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The Effect of Feeding Level and Physiological Status on Total Flow and Amino Acid Composition of Endogenous Protein at the Distal Ileum in Swine[1,2]

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ABSTRACT: An experiment was conducted to investigate the effects of BW, feed intake, and the physiological condition of the animal on the loss and amino acid composition of endogenous protein in swine. Ten growing barrows and five multiparous sows were equipped with a T-cannula in the distal ileum for digesta collection. A protein-free diet was fed to all animals. The barrows were given free access to the experimental diet. The sows also were allowed to consume the diet on an ad libitum basis, and digesta were collected during lactation and in the following gestation period. In addition, digesta from the gravid sows were collected after restricting the sows to 2 kg of feed per day. For each animal group, the endogenous losses of protein and amino acids were calculated in relation to DMI, and the amino acid composition of endogenous protein was calculated. The total endogenous gut protein loss at the distal ileum of growing pigs, lactating sows, and gestating sows, given free access to feed, was 12.4, 9.4, and 11.2 g/kg DMI, respectively. These values were not different ($P > .10$). However, when gestating sows were fed only 2 kg/d, 17.8 g of endogenous protein was lost per kilogram of DMI, which was higher ($P < .05$) than for any of the other groups. This difference was mainly caused by higher ($P < .05$) losses of glycine, proline, and serine. There were no differences ($P > .05$) in amino acid composition of endogenous protein between growing pigs, lactating sows, and gestating sows given free access to feed, but restricted-fed gestating sows had an amino acid composition of endogenous protein that was significantly different from that of the other groups. The results from the experiment showed that age, BW, and the physiological condition of the animal have little or no effect on the amount of endogenous protein and amino acids lost at the distal ileum of hogs if calculated in relation to DMI. Likewise, the amino acid composition was not affected by the BW or physiological condition of the animal. However, DMI had a significant effect on endogenous protein losses in sows as well as on amino acid composition of endogenous protein.

Key Words: Sows, Endogenous Protein, Amino Acids, Feed Intake

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Introduction

Estimates of endogenous protein losses in pigs are needed to determine true or standardized ileal digestibility coefficients for feed ingredients. Because the total amount and amino acid composition of protein is altered in the hindgut, protein and amino acid losses should be determined at the distal ileum (Sauer and Ozimek, 1986; Sauer and de Lange, 1992).

Several factors influence the amount of endogenous protein and amino acids recovered at the distal ileum in pigs (Souffrant, 1991; Tamminga et al., 1995; Boisen and Moughan, 1996). Nutritional factors such as the source and amount of fiber (Larsen et al., 1993; Schulze et al., 1994, 1995b; Leterme et al., 1996b), fat (Imbeah and Sauer, 1991; Li and Sauer, 1994), CP (Poppe et al., 1983; Bartelt et al., 1994), and antinutritional factors (le Guen et al., 1995; Schulze et al., 1995a) may increase the amount of endogenous losses at the distal ileum. The total DMI may also affect endogenous amino acid losses (Fuller and

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Cadenhead, 1991; Furuya and Kaji, 1992; Butts et al., 1993).

Nutrient digestibilities and endogenous protein losses are usually determined in weanling or growing pigs. Nevertheless, these numbers are applied to all categories of swine, and it has been proposed that the amount of endogenous losses as well as the amino acid composition of endogenous protein is constant regardless of the BW of the animal (Boisen and Moughan, 1996). However, to the best of our knowledge, the hypothesis that values for endogenous losses obtained in growing pigs also can be applied to gestating and lactating sows has never been tested. Likewise, it is not documented that the amino acid composition of endogenous protein is constant, regardless of the physiological status of the animal. The objective of the present work was to test these hypotheses.

Materials and Methods

Animals and Housing

Ten growing barrows (initial BW: 94 ± 3.9 kg) arising from the matings of Camborough 15 sows to PIC line 326 boars (PIC, Franklin, KY) were used to measure endogenous protein losses for growing pigs. Five adult sows (Camborough 15, PIC) were used to determine endogenous losses for sows under different physiological conditions and subjected to different feeding regimens. All animals were equipped with a T-cannula surgically installed in the distal ileum. Pigs were cannulated at an average BW of 42 kg (± 4 kg), and they had been used in a different experiment prior to the present one. Sows were cannulated in the previous gestation period on d 40 (± 5 d) according to the procedure described previously (Stein et al., 1998).

Pigs and gestating sows were penned individually in 5- × 5-m pens with a partly slatted concrete floor. A feeder was suspended at the front of each pen, and water was available 24 h a day from a nipple drinker suspended at one of the side panels. The barn temperature was maintained at a minimum of 16°C. Lactating sows were housed in regular farrowing stalls (.66 × 2.13 m) located on a plastic-coated expanded-metal floor. The farrowing barn was environmentally regulated, and the temperature was maintained at approximately 22°C. The farrowing stalls had horizontal bars and vertical fingers on the lowest side-bar. A feeder and a nipple drinker was suspended at the front of the stall, and water was available at all times.

The experiment was approved by the University of Illinois Laboratory Animal Care Committee (protocol no. A3S-164).

Diets and Feeding

A cornstarch-based protein-free diet (Table 1) was formulated. Vitamins, minerals, soybean oil, and Solka floc (a source of fiber) were included in the diet. Sucrose (5%) was added to the diet to enhance palatability, and chromium oxide was included as an indigestible marker at a level of .25%.

Table 1. Composition (as feed) of the experimental diet[a]

Ingredient	g/100 g
Cornstarch	81.6
Soybean oil	4.0
Sucrose	5.0
Solka floc[b]	5.0
Dicalcium phosphate	3.2
Limestone	.4
Trace mineral salt[c]	.35
Vitamin premix[d]	.2
Chromium oxide	.25

[a]7 g of Ca and 6 g of P/kg of diet.
[b]James River, Berlin, NH.
[c]The trace mineral salt provided the following quantities of minerals per kilogram of diet: Se, .30 mg; I, .35 mg; Cu, 8 mg; Mn, 20 mg; Fe, 90 mg; Zn, 100 mg; and NaCl, 2,730 mg.
[d]The vitamin premix provided the following quantities of vitamins per kilogram of diet: Vitamin A, 5,250 IU; vitamin D_3, 525 IU; vitamin E, 40 IU; menadione K, 2 mg; vitamin B_{12}, .016 mg; riboflavin, 4 mg; D-pantothenic acid, 11 mg; niacin, 15 mg; and choline chloride, 110 mg.

The experiment consisted of four collection periods. Digesta from the growing pigs were collected once, and digesta from the sows were collected in lactation and twice in gestation. The growing pigs and the lactating sows were allowed ad libitum access to the experimental diet. Gestating sows were restricted to 2 kg feed/d fed in two equal meals at 0800 and 2000 in the first collection period, but the diet was fed to appetite in the second collection period. However, only four sows were used in this last period.

All animals were fed the experimental diet for 7 d, and digesta were collected over two 12-h periods on d 6 and 7 as previously described (Stein et al., 1998). Samples from the growing pigs and restricted-fed gestating sows were collected over a 5-wk period, and two pigs or one sow was fed the experimental diet each week. Likewise, samples from the gestating sows allowed ad libitum access to the diet were collected over a 4-wk period. Digesta from lactating sows were collected over a 5-wk lactation period; samples from one sow were collected each week. Digesta from restricted-fed gestating sows and from gestating sows fed to appetite were collected in midgestation.

Sample Analysis

Samples were frozen immediately after being collected. At the end of the experiment, digesta samples were thawed and mixed within animal in each physiological state and feeding level, and a subsample was removed and frozen. Prior to chemical analysis, samples were freeze-dried and finely ground. Proximate analyses were performed on all samples accord-

ing to AOAC procedures (AOAC, 1990). The amino acid content of feed and digesta samples was determined by HPLC using a Beckman 6300 Amino Acid Analyzer (Beckman Instruments Corp., Palo Alto, CA) using ninhydrin for postcolumn derivatization (AOAC, 1990). Norleucine was used as the internal standard. All samples were hydrolyzed for 24 h at 110°C with 6 *N* HCl prior to amino acid analysis. Sulfur-containing amino acids were analyzed after cold performic acid oxidation overnight and subsequent hydrolysis. Tryptophan was determined after alkaline hydrolysis for 22 h at 110°C.

The chromium content of feed, feces, and digesta was determined by atomic spectrophotometry (Williams et al., 1962).

Calculations and Statistical Analysis

Data for feed intake were summarized at the end of each collection period, and average daily feed intake during the collection period was calculated for each pig and period on a total basis as well as in relation to the metabolic body weight ($kg^{.75}$) of the animals.

The endogenous flow of each amino acid was calculated for each animal and period as milligrams lost per kilogram of DMI using the following formula (Moughan et al., 1992): EAL = [AAd × (Crf/Crd)], where EAL is the total endogenous loss of an amino acid (mg/kg DMI), AAd is the concentration of that amino acid in digesta DM, and Crf and Crd are the chromium content in feed DM and digesta DM, respectively. The same formula was used to calculate the loss of protein.

The amino acid composition of endogenous protein was calculated for each animal group by expressing each amino acid as a percentage of total endogenous protein.

Results were subjected to analysis of variance using PROC GLM of SAS (1989), and treatment means were separated using the least significant difference test.

Results

Animals remained healthy throughout the experiment and readily consumed their diets (Table 2). Growing pigs consumed an average of 2.67 kg/d of feed, but lactating sows and gestating sows given free access to feed consumed more ($P < .05$), 5.05 and 4.35 kg/d, respectively. However, if feed intake was calculated in relation to metabolic BW of the animals, there were no differences in daily feed intake ($P > .05$) among these three groups. Restricted-fed gestating sows were allowed to eat only 2 kg of feed/d, which was less ($P < .05$) than what sows given free access to feed consumed on a daily basis as well as in relation to metabolic BW.

All animals lost weight during the week they were fed the protein-free diet (Table 2). Lactating sows lost more weight ($P < .05$) than did any of the other groups during this week.

Endogenous losses of amino acids and protein for each animal group are presented in Table 3. Numerically, the endogenous protein loss of lactating sows was lower than, but not significantly different ($P = .11$) from, that of growing pigs or gestating sows given free access to feed. However, lactating sows had the numerically lowest loss of all amino acids except for tryptophan and glycine compared with the other groups. Of the indispensable amino acids, the loss of arginine, isoleucine, lysine, methionine, and valine in lactating sows was lower ($P < .05$) than in growing pigs and gestating sows that were fed only 2 kg/d. Likewise, the losses of all dispensable amino acids except proline, glycine, and serine were lower ($P < .05$) in lactating sows than in growing pigs. Except for isoleucine, the losses of protein and amino acids in lactating sows were not different ($P > .05$) from those obtained in gestating sows given free access to feed.

The gestating sows fed only 2 kg/d had a greater ($P < .05$) loss of endogenous protein than any of the other groups. Likewise, with the exception of isoleucine, the losses of all amino acids were numerically higher in restricted-fed sows than in other groups, and the loss of arginine, histidine, glycine, proline, and serine was higher ($P < .05$) than for any of the other groups.

No differences ($P > .05$) in the amino acid composition of endogenous protein from lactating sows and gestating sows given free access to feed was observed. Furthermore, the amino acid composition of endogenous protein from these two groups was not different ($P > .05$) from the composition of endogenous protein in growing pigs, except for glycine, in lactating sows, which contributed more ($P < .05$) to total protein losses than in any of the other groups (Table 4). The amino acid composition of endogenous protein in gestating sows fed only 2 kg/d was different ($P < .05$) from that in growing pigs for all amino acids except arginine, histidine, glycine, and serine. Furthermore, these sows had a lower ($P < .05$) amount of indispensable amino acids and a higher ($P < .05$) amount of dispensable amino acids in endogenous protein than the other groups. In particular, the loss of proline in sows restricted in their feed intake was higher than in any of the other groups, and proline accounted for more ($P < .05$) of the total protein loss in these sows than in the sows and growing pigs given free access to the diet.

Discussion

Endogenous nitrogen mainly consists of nitrogen from digestive enzymes, mucoproteins, desquamated cells, serum albumin, peptides, free amino acids,

Table 2. Feed intake and average daily gain of animals fed the experimental diet

Item	Growing pigs	Lactating sows	Gestating sows		SEM[a]
			Restricted-fed	Ad libitum intake	
n	10	5	5	4	—
BW, kg	111.67[b]	215.30[c]	213.00[c]	234.63[c]	8.74
BW, $kg^{.75}$	34.31[b]	56.11[c]	55.72[c]	59.90[c]	1.76
ADG, g	−132[b]	−2,800[c]	−687[b]	−422[b]	369
ADFI, kg	2.67[b]	5.04[c]	2.0[b]	4.35[c]	.28
ADFI, $g/kg^{.75}$	79[b]	90[b]	36[c]	73[b]	5.68

[a]Pooled standard error of the mean.
[b,c]Means within a row lacking a common superscript differ ($P < .05$).

amines, and urea (Moughan and Schuttert, 1991). The main sources of endogenous protein are saliva, gastric secretions, pancreatic enzymes, bile acids, and intestinal secretions (Low and Zebrowska, 1989; Souffrant, 1991; Tamminga et al., 1995). However, 70 to 80% of secreted endogenous protein is hydrolyzed and reabsorbed before reaching the distal ileum (Souffrant et al., 1993; Krawielitzki et al., 1994). The major part of the remaining endogenous protein originates from deconjugated bile salts and mucin glycoprotein, because these components are largely resistant to proteolysis and, therefore, escape reabsorption (Taverner et al., 1981; Fuller and Cadenhead, 1991; Moughan and Schuttert, 1991). Glycine accounts for more than 90% of the total amino acid content of bile, and mucin glycoprotein is rich in proline, glutamic acid, aspartic acid, serine, and threonine (Souffrant, 1991; Lien et al., 1997). It has

Table 3. Endogenous losses (mg/kg DMI) of protein and amino acids in growing pigs and sows fed a protein-free diet[a]

Group	Growing pigs	Lactating sows	Gestating sows		SEM[a]
			Restricted-fed	Ad libitum intake	
n	10	5	5	4	—
Crude protein	12,437[c]	9,396[c]	17,780[d]	11,218[c]	1,311
Indispensable amino acid					
Arginine	361[c]	266[d]	528[e]	303[cd]	32
Histidine	156[c]	136[c]	222[d]	153[c]	16
Isoleucine	392[c]	252[d]	376[c]	317[c]	42
Leucine	591[cd]	446[c]	644[d]	498[cd]	46
Lysine	428[c]	292[d]	522[c]	413[cd]	46
Methionine	123[c]	80[d]	128[c]	105[cd]	12
Phenylalanine	341[cd]	268[c]	372[d]	293[cd]	32
Threonine	527[cd]	454[c]	606[d]	508[cd]	45
Tryptophan	151	130	162	125	13
Valine	491[c]	340[d]	532[c]	430[cd]	51
Total	3,561[cd]	2,664[d]	4,092[c]	3,143[cd]	332
Dispensable amino acid					
Alanine	591[c]	406[d]	650[c]	510[cd]	57
Aspartate	878[c]	604[d]	1,010[c]	800[cd]	85
Cysteine	236[de]	174[c]	268[e]	188[cd]	16
Glutamate	1,139[c]	752[d]	1,270[c]	958[cd]	111
Glycine	857[c]	1,020[c]	1,446[d]	778[c]	107
Proline	1,977[c]	782[c]	5,044[d]	1,090[c]	562
Serine	450[c]	376[c]	622[d]	455[c]	43
Tyrosine	299[c]	214[d]	328[c]	235[cd]	28
Total	6,427[c]	4,328[c]	10,638[d]	5,013[c]	860
All amino acids	9,988[c]	6,992[c]	14,730[d]	8,155[c]	1,067

[a]The endogenous loss of protein and each amino acid was calculated as the amino acid or protein concentration in digesta DM multiplied by the ratio between chromium in digesta DM and chromium in feed DM.
[b]Pooled standard error of the mean.
[c,d,e]Means within a row lacking a common superscript differ ($P < .05$).

Table 4. Amino acid composition of endogenous protein in growing pigs and sows[a]

Group	Growing pigs	Lactating sows	Gestating sows		SEM[b]
			Restricted-fed	Ad libitum intake	
n	10	5	5	4	
Crude protein	100	100	100	100	—
Indispensable amino acid					
Arginine	2.93	2.87	3.00	2.74	.13
Histidine	1.29	1.45	1.25	1.39	.08
Isoleucine	3.19[c]	2.69[cd]	2.11[d]	2.84[c]	.20
Leucine	4.88[c]	4.81[c]	3.64[d]	4.49[cd]	.29
Lysine	3.48[c]	3.12[cd]	2.96[d]	3.67[c]	.18
Methionine	1.01[c]	.85[cd]	.72[d]	.93[cd]	.06
Phenylalanine	2.82[c]	2.87[c]	2.10[d]	2.62[cd]	.16
Threonine	4.35[c]	4.96[c]	3.42[d]	4.70[c]	.27
Tryptophan	1.27[c]	1.41[c]	.92[d]	1.16[cd]	.08
Valine	3.99[c]	3.62[cd]	3.00[d]	3.93[c]	.24
Total	29.21[c]	28.64[c]	23.12[d]	28.46[c]	1.51
Dispensable amino acid					
Alanine	4.81[c]	4.34[c]	3.66[d]	4.59[c]	.19
Aspartate	7.20[c]	6.50[cd]	5.69[d]	7.18[c]	.42
Cysteine	1.94[c]	1.87[cd]	1.52[d]	1.75[cd]	.10
Glutamate	9.26[c]	8.06[cd]	7.12[d]	8.64[c]	.42
Glycine	6.85[c]	11.55[d]	8.19[c]	7.13[c]	.86
Proline	14.38[c]	7.80[c]	28.30[d]	8.88[c]	3.23
Serine	3.70	4.09	3.49	4.15	.20
Tyrosine	2.46[c]	2.30[cd]	1.85[d]	2.07[cd]	.14
Total	50.61[c]	46.52[c]	59.83[d]	44.39[c]	2.66
All amino acids	79.82[cd]	75.17[c]	82.95[d]	72.85[c]	2.35

[a]The endogenous loss of each amino acid was calculated as the percentage of total endogenous protein loss.
[b]Pooled standard error of the mean.
[c,d]Means within a row lacking a common superscript differ ($P < .05$).

been suggested that the activity of pyrroline-5-carboxylate reductase (the enzyme that catalyzes proline synthesis) is higher than that of the proline-degrading enzyme, proline oxidase (Mariscal-Landin et al., 1995). Therefore, proline will accumulate in the enterocytes and diffuse into the lumen. Gardner (1975) also provided evidence for a substantial flux of proline and glycine from the enterocytes into the intestinal lumen. There is evidence that proline, glycine, threonine, serine, aspartic acid, and glutamic acid are more slowly absorbed from the intestinal lumen than are most other amino acids (Taverner et al., 1981). Therefore, endogenous protein usually has a high content of these amino acids (Holmes et al., 1974; Taverner et al., 1981). The amino acid composition of endogenous protein in the present experiment is in agreement with this hypothesis.

The values for endogenous losses of protein and amino acids for growing pigs are within the wide range of values reported in studies in which a protein-free diet had been fed (e.g., de Lange et al., 1989a,b; Wang and Fuller, 1989; Chung and Baker, 1992; Leterme et al., 1996a). Furthermore, the amino acid composition of endogenous protein from growing pigs in this study parallels previous estimates (Wünsche et al., 1987).

The values for endogenous losses obtained in growing pigs were close to those obtained in gestating sows given free access to feed, but the levels were somewhat lower in lactating sows. However, lactating sows had a significantly higher feed intake than did the growing pigs, which may explain this difference.

Furuya and Kaji (1992) compared endogenous losses in growing pigs at 45 and 92 kg BW fed at three levels of feed intake, and they found no significant differences in the endogenous nitrogen losses between these two groups of pigs when expressed as grams per kilogram of DMI. Our results with growing pigs and sows allowed ad libitum access to feed are in agreement with these observations. Mariscal-Landin et al. (1995) suggested that the endogenous output of protein is related to BW rather than to DMI in growing pigs fed less than 70 g DM/kg$^{.75}$. In the present experiment, growing pigs, lactating sows, and one of the groups of gestating sows were allowed ad libitum access to feed, and daily feed intake exceeded 70 g/kg$^{.75}$, which might explain why we obtained a different result in our study. Leibholz and Mollah (1988) hypothesized that the BW of the animal significantly affected the loss of endogenous protein, but they were working with younger pigs. We have

previously demonstrated that endogenous protein losses change with BW in pigs that are less than 60 kg (Stein, 1998). The mucosal surface of the intestines increases more than BW of the animal from birth to approximately 120 d of age (Low and Zebrowska, 1989). Therefore, it is likely that the production of mucin also increases relatively faster than the BW of the animals. Mucin protein significantly contributes to the endogenous protein flow at the distal ileum, and this may explain why the endogenous losses are influenced by BW in young pigs. However, results from the present experiment as well as the results reported by Furuya and Kaji (1992) indicate that there is no effect of BW on the endogenous losses in older pigs.

When gestating sows were restricted to 2 kg/d, the endogenous loss of protein was higher than that for any of the other groups. The values for arginine, histidine, glycine, serine, and proline were significantly higher than those obtained with the other groups, and, for all other amino acids, the numerically highest values were obtained in gestating sows fed 2 kg/d. This finding indicates that feed intake per se has a significant effect on endogenous losses of protein and amino acids if calculated in relation to DMI. A similar finding has previously been reported (Fuller and Cadenhead, 1991; Furuya and Kaji, 1992; Butts et al., 1993). Therefore, it is important to consider daily feed intake when values for endogenous losses are compared among different experiments. In the restricted-fed gestating sows, proline, glutamate, aspartate, and glycine accounted for almost 60% of the amino acids lost, and this was considerably more than in the animals given free access to feed. The loss of proline in restricted-fed gestating sows was more than four times higher than in gestating sows allowed to eat their diet on an ad libitum basis and accounted for one-third of total amino acid losses in these animals. One explanation for the abundance of proline in the digesta from animals fed a protein-free diet may be that a substantial amount of muscle protein is broken down in these animals to meet the amino acid requirement for maintenance (de Lange et al., 1989b). Protein released from muscle tissue contains large amounts of glutamine, which is taken up by the enterocytes and metabolized to glutamate, ammonia, citrulline, and proline. Because of the flux of proline into the intestinal lumen and the slow reabsorption, ileal digesta from animals fed a protein-free diet would be expected to have a high content of proline. However, if one assumes that muscle breakdown in animals fed a protein-free diet is not influenced by the feeding level, the daily production of proline due to this mechanism would be expected to be constant regardless of the daily feed intake of the animals. In the present experiment, gestating sows fed 2 kg/d lost approximately twice as much proline on a daily basis as gestating sows allowed free access to feed. Furthermore, due to the high amino acid requirements for milk production in lactating sows, it is likely that more body protein was catabolized in lactating sows than in any of the other groups, as indicated by the high weight losses in lactating sows. Thus, a greater amount of glutamine would be produced in lactating sows, and a higher proline synthesis and, subsequently, a higher proline loss would be expected. However, lactating sows had the least loss of proline of any of the groups, also if calculated on a daily basis. Because glutamine is the most abundant amino acid in sow's milk (Wu and Knabe, 1994; Wu et al., 1996), it could be speculated that the reason for the relatively low losses of proline in lactating sows is that glutamine in lactating sows is excreted in the milk, thus preventing the synthesis of proline. However, even if this mechanism is true in lactating sows, this would not explain the differences in proline losses between gestating sows fed 2 kg/d and gestating sows fed to appetite. Therefore, the above mechanism cannot fully explain the high losses of proline in restricted-fed gestating sows.

The composition of endogenous protein was not significantly different among the three groups of animals that were fed to appetite, but the restricted-fed gestating sows had a significantly different amino acid composition of endogenous protein. This indicates that neither the BW nor the physiological state of the animal affects the amino acid composition of endogenous protein if calculated proportionally to DMI. However, as was the case for the total flow of endogenous protein, the amino acid composition was influenced by the feeding level of the animals.

In conclusion, the present experiment showed that there are only minor differences between 100 kg growing pigs and sows in values for endogenous losses of protein and amino acids as well as the amino acid composition of endogenous protein as long as daily feed intake relative to BW is the same.

Implications

Growing pigs at or above 100 kg of body weight are good models for estimating the endogenous losses of protein and amino acids at the distal ileum in gestating and lactating sows. Furthermore, the amino acid composition of endogenous protein in sows is not different from that in growing pigs. However, daily feed intake affects the amount of endogenous protein and amino acids lost at the distal ileum, as well as the amino acid composition of endogenous protein. Because lactating sows usually consume more feed and gestating sows usually consume less feed than growing pigs, they may also have different losses of endogenous protein and amino acids. Consequently, values for apparent ileal digestibilities of amino acids may be different between growing pigs and sows.

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