table>
<thead>
<tr>
<th>Item</th>
<th>Proximal jejunum</th>
<th>Distal jejunum</th>
<th>Proximal ileum</th>
<th>Distal ileum</th>
<th>Proportion (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starch</td>
<td>0.543</td>
<td>0.678</td>
<td>0.812</td>
<td>0.858</td>
<td>79.0</td>
</tr>
<tr>
<td>Protein (N)</td>
<td>0.333</td>
<td>0.538</td>
<td>0.727</td>
<td>0.719</td>
<td>74.8</td>
</tr>
<tr>
<td>Arginine</td>
<td>0.533</td>
<td>0.710</td>
<td>0.832</td>
<td>0.862</td>
<td>82.4</td>
</tr>
<tr>
<td>Histidine</td>
<td>0.427</td>
<td>0.612</td>
<td>0.752</td>
<td>0.785</td>
<td>78.0</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>0.363</td>
<td>0.568</td>
<td>0.726</td>
<td>0.774</td>
<td>73.4</td>
</tr>
<tr>
<td>Leucine</td>
<td>0.359</td>
<td>0.536</td>
<td>0.695</td>
<td>0.748</td>
<td>71.7</td>
</tr>
<tr>
<td>Lysine</td>
<td>0.606</td>
<td>0.758</td>
<td>0.847</td>
<td>0.867</td>
<td>87.4</td>
</tr>
<tr>
<td>Methionine</td>
<td>0.730</td>
<td>0.846</td>
<td>0.916</td>
<td>0.947</td>
<td>89.3</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>0.413</td>
<td>0.584</td>
<td>0.734</td>
<td>0.781</td>
<td>74.8</td>
</tr>
<tr>
<td>Threonine</td>
<td>0.405</td>
<td>0.580</td>
<td>0.715</td>
<td>0.744</td>
<td>78.0</td>
</tr>
<tr>
<td>Valine</td>
<td>0.352</td>
<td>0.560</td>
<td>0.715</td>
<td>0.760</td>
<td>73.7</td>
</tr>
<tr>
<td>Alanine</td>
<td>0.359</td>
<td>0.536</td>
<td>0.687</td>
<td>0.733</td>
<td>73.1</td>
</tr>
<tr>
<td>Aspartic acid</td>
<td>0.416</td>
<td>0.585</td>
<td>0.732</td>
<td>0.767</td>
<td>76.3</td>
</tr>
<tr>
<td>Glutamic acid</td>
<td>0.470</td>
<td>0.625</td>
<td>0.755</td>
<td>0.794</td>
<td>78.7</td>
</tr>
<tr>
<td>Glycine</td>
<td>0.355</td>
<td>0.561</td>
<td>0.716</td>
<td>0.752</td>
<td>74.6</td>
</tr>
<tr>
<td>Proline</td>
<td>0.368</td>
<td>0.531</td>
<td>0.681</td>
<td>0.722</td>
<td>73.5</td>
</tr>
<tr>
<td>Serine</td>
<td>0.384</td>
<td>0.555</td>
<td>0.715</td>
<td>0.754</td>
<td>73.6</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>0.342</td>
<td>0.534</td>
<td>0.715</td>
<td>0.763</td>
<td>70.0</td>
</tr>
</tbody>
</table>

1 The proportion of amino acid digested in the jejunum relative to the distal ileal digestibility coefficient.

average of 74.9% for the 13 protein-bound amino acids. This reflects the inherent differences in the digestive dynamics of supplemental (or crystalline or synthetic) amino acids as opposed to protein-bound amino acids.

It is noteworthy that in a meta-analysis of 5 feeding studies involving sorghum-based broiler diets, distal ileal starch (r = 0.013; P = 0.349) and protein (r = 0.349; P = 0.019) digestibility coefficients were not significantly correlated with FCR [23]. In contrast, there were significant correlations between proximal jejunal starch (r = 0.446; P = 0.041) and protein (r = 0.538; P = 0.029) digestibility coefficients with FCR. This comparison illustrates the merits of considering apparent digestibility coefficients in more proximal sites than the terminal ileum.

Rates of Starch and Protein Digestion

Starch and protein digestion rate constants may be determined using an exponential mathematical model to relate digestion coefficients at proximal jejunum, distal jejunum, proximal ileum, and distal ileum with their corresponding retention times in small intestinal segments:

\[ D_t = D_\infty (1 - e^{-kt}) \]

In this mathematical model, \( D_t (g/100 g\ starch or protein) \) is the percentage of starch/protein that is digested at time t (min), the fraction is the amount of potential digestible starch or protein (asymptote), and k is the digestion rate constant per unit time. The mean retention time in the 4 small intestinal segments is calculated from the concentrations of acid insoluble ash in dry digesta from 4 small intestinal segments and the daily intake of acid insoluble ash (or an alternative dietary marker).

The effects of phytase supplementation in broiler chickens offered nutritionally equivalent corn-, sorghum-, and wheat-based diets from 7 to 27 d post-hatch was investigated [24]. The FCR of these birds ranged from 1.532 to 1.457 about a mean value of 1.495. A contour plot of the relationship between protein and starch digestion rate constants with FCR from the study is shown in Figure 1. The minimal FCR is in the order of 1.400 that corresponds to a narrow range of protein digestion rates but a relatively wide range of starch digestion rate constants. This suggests that protein digestion rate constants are more important than starch in that they have to be met with greater precision if feed conversion efficiencies are to be enhanced. Although speculative, our contention is that protein digestive
dynamics may be a more potent force than starch as a relatively precisely defined protein digestion rate constant supported superior FCR in this study.

**Starch: Protein Disappearance Rate Ratios**

Starch: protein disappearance rate ratios may be calculated from starch and protein apparent digestibility coefficients ($ADC_i$) in any 1 of 4 small intestinal segments, dietary starch, and protein concentrations and daily feed intakes ($DFI$) from the following equation:

$$\text{Disappearance rate (g/bird/day)} = ADC \times \text{dietary concentration (g/kg)} \times DFI \, (g/day).$$

The starch: protein disappearance rate ratio is calculated to eliminate the potentially confounding effect of feed intake rates.

Broiler chickens were offered 6 dietary treatments from 7 to 28 d post-hatch based on a red sorghum (600 g/kg) and the sorghum in question, Buster, contained 121 g/kg protein and 706 g/kg starch on a dry matter basis [21]. The 6 dietary treatments were offered as mash, intact pellets steam-pelleted at conditioning temperatures of 65, 80, and 95°C, reground mash following pelleting at 95°C, and with protease added to the 80°C diet. In this study, FCR ranged from 1.473 to 1.659 about a mean of 1.523. Retrospectively calculated starch disappearance rates ranged from 29.8 to 39.5 g/bird/d, protein disappearance rates from 14.2 to 18.6 g/bird/d, and the starch: protein disappearance rate ratios ranged from 1.74 to 2.25 about a mean ratio of 2.03. Individually, starch and protein disappearance rates in the distal ileum were not linearly ($P > 0.20$) or quadratically ($P > 0.40$) related to FCR. However, the distal ileal disappearance rate ratio was quadratically related to FCR ($r = 0.458; \ P = 0.01$) as expressed in the following equation:

$$y(FCR) = 5.239 + 0.980 \times \text{ratio}^2 - 3.823 \times \text{ratio}.$$  

It may be deduced from the quadratic regression equation that an optimum starch: protein disappearance rate of 1.95 would generate the minimal FCR of 1.511 as shown in Figure 2. A relative excess in the disappearance rate of either component would disturb this balance and depress feed conversion efficiency.

A more recent study [25] investigated the impacts of fishmeal and corn starch inclusions in sorghum-soybean meal diets for broiler chickens. Instructively, proximal jejunal starch: protein disappearance rate ratios were quadratically related to weight gain ($r = 0.849; \ P < 0.001$) and FCR ($r = 0.838; \ P < 0.001$) from 15 to 28 d post-hatch, as shown in Figures 3 and 4, respectively. It may be deduced from the relevant equations that a disappearance rate ratio of 3.59:1 would generate the maximum weight gain of 1265 g/bird and a similar, but not identical, ratio of 3.88:1 would generate the minimum FCR of 1.287. It is noteworthy that these theoretical values surpass Ross 308 performance objectives by 22.7% (1265 vs. 1031 g/bird) in weight gain and by 16.8% (1.287 vs. 1.546) in...
The quadratic relationship between starch: protein disappearance rate ratios in the proximal jejunum with weight gain ($r = 0.849; P < 0.001$) in broiler chickens from 15 to 28 d post-hatch [25].

Figure 4. The quadratic relationship between starch: protein disappearance rate ratios in the proximal jejunum with FCR ($r = 0.838; P < 0.001$) in broiler chickens from 15 to 28 d post-hatch [25].

FCR. The outcomes of both studies confirm the relevance of starch and protein digestive dynamics in poultry and demonstrate the potential advantages to be gained from harnessing digestive dynamics.

CATABOLISM OF AMINO ACIDS AND GLUCOSE IN THE GUT MUCOSA

Amino acids are considered to be critical energy sources for the gut mucosa [26]. However, whether the regulation of these pathways may be manipulated by dietary strategies then remained to be investigated; essentially, this remains the case in poultry. The processes of the digestive tract may account for more than 20% of incoming dietary energy [4]. As a consequence, either glucose or amino acids, probably glutamate and glutamine in particular, are catabolized in avian enterocytes for energy provision during their transition across the gut mucosa to meet the energy demand of the gut [3]. Thus, glucose and amino acids are denied entry into the portal circulation to varying extents. In rats, glucose and glutamine provide similar proportions of energy to the gut mucosa but the likelihood is that energy is derived more efficiently from glucose than amino acids [27]. The proportion of dietary amino acids that are catabolized may be in the order of 20%, which is potentially importance. This estimate is based on data where the net portal outflow of ammonia accounted for 18% of total amino acid nitrogen in the diet in young pigs [28]. It has been suggested that catabolism of branched-chain amino acids in the gut mucosa in pigs may play an important role in regulating the balance of dietary amino acids that gain entry into the portal circulation [29]. The probability is that if the glucose to amino acid “catabolic ratio” in the gut mucosa can be manipulated so that more glucose undergoes catabolism then more amino acids would be spared to enter the portal circulation and become available for protein accretion and energy would be derived more efficiently from glucose.

The relevance of concentrations of free amino acids in the portal circulation was illustrated in a preliminary investigation [30]. Free concentrations of threonine in plasma from the anterior mesenteric vein were positively correlated with weight gain ($r = 0.915; P < 0.001$) and negatively correlated with FCR ($r = 0.773; P < 0.01$) in broilers from 7 to 28 d post-hatch. The caveat is that the threonine in the portal circulation could have been derived from either the gut lumen or the arterial blood supply to the gut mucosa. In poultry [31], concentrations of free amino acids in the portal circulation derived from oligopeptides of fishmeal and soybean meal were reported to be higher than from cottonseed and rapeseed meals. Also the profile of portal free amino acid concentrations was more similar to the oligopeptide profile in the case of fishmeal and soybean meal. This indicates that the digestive dynamics of protein/amino acids vary between dietary protein sources.

The manipulation of the “catabolic ratio” of starch to protein in the gut mucosa by dietary strategies may become a pivotal issue. Moreover, there is some evidence in pigs to indicate that the dietary provision of slowly digestible starch
Table 2. Net portal flux (mmol) of amino acids in pigs offered diets containing either maize starch or pea starch [32].

<table>
<thead>
<tr>
<th>Amino acid</th>
<th>Maize starch starch</th>
<th>Pea starch starch</th>
<th>Difference (%)</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arginine</td>
<td>17.1</td>
<td>20.1</td>
<td>17.5</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Histidine</td>
<td>7.2</td>
<td>8.6</td>
<td>19.4</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>19.8</td>
<td>24.0</td>
<td>21.2</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Leucine</td>
<td>35.0</td>
<td>40.9</td>
<td>16.9</td>
<td>NS</td>
</tr>
<tr>
<td>Lysine</td>
<td>24.1</td>
<td>31.0</td>
<td>28.6</td>
<td>P &lt; 0.05</td>
</tr>
<tr>
<td>Methionine</td>
<td>8.4</td>
<td>9.6</td>
<td>14.3</td>
<td>NS</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>19.5</td>
<td>22.8</td>
<td>16.9</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Threonine</td>
<td>10.9</td>
<td>15.2</td>
<td>39.4</td>
<td>NS</td>
</tr>
<tr>
<td>Tryptophan</td>
<td>2.6</td>
<td>3.7</td>
<td>42.3</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Valine</td>
<td>22.1</td>
<td>28.6</td>
<td>29.4</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Alanine</td>
<td>57.2</td>
<td>65.4</td>
<td>14.3</td>
<td>NS</td>
</tr>
<tr>
<td>Aspartic acid</td>
<td>3.7</td>
<td>2.6</td>
<td>-29.7</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Asparagine</td>
<td>22.3</td>
<td>23.3</td>
<td>4.48</td>
<td>NS</td>
</tr>
<tr>
<td>Cysteine</td>
<td>1.9</td>
<td>2.8</td>
<td>47.4</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Glutamic acid</td>
<td>-7.4</td>
<td>-8.8</td>
<td>-18.9</td>
<td>NS</td>
</tr>
<tr>
<td>Glutamine</td>
<td>-66.2</td>
<td>-62.9</td>
<td>4.98</td>
<td>NS</td>
</tr>
<tr>
<td>Glycine</td>
<td>23.1</td>
<td>25.5</td>
<td>10.4</td>
<td>NS</td>
</tr>
<tr>
<td>Proline</td>
<td>12.7</td>
<td>14.6</td>
<td>15.0</td>
<td>NS</td>
</tr>
<tr>
<td>Serine</td>
<td>25.8</td>
<td>28.8</td>
<td>11.6</td>
<td>P &lt; 0.10</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>13.5</td>
<td>16.7</td>
<td>23.7</td>
<td>P &lt; 0.05</td>
</tr>
<tr>
<td>Mean</td>
<td>12.7</td>
<td>15.6</td>
<td>22.8</td>
<td></td>
</tr>
</tbody>
</table>

can influence the transport of amino acids into the portal circulation [32]. Overall, the transition from maize to pea starch increased the mean net portal flux of 20 amino acids by 22.8%, from 12.7 to 15.6 mmol, and the details are shown in Table 2. It was concluded that more glucose was used as an oxidative substrate by the gut mucosa following the feeding of slowly digestible pea starch thereby permitting more amino acids to enter the portal circulation as they were spared from catabolism in the gut mucosa.

Somewhat contradictory findings in pigs have been reported [33]. These researchers investigated the impacts of maize starch and sticky rice starch on the ileal digestibility and concentrations in systemic blood samples of amino acids derived from zein. Sticky rice starch (81.9% digested in the proximal jejunum) was more rapidly digested than maize starch (47.2%). Interestingly, sticky rice starch supported higher mean ileal digestible coefficients of 18 amino acids by 7.21% (0.818 vs. 0.763) in comparison to maize starch as shown in Table 3. Also mean concentrations of amino acids in systemic serum samples were higher in birds offered diets containing sticky rice starch by 14.2% (258 vs. 226 mmol/l) in comparison to maize starch as shown in Table 4. Thus, this study suggests that rapidly digestible starch will enhance the ileal digestibility of amino acids. One possible explanation put forward by the researchers was that increases in gut viscosity prompted by maize starch, relative to sticky rice starch, impeded protein digestion and amino acid absorption.

In a subsequent poultry study [34], the addition of 500 fytase units/kg phytase significantly increased proximal jejunal starch digestibility coefficients by 26.6% (0.681 vs. 0.538) and increased starch disappearance rates in the proximal jejunum by 33.6% (35.8 vs. 43.4 g/bird/d) in corn-based diets. However, this alteration to starch digestive dynamics was associated with pronounced increases in proximal jejunal amino acid digestibility coefficients; the mean digestibility of 16 amino acids was increased by 49.7% (0.720 vs. 0.481) and the increase for each amino acid was highly significant (P < 0.001).

Thus, increases in amino acid digestibility coefficients in the distal ileum in pigs [33] and proximal jejunum in poultry [34] were both associated with accelerated starch digestion rates. Given these associations are valid, it is tempting to conjecture that they may be related to the insertion of the glucose transporter GLUT-2
into the apical membrane of enterocytes [35].

Classically, glucose is co-absorbed with sodium into enterocytes via the Na^+^-dependent transporter SGLT-1 [36]. However, the insertion of GLUT-2 into the apical membrane may increase intestinal uptakes of glucose by a 2- or even a 3-fold factor [37, 38]. Thus, in the event of increased quantities of starch being digested and glucose being made available for absorption, the insertion of GLUT-2 into the apical membrane of enterocytes might reduce the dependence of glucose absorption via Na^+^-dependent SGLT-1 transporters and, in turn, permit increased co-absorption of amino acids and sodium via
Na\(^+\)-dependent transport systems orientated toward amino acids. However, regardless of the underlying mechanisms, it is evident that starch and protein digestive dynamics are interactive and should not be considered in isolation.

**SLOWLY DIGESTIBLE STARCH**

The slowly digestible starch concept has been reviewed in overall terms [39]. It has been claimed [40] that dietary provisions of slowly digestible starch (starch digested in distal jejunum, proximal, distal ileum) enhance broiler performance relative to rapidly digestible starch (starch digested in proximal jejunum). In the comparison [40], slowly digestible starch significantly improved body weight by 5.44% (1823 vs. 1729 g/bird) and FCR by 2.42% (1.734 vs. 1.777) in birds to 38 d post-hatch. However, there were tangible differences between the formulations of the dietary treatments containing either high or low amounts of slowly digestible starch; thus, the growth performance advantages observed cannot be attributed to slowly digestible starch entirely. Steam-flaking feed grains have been shown to accelerate starch digestion under in vitro conditions [41]. A comparison of unprocessed vs. processed (pelleting and expansion) blends of corn and peas as starch sources in broiler diets on the basis that processing would accelerate starch digestion rates has been completed [42]. The unprocessed, slowly digestible starch diet supported a numerical improvement in FCR of 2.50% (1.675 vs. 1.718) from 14 to 30 d post-hatch in this study.

In a further study [43], diets based on corn and tapioca were compared with diets based on corn and peas, as pea starch is digested more slowly than tapioca starch. The 2 basal diets contained 5 concentrations of digestible lysine ranging from 8.50 to 11.00 g/kg. The slow-starch corn-peas diet supported significant improvements of 1.28% in weight gain (473 vs. 467 g/bird) and 3.19% in FCR (1.366 vs. 1.411) in comparison to the rapid-starch corn-tapioca diets from 9 to 18 d post-hatch as a main effect. However, there was a significant interaction between starch digestion rates and digestible lysine concentrations where the most robust FCR response to slowly digestible starch was an improvement of 4.33% (1.414 vs. 1.478). This was observed at the lowest lysine level of 8.50 g/kg. The implication is that the impact of slowly digestible starch sparing amino acids from catabolism in the gut mucosa was declared most in diets containing inadequate protein/amino acid levels. However, a considerable amount of further research in this area is required for verification.

In a study in which broiler chickens were offered “all-sorghum” (> 900 g/kg) diets [44], the dietary inclusion of a sulfite reducing agent (5.0 g/kg sodium metabisulfite) decreased the amount of rapidly digestible starch from 293 to 246 g/bird but increased the amount of slowly digestible starch from 88 to 100 g/bird from 14 to 21 d post-hatch. This increase in slowly digestible starch was associated with a significant improvement in AME of 0.53 MJ (14.94 vs. 14.41 MJ/kg; \(P < 0.01\)) and a numerical improvement in N retention.

Broiler diets essentially based on diverse wheat varieties with different starch digestion rates have been compared [45]. Starch digestion rates (KDS) influenced weight gain and FCR in a quadratic manner with an optimal KDS in the order of 2.2/h for bird growth. This outcome suggests that there may be an ideal balance between rapidly and slowly digestible starch to maximize broiler performance, but this balance is probably influenced by digestion rates of protein.

**RAPIDLY DIGESTIBLE PROTEIN**

As mentioned earlier, the starch digestion rate was 67% higher than the protein (N) digestion rate in a study where broilers were offered sorghum-based diets [20]. One tenet of digestive dynamics is the proposition that starch is digested too rapidly, and protein too slowly, and it would be beneficial to correct this imbalance. Moreover, if slowly digestible starch is advantageous then the reciprocal, or rapidly digestible protein, may be equally or even more advantageous.

The impact of providing rapidly digestible protein in diets for male broiler chickens has been investigated [46]. In the 220 g/kg protein “slow” foundation diet, protein was derived from soybean and canola meals, corn, and limited quantities of synthetic lysine, methionine, and threonine. The 208.6 g/kg protein “rapid” summit diet contained less soybean meal but was...
fortified with 50 g/kg casein and additional synthetic amino acids (arginine, isoleucine, lysine, methionine, threonine, tryptophan) so that digestible amino acid levels in the dietary treatments were comparable. An equal blend of these 2 diets was used as an intermediate treatment so that linear effects of protein digestion rates could be established. These diets were offered from 7 to 28 d post-hatch and the summit diet generated numerical improvements in weight gain by 4.48% (1610 vs. 1541 g/bird) and FCR by 1.76% (1.450 vs. 1.476) relative to the foundation diet.

The summit diet linearly increased protein (N) digestibility coefficients and disappearance rates in the distal jejunum, proximal ileum, and distal ileum to highly significant extents. However, rapidly digestible protein also significantly rates in the distal jejunum, proximal ileum, and (N) digestibility coefficients and disappearance (1.450 vs. 1.476) relative to the foundation diet.

The summit diet significantly increased starch digestibility coefficients in both ileal segments ($P < 0.005$) and starch disappearance rates in all 4 small intestinal segments ($P < 0.01$). This was associated with significant linear improvements in nutrient utilization (AME, ME: GE ratios, N retention, AMEn) with the transition from slowly to rapidly digested protein diets. Thus, this study [46] demonstrates the relevance and complexities of starch and protein digestive dynamics in poultry and the advantages of rapidly digestible protein sources.

A direct comparison of the impact of the “rapid” summit diet and the “slow” protein foundation diet on amino acid concentrations in the portal circulation is instructive [46]. The summit diet significantly increased concentrations of free methionine by 42.2% ($P < 0.001$), threonine by 39.1% ($P < 0.001$), and proline by 23.2% ($P = 0.01$) in plasma taken from the anterior mesenteric vein on the basis of pairwise comparisons. Methionine and threonine are 2 of the first 3 limiting amino acids in poultry diets. Alternatively, glycine concentrations were decreased by 20.3% ($P = 0.004$) and the balance of amino acids was not influenced ($P > 0.125$) by the transition from foundation to summit diets. Six amino acids were present in the summit diet in both synthetic and protein-bound forms, and the transition from slow to rapid protein diets increased their collective concentrations in the portal circulation by 17.4% from 219 to 257 μg/mL. In contrast, there were 12 protein-bound amino acids in the summit diet and the transition fractionally decreased their concentrations by 0.84% (709 vs. 715 μg/mL). Although not conclusive, this contrast is consistent with the possibility that crystalline amino acids are less prone to catabolism in the gut mucosa than their protein-bound counterparts. Possibly because synthetic amino acids are rapidly absorbed in the anterior small intestine, where more glucose is available as an alternative energy substrate, and are, therefore, spared from catabolism. Thus, this preliminary investigation into free amino acid plasma concentrations in the portal circulation suggests that accelerating protein digestion rates may favorably manipulate the catabolic ratio between amino acids and glucose.

Ileal digestibilities of amino acids from fishmeal and soybean meal are comparable in poultry [47]. However, a study based on sorghum-soybean diets in which either soybean meal was partially substituted by fishmeal (175 g/kg) or sorghum was partially substituted by maize starch (200 g/kg) has been completed [25]. This 2 x 2 factorial array of dietary treatments was offered to broiler chicks from 15 to 28 d post-hatch. As a main effect, fishmeal significantly increased ($P < 0.001$) protein (N) digestibility coefficients in the proximal ileum by 12.2% (0.706 vs. 0.629) and in the distal ileum by 13.9% (0.728 vs. 0.639). There were corresponding significant increases ($P < 0.001$) in protein (N) disappearance rates in the proximal ileum of 13.8% (19.0 vs. 16.7 g/bird/d) and in the distal ileum of 16.5% (19.8 vs. 17.0 g/bird/d). Thus, in this study fishmeal protein was more rapidly and extensively digested than soy protein. However, fishmeal significantly increased ($P < 0.001$) starch digestibility coefficients in the proximal jejunum by 70.1% (0.597 vs. 0.351), in the distal jejunum by 37.6% (0.809 vs. 0.588), in the proximal ileum by 26.7% (0.902 vs. 0.712), and in the distal ileum by 18.9% (0.937 vs. 0.788). The unexpected but pronounced impacts of fishmeal on starch digestibility were effectively validated by the significant relationships between starch digestibilities and parameters of growth performance and nutrient utilization. However, it is noteworthy that dietary fishmeal inclusions increased total retention times in 4 small intestinal segments from 210 to 289 min and total retention times were positively correlated with distal ileal starch
digestibility coefficients ($r = 0.759; P < 0.001$). In addition, there were significant, positive correlations between retention times and starch digestibility coefficients in each of the 4 small intestinal segments. The mechanisms whereby fishmeal increased retention times along the small intestine are not clear, but this impact coupled with remarkably low starch digestibility coefficients of the basal sorghum-soybean appeared to be involved in these outcomes. In contrast, the substitution of grain sorghum with corn starch did not influence starch digestibilities, which was not anticipated. It is again evident in this study [25] that starch and protein digestive dynamics are interdependent and should not be considered in isolation.

**STARCH–PROTEIN INTERACTIONS**

The importance of starch–protein interactions that occur in the endosperm of feed grains is recognized [48], although these interactions have yet to be fully defined [19]. In this context, sorghum is probably the most relevant feed grain where biophysical and biochemical interactions between kafirin protein bodies and starch granules in sorghum endosperm almost certainly impede starch digestion and energy utilization in poultry [49]. However, the subject of starch–protein interactions should not be confined to the endosperm of feed grains and these interactions can probably be triggered by both steam-pelleting of poultry diets and the passage of digesta along the digestive tract, perhaps especially in the gizzard, which would be amplified by whole grain feeding [50]. Also, more specifically, glucose–amino acid interactions in the gut lumen may hold equal or more relevance than starch–protein interactions.

A vivid example of starch–protein interactions occurring in poultry is provided in one study [51], which investigated the impact of digestive dynamics in broiler chickens offered low-protein diets. The positive control diet contained 465 g/kg maize grain but this was reduced to 100 g/kg in 5 low-protein diets containing various additions of supplemental amino acids coupled with an average inclusion of 479 g/kg maize starch. This had the net effect of increasing the analyzed starch concentration of the control diet from 269 g/kg in the control diets to 436 g/kg in the 5 low-protein diets and decreasing the analyzed protein (N) concentration of the control diet from 219 g/kg to an average of 199 g/kg in the 5 low-protein diets. As a consequence, the distal ileal starch digestibility coefficient in the control diet was significantly increased by 10.9% (0.968 vs. 0.873) in the 5 low-protein diets but the distal ileal protein (N) digestibility coefficient in the control diet was significantly decreased by 6.36% (0.721 vs. 0.770) in the 5 low-protein diets. In general terms, amino acid digestibilities were compromised in the 5 low-protein diets despite the supplemental amino acid inclusions, which are notionally 100% bioavailable [52]. For example, the transition from positive control to 5 low protein diets reduced average distal ileal digestibility coefficients of lysine by 4.12% (0.814 vs. 0.849), methionine by 2.93% (0.894 vs. 0.921), and threonine by 7.06% (0.698 vs. 0.751). As a consequence of the higher starch contents and higher starch digestibilities in the low-protein diets, the starch disappearance rate in the distal ileum was increased by 91% from 22.1 g/bird/d in the positive control diet to an average of 42.2 g/bird/d in the 5 low-protein diets. Thus glucose absorption along the small intestine was nearly doubled by the dietary transition and this glucose “overload” appeared to compromise the absorption of amino acids, which raises the real possibility that there is competition for intestinal uptakes between glucose and amino acids.

**Competition for Intestinal Uptakes Between Glucose and Amino Acids**

The opinion has been expressed that the regulation of sugar and amino acid transport in the intestine constitutes a neglected area [53]. The role of transporters in the gastrointestinal tract involved in the absorption of glucose and peptides has been reviewed [54], and the possibility that there are interactions between glucose and peptides transporters has been advanced [55].

Leptin has been shown to regulate both SGLT-1 glucose transport and some specific amino acid transport systems in human intestinal cells [56]. The possibility that there is a competition between glucose and amino acids
for intestinal uptakes of nutrients in broiler chickens is an attractive proposition given the limited amount of time digesta is retained along the small intestine. Average retention times of 25, 36, 51, and 53 min in the proximal and distal jejunum, proximal and distal ileum, respectively have been reported [57]. Thus, in sorghum-based diets steam-pelleted at 3 different conditioning temperatures digesta was retained in 4 small intestinal segments for a total of only 2.8 h. The likelihood is that intestinal uptakes of nutrients by both Na⁺-independent and perhaps Na⁺-dependent transport systems especially could simply become overloaded resulting in compromised intestinal uptakes of glucose and amino acids. Several review papers hold relevance [58–60] and, subsequently, the mutual inhibition of intestinal absorption for sugars and amino acids was specifically discussed [2].

It is also probable that there are interactions between amino acids for intestinal uptakes. The addition of 1.8 g/kg lysine, as lysine HCl, to broiler diets based on a wheat-sorghum blend significantly increased \((P < 0.02 \text{ to } <0.001)\) the ileal digestibility of 8 amino acids [61]. These included (increases in parentheses) isoleucine (4.07%), lysine (5.42%), methionine (1.10%), phenylalanine (5.45%), valine (4.29%), aspartic acid (3.89%), glutamic acid (2.97%), and tyrosine (3.81%). Earlier, the effects of enriching broiler diets with lysine on lysine transport in the jejunal brush-border membrane were investigated [62] and both \(b_o, +\) and \(y^-\)-like transport systems were upregulated by dietary lysine; both these transport systems are Na-independent. The \(b_o, +\)-like transport system has a broad specificity incorporating cationic and neutral amino acids and playing a key role in the intestinal absorption of amino acids [63]. Thus, it follows that when the \(b_o, +\)-like system, in particular, is upregulated by dietary lysine enrichment, then there is the possibility that absorption of certain other amino acids will be influenced.

Researchers suggested that slowly digestible starch may generate more sustained insulin peaks that would benefit broiler performance [40]. Glucose absorption generates insulin secretion from the pancreas but the role of this powerful peptide hormone in avian species needs clarification. Blood glucose levels in chickens are considerably higher than in most mammals [64] and chickens exhibit a relative resistance to insulin and higher levels are required to obtain hypoglycemic effects than in mammals [65]. That there are fundamental differences in avian and mammalian responses to insulin is generally accepted although there is the contention that broiler chickens are an instructive model to investigate the roles of insulin [66]. Potentially, insulin may both depress hepatic gluconeogenesis and promote net protein accretion in poultry. Glucose uptakes by skeletal muscle in broilers were found to be doubled within 10 min of insulin administration [67]. This suggests that an insulin-responsive glucose transport mechanism is present in chickens despite the absence of the GLUT-4 homologous gene, the insulin-responsive glucose transporter in mammals. The role of insulin-like growth factors in poultry has been reviewed [68]. Clarification of these roles would be desirable as, according to the review, insulin-like growth factors may be involved in the etiology of disease states associated with rapid growth in poultry. Interestingly, insulin-like growth factor has been reported to promote lean growth and feed efficiency in broiler chickens that was attributed, in part, to the attenuation of rates of protein breakdown [69]. Therefore, a better comprehension of the starch–insulin axis in avian physiology is necessary to interpret its impacts on digestive dynamics with certainty.

**THE STARCH–GLUCOSE–INSULIN AXIS IN BROILER CHICKENS**

The benefits of slowly digestible starch may be due, in part, to its positive influence on the starch–glucose–insulin axis in poultry. Researchers suggested that slowly digestible starch may generate more sustained insulin peaks that would benefit broiler performance [40]. Glucose absorption generates insulin secretion from the pancreas but the role of this powerful peptide hormone in avian species needs clarification. Blood glucose levels in chickens are considerably higher than in most mammals [64] and chickens exhibit a relative resistance to insulin and higher levels are required to obtain hypoglycemic effects than in mammals [65]. That there are fundamental differences in avian and mammalian responses to insulin is generally accepted although there is the contention that broiler chickens are an instructive model to investigate the roles of insulin [66]. Potentially, insulin may both depress hepatic gluconeogenesis and promote net protein accretion in poultry. Glucose uptakes by skeletal muscle in broilers were found to be doubled within 10 min of insulin administration [67]. This suggests that an insulin-responsive glucose transport mechanism is present in chickens despite the absence of the GLUT-4 homologous gene, the insulin-responsive glucose transporter in mammals. The role of insulin-like growth factors in poultry has been reviewed [68]. Clarification of these roles would be desirable as, according to the review, insulin-like growth factors may be involved in the etiology of disease states associated with rapid growth in poultry. Interestingly, insulin-like growth factor has been reported to promote lean growth and feed efficiency in broiler chickens that was attributed, in part, to the attenuation of rates of protein breakdown [69]. Therefore, a better comprehension of the starch–insulin axis in avian physiology is necessary to interpret its impacts on digestive dynamics with certainty.

**THE CHALLENGE OF HIGH SUPPLEMENTAL AMINO ACID INCLUSIONS IN BROILER DIETS**

There is considerable interest in the successful development of low-protein diets because of their potential economic, environmental, and bird welfare advantages. Axiomatically low-protein diets will contain high levels of supplemental amino acids. Almost certainly, an expanding array of supplemental amino acids
will be incorporated into broiler diets and this development should have profound impacts on the digestive dynamics of protein and amino acids [18]. Intestinal uptakes of supplemental amino acids are more rapid and take place more proximally in the small intestine than the corresponding protein-bound amino acids. Supplemental amino acids do not undergo digestion and are directly available for absorption in the upper small intestine and appear in the portal circulation more rapidly than protein-bound amino acids [70]. This may apply to branched-chain amino acids in particular as their digestion rates are relatively slow due to their hydrophobicity [71]. The digestion rate constants of branched-chain amino acids were lower than all protein-bound amino acids, with the exception of tyrosine, in broilers offered sorghum-based diets [57]. It seems possible that supplemental amino acids would be less likely to undergo catabolism in the gut mucosa than their protein-bound counterparts which is just one of the many questions that need to be addressed if the challenge of low-protein diets is going to be met.

CONCLUSIONS

1. The contention of this review is that digestive dynamics of starch and protein are of relevance to chicken-meat production.

2. A better understanding of the underlying mechanisms whereby starch and protein digestive dynamics influence the performance of broiler chickens is required; this certainly represents a challenge due to the complexity of the topic. Nevertheless, there is the potential to formulate poultry diets that will be more efficiently utilized when digestive dynamics can be taken into consideration.

3. It would appear that the formulation of diets based on static ileal amino acid digestibilities can only be improved by the incorporation of kinetic parameters into the relevant computer programs.

4. Moreover, the likelihood is that the relevance of starch and protein digestive dynamics will become increasingly apparent if the challenge of successfully developing low-protein diets is to be met in the future.

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