

Dietary inclusion of fibrous ingredients and bird type influence apparent ileal digestibility of nutrients and energy utilization

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ABSTRACT The interaction between inclusion of fibrous ingredients and bird type on the coefficient of apparent ileal digestibility (CAID) of nutrients and energy utilization was investigated in the current study. A 2 × 3 factorial arrangement of treatments was utilized with 2 fiber contents (10.3 and 19.3 g/kg neutral detergent fiber) and 3 bird types (broilers, pullets and layers). The low-fiber diet was based on corn and soybean meal, and the high-fiber diet was developed by the inclusion of palm kernel meal, canola meal, and oat hulls. Titanium dioxide was used as an inert marker to calculate the CAID. The digesta were collected from the terminal ileum following the feeding of experimental diets for 7 d. Significant interactions ($P < 0.05$) between dietary fiber content and bird type were observed for the CAID of DM, starch, fat, neutral detergent fiber and energy, and AMEn. In general, the CAID coefficients were higher in broilers, intermediate in pullets, and lowest in layers at both

fiber contents. The CAID of nutrients in the 3 bird types was higher ($P < 0.05$) in the high-fiber diet than in the low-fiber diet, but the magnitude of responses differed. Layers showed markedly higher digestibility responses to increased dietary fiber content compared to broilers and pullets. There were interactions ($P < 0.05$ to 0.001) between the dietary fiber content and bird type for the CAID of nitrogen and all amino acids, except for Asp and Lys. The CAID of Asp and Lys was highest ($P < 0.05$) in broilers, intermediate in pullets, and lowest digestibility in layers. The CAID coefficients of nitrogen and amino acid increased with increased fiber content, with distinctly greater responses in layers compared to broilers and pullets. Overall, layers showed greater digestibility of nutrients in response to the increased fiber content, suggesting that layers require high-dietary fiber contents to efficiently utilize nutrients compared to broilers and pullets.

Key words: bird type, energy utilization, fiber, nutrient digestibility

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INTRODUCTION

A large volume of published reports is available on the ileal amino acid (AA) digestibility of feed ingredients for broilers (Bryden et al., 2009; Evonik, 2016) and, despite differences in age, gender, and nutrient requirements, these values are widely applied in feed formulations for pullets and layers. Nutrient digestibility estimates can vary depending on assay methodology, bird factors (bird type, strain, age, and gender), and dietary factors (e.g., type and content of fiber and antinutritional factors) (Ravindran et al., 1999a; Batal and Parson, 2002; Huang et al., 2005; Ravindran et al., 2005; Adedokun et al., 2009; Ravindran et al., 2017). However, contradictory results on nutrient digestibility have been reported due to the influence of bird type, age, gender of birds (Batal and Parsons 2002; Huang

et al., 2005), and fiber inclusion in the diet (Svihus and Hetland 2001). Limited data are available concerning the effect of bird type on the digestibility of AA in feed ingredients (Huang et al., 2006, 2007; Adedokun et al., 2009).

Dietary fiber has been reported to reduce feed intake and nutrient digestibility in poultry, but the extent of reduction depends on the type and content of fiber source (Mateos et al., 2012). The optimum dietary fiber inclusion level for different type of chickens is not well characterized. Some studies in broilers (Hetland and Svihus 2001; González-Alvarado et al., 2010; Mateos et al., 2012), pullets (Guzmán et al., 2015; Kimiaetalab et al., 2017), and layers (Hetland et al., 2003) have reported increased nutrient digestibility in birds-fed diets with moderate inclusion levels of dietary fiber. These improvements were ascribed to the positive effect of fiber on the development of gizzard. Moderate amounts of fibrous ingredients, such as oat hulls (OH), pea hulls, or wood shavings, have been shown to improve the development and functionality of the gizzard (Hetland

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et al., 2005; Amerah et al., 2009; Mateos et al., 2012). A well-developed gizzard has been suggested to reduce gizzard pH, improve enzyme activities, and enhance the antiperistaltic reflux in the gastrointestinal tract. The retention time in the upper digestive tract is increased, thereby improving the nutrient digestibility by allowing more time for enzymatic action (Svihus, 2013; Singh et al., 2014; Rodrigues and Choct, 2018).

Bird type also seems to influence the responses in the digestibility of nutrients to dietary fiber. The inclusion of corn distillers dried grains with solubles and wheat bran (60 to 80 g/kg) improved the nutrient digestibility in layer chicks compared to broiler chicks (Walugembe et al., 2014). These differences might suggest an improved capability of digestive tract in layers, compared to broilers, to more efficiently utilize nutrients in the presence of fibrous materials, possibly due to the physical characteristics of the fiber source.

The effects of type and content of dietary fiber sources on the performance have been investigated in different bird types (Hetland et al., 2005; Mateos et al., 2012); however, no research to date has examined the interaction between dietary fiber content and bird type on nutrient digestibility in the same study. It was hypothesized that an interaction will exist for digestibility responses of layers, pullets, and broilers, and that, due to the well-known tolerance of layers to fibrous feed ingredients, layers will have a higher digestibility when fed diets with high-fiber content. The aim of the present study was to examine the influence of dietary fiber content (low and high fiber), achieved by the inclusion of fibrous feed ingredients, and bird type (broilers, pullets, and layers) on apparent ileal nutrient digestibility and energy utilization.

MATERIALS AND METHODS

The experiment was conducted according to the New Zealand Revised Code of Ethical Conduct for the use of live animals for research, testing, and teaching and approved by the Massey University Animal Ethics Committee.

The experimental design was a 2 × 3 factorial arrangement of treatments testing two fiber contents (low, 23.8 g/kg and high, 50.6 g/kg) and three bird types (broilers, pullets and layers). The diets were formulated and mixed using the same batch of ingredients (Table 1). The low fiber diet was based on corn and soybean meal. In the high fiber diet, palm kernel meal, canola meal and OH were included to increase the fiber content. Because the nutrient utilization, and not the performance, was the main focus of this study and the primary objective was to establish diets with different fibre contents rather than diets equivalent in energy contents, no attempt was made to adjust the energy density in the low and high fibre diets. Titanium dioxide (5.0 g/kg) was included in the diets as an indigestible marker.

Table 1. Composition and analysis of the experimental diets (g/kg, as fed basis).

Ingredient	Low fiber	High fiber
Corn	712.0	546.1
Soybean meal (CP, 480 g/kg)	248.6	217.1
Palm kernel meal (crude fiber, 197 g/kg)	0.0	80.0
Canola meal (CP, 350 g/kg; crude fiber, 105 g/kg)	0.0	40.0
Oat hulls (crude fiber, 283 g/kg)	0.0	40.0
Soybean oil	0.0	38.8
Dicalcium phosphate	16.5	16.2
Limestone	10.7	9.6
Sodium chloride	2.3	2.1
Sodium bicarbonate	2.6	2.8
Vitamin premix ¹	0.8	0.8
Trace mineral premix ¹	1.5	1.5
Titanium dioxide ²	5.0	5.0
Calculated values		
AMEn (kcal/kg)	3,000	2,900
CP	180	180
Crude fiber	23.8	50.6
Crude fat	29.8	69.8
Lys	9.2	9.0
Met	3.0	3.0
Met + Cys	6.0	6.0
Thr	6.7	6.7
Trp	2.3	2.2
Ca	8.5	8.5
Total P	6.6	6.8
Non-phytate P	4.2	4.2
Sodium	1.8	1.8
Chloride	1.8	1.8
Analyzed values		
Starch	410	356
Fat	20	51
CP	183	161
Gross energy (kcal/kg)	3,750	4,020
Neutral detergent fiber	10.3	19.3
Ca	10.5	10.6
Total P	6.0	6.5

¹Supplied per kg diet: vitamin A (trans-retinyl acetate), 12,000 IU; vitamin D3 (cholecalciferol), 4000 IU; vitamin E (DL- α -tocopherol), 80 IU; biotin, 0.25 mg; pantothenic acid (D-Ca pantothenate), 15 mg; vitamin B12 (cyanocobalamin), 0.02 mg; folic acid, 3.0 mg; vitamin K3 (menadione nicotinamide bisulphite), 4.0 mg; niacin (nicotinic acid), 60 mg; pyridoxine (pyridoxine. HCl), 10 mg; riboflavin, 9.0 mg; thiamine (thiamine-mononitrate), 3.0 mg; antioxidant (ethoxyquin), 100 mg; choline (choline chloride 60%), 360 mg; Co (cobalt sulfate), 0.15 mg; Cu (copper sulfate), 6.0 mg; organic Cu (B-Traxim Cu), 3.0 mg; Fe (iron sulfate), 36 mg; I (calcium iodate), 0.93 mg; Mn (manganese oxide), 60 mg; Mo (sodium molybdate), 0.15 mg; Se (sodium selenite), 0.26 mg; organic Se (enriched yeast), 0.14 mg; Zn (zinc sulfate), 48 mg; organic Zn (B-Traxim Zn), 24 mg.

²Inert marker for ileal digestibility measurements (Merck KGaA, Darmstadt, Germany).

Day-old male broilers (Ross 308) were obtained from a commercial hatchery, raised in floor pens and, fed commercial broiler starter (d 1 to 21) and finisher (d 22 to 35) diets. The broilers were 35-d-old (average BW, 2.60 kg) at the start of the test period. The pullets (Hy-Line Brown, 10-wk-old, average BW, 1.05 kg) and layers (Hy-Line Brown, 59-wk-old, average BW, 1.95 kg) were obtained from a commercial farm. Within each bird type, 96 birds with uniform BW were selected and assigned to 24 colony cages, so that the average weight per cage was similar. For broilers and pullets, 2 adjacent cages were treated as a replicate (4 birds

per cage, 8 birds per replicate). For layers, 4 adjacent cages were treated as a replicate (2 birds per cage, 8 birds per replicate) each diet was randomly assigned to 6 replicates. Birds were fasted for 12 h before the introduction of treatment diets. The diets, in mash form, were offered ad libitum for 7 d prior to the collection of ileal digesta. Water was freely available.

Total feed intake and excreta output were recorded over the last 4 d of the experimental period for AME determination. Daily excreta collections were pooled within replicate cages, mixed well and sub-sampled. In the case of layers, no eggshell quality issues were observed during the 7 d test period and there was no contamination of excreta with shell-less eggs. The sub-samples were lyophilized, ground to pass through a 0.5 mm sieve and stored in airtight plastic containers at 4°C until laboratory analysis. Excreta samples were analyzed for DM, gross energy (GE) and nitrogen (N).

After 7 d on the treatment diets, all birds were euthanized by intravenous injection (0.5 ml per kg BW) of sodium pentobarbitone (Provet NZ Pty Ltd., Auckland, New Zealand) and ileal digesta was collected from the lower half of the ileum (Ravindran et al., 2005). The ileum was defined as the portion of the small intestine extending from Meckel's diverticulum to ~40 mm proximal to ileo-cecal junction. The ileum was divided into two halves and the digesta were collected from the lower half towards the ileo-cecal junction by gentle flushing with distilled water. Digesta were pooled within replicates, giving 6 samples per treatment. The digesta were immediately frozen, lyophilized, ground to pass through a 0.5-mm sieve and stored at 4°C until laboratory analysis for DM, GE, N, AA, starch, fat, neutral detergent fiber (NDF) and titanium (Ti).

Dry matter was determined using standard procedures (methods 930.15 and 925.10; AOAC, 2005). Gross energy was determined by adiabatic bomb calorimetry (Gallenkamp Autobomb, London, UK) standardized with benzoic acid. Neutral detergent fiber was determined using AOAC (2005) procedures (method 2002.04/973.18). Titanium was determined on a UV spectrophotometer following the method of Short et al. (1996). Nitrogen was determined by combustion (method 968.06; AOAC, 2005) using the Leco CNS 2000 auto-analyser (LECO Corporation, St. Joseph, MI). Crude protein content was calculated as N X 6.25. Starch was determined using the Megazyme total starch assay kit (Megazyme International Ireland Ltd., Wicklow, Ireland) based on thermostable α -amylase and amyloglucosidase. Fat was determined using the Soxhlet extraction procedure (method 991.36; AOAC, 2005). Amino acids were detected in an AA analyzer (Biochrom, Version 30 plus, Biochrom Ltd., Cambridge, England) and the chromatograms were integrated using dedicated software (Agilent Open Lab software) with the amino grams simultaneously detected at 570 and 440 nm. Cysteine and methionine were analyzed as cysteic acid and methionine sulphone, respectively, by oxidation with performic acid-phenol

for 16 h at 0°C prior to hydrolysis. Tryptophan was not measured.

For mineral analysis, the samples were wet acid digested with a mixture of nitric and perchloric acid, and concentrations of Ca, P, K, Mg and Na were determined by Inductively Coupled Plasma-Optical Emission Spectroscopy (ICP-OES) using a Thermo Jarrell Ash IRIS instrument (Thermo Jarrell Ash Corporation, Franklin, MA). The concentrations of Cu, Mn and Zn were determined by Inductively Coupled Plasma-Mass Spectrometry (ICP-MS) using a Perkin Elmer Elan 6000 instrument (Melbourne, Victoria, Australia).

The AME was calculated using the following formula with appropriate corrections made for differences in DM content.

$$\text{AME (kcal/kg)} = \frac{[(\text{FI} \times \text{GE}_{\text{diet}}) - (\text{Excreta output} \times \text{GE}_{\text{excreta}})]}{\text{FI}}$$

The AMEn was calculated by correction for zero N retention by assuming 8.22 kcal per g N retained in the body as described by Hill and Anderson (1958).

The coefficient of apparent ileal digestibility (CAID) of nutrients was calculated using the following formula:

$$\text{Digestibility of diet component} = \frac{[(\text{Component/Ti})_{\text{diet}} - (\text{Component/Ti})_{\text{ileal}}]}{(\text{Component/Ti})_{\text{diet}}}$$

Where,

(Component/Ti) diet

= ratio of component to titanium in the diet, and

(Component/Ti) ileal

= ratio of component to titanium in the ileal digesta.

Replicate cages were considered as the experimental unit. The data were analyzed by two-way ANOVA to determine the main effects (fiber content and bird type) and their interaction using the GLM procedure of SAS (SAS Inst. inc., Cary, NC). Differences were considered to be significant at $P < 0.05$ and significant differences between means were separated by the Least Significant Difference test.

RESULTS

The influence of dietary fiber content and bird type on the CAID of DM, starch, fat, NDF and GE of the diets for the three bird types is shown in Table 2. There were significant ($P < 0.05$ to 0.001) interactions between the dietary fiber content and bird type for the digestibility of all nutrients, with responses to increased fiber content differing among bird types. Digestibility

Table 2. Influence of fiber content and bird type on the coefficient of apparent ileal digestibility of DM, starch, fat, neutral detergent fiber (NDF) and gross energy (GE), and AMEn (kcal/kg DM).¹

Fiber content	Bird type	Ileal digestibility					
		DM	Starch	Fat	NDF	GE	AMEn
Low fiber	Broiler	0.685 ^a	0.950 ^b	0.696 ^c	0.275 ^a	0.736 ^a	3,090 ^{b,c}
	Pullet	0.604 ^c	0.981 ^{a,b}	0.749 ^b	-0.058 ^b	0.661 ^c	3,190 ^a
	Layer	0.495 ^d	0.771 ^c	0.569 ^d	-0.051 ^b	0.550 ^d	2,800 ^e
High fiber	Broiler	0.666 ^{a,b}	0.978 ^{a,b}	0.943 ^a	0.340 ^a	0.738 ^a	3,025 ^c
	Pullet	0.628 ^{b,c}	0.994 ^a	0.952 ^a	0.234 ^a	0.712 ^{a,b}	3,118 ^{a,b}
	Layer	0.627 ^{b,c}	0.963 ^{a,b}	0.924 ^a	0.270 ^a	0.688 ^{b,c}	2,908 ^d
SEM		0.019	0.014	0.014	0.044	0.017	28.6
Main effects							
Fiber content							
	Low fiber	0.595	0.901	0.671	0.055	0.649	3,027
	High fiber	0.640	0.978	0.940	0.281	0.712	3,017
Bird type							
	Broiler	0.675	0.964	0.820	0.307	0.737	3,057
	Pullet	0.616	0.988	0.850	0.088	0.686	3,154
	Layer	0.561	0.867	0.746	0.110	0.619	2,854
Probabilities, P ≤							
	Fiber content	0.007	0.001	0.001	0.001	0.001	0.679
	Bird type	0.001	0.001	0.001	0.001	0.001	0.001
	Fiber content x Bird type	0.002	0.001	0.001	0.013	0.001	0.005

Means in a column not sharing a common letter are significantly different ($P < 0.05$).

¹Each value represents the mean of 6 replicates (8 birds per replicate), measured after 7 d on treatment diets.

of all nutrients, in general, increased in the high fiber diet, but the responses were markedly greater in layers compared to those in the broilers and pullets. The digestibility improvements in layers ranged from 16.5 (for N) to 62.0% (for fat). The improvements in broilers and pullets ranged from 0.3 (for GE) to 35.0% (for fat) and 1.3 (for starch) to 27.0% (for fat), respectively.

In the low fiber diet, the DM digestibility in broilers was higher ($P < 0.05$) than those in pullets and layers, whereas in the high-fiber diet, the digestibility was similar ($P > 0.05$) among the bird types. The ileal digestibility of starch was higher ($P < 0.05$) in broilers and pullets than in layers fed the low fiber diet, but all bird types showed similar ($P > 0.05$) starch digestibility in the high fiber diet. In the low fiber diet, the highest ($P < 0.05$) fat digestibility observed with pullets and the lowest ($P < 0.05$) in layers. Fat digestibility in broilers was lower ($P < 0.05$) than that in pullets, but higher ($P < 0.05$) than that in layers. In the high fiber diet, fat digestibility was similar ($P > 0.05$) among all bird types. In the low fiber diet, NDF was digested only in broilers and the digestibility estimates were negative in pullets and layers. However, in the high fiber diet, NDF was digested in all bird types and the digestibility estimates were similar ($P > 0.05$). In the low fiber diet, ileal GE digestibility in broilers was higher ($P < 0.05$) than those in pullets and layers, and the energy digestibility in layers was lower ($P < 0.05$) than that in pullets. In the high fiber diet, layers showed lower ($P < 0.05$) GE digestibility than broilers, but similar digestibility ($P > 0.05$) to that of pullets.

The interaction between bird type and fiber content was significant ($P < 0.05$) for the AMEn (Table 2). At both fiber contents, the AMEn in pullets was higher than those in the broilers and layers, and that in layers

was lower ($P < 0.05$) than that of broilers. The magnitude of differences among bird types, however, were lower in the high fiber diet, and only the layers showed positive AMEn response to increased fiber content.

The influence of dietary fiber content and bird type on the CAID of N and AA is summarized in Table 3. The ileal N digestibility increased with increase in dietary fiber content in all bird types, but the magnitude of responses differed resulting in a fiber content x bird type interaction ($P < 0.05$). The improvements were distinctly greater in the layers. The increases in broilers, pullets and layers were 4.6, 6.5 and 16.5%, respectively.

Both the dietary fiber content and bird type had significant ($P < 0.001$) effects on the ileal digestibility of AA. However, there were interactions ($P < 0.05$ to 0.001) between fiber content and bird type for all AA, except Asp and Lys. The digestibility of AA in the 3 bird types was higher in the high fiber diet ($P < 0.05$) compared to the low fiber diet, but the magnitude of increases differed. The digestibility of AA was higher in broilers ($P < 0.05$), compared to pullets and layers, at both fiber contents. The response to increased dietary fiber content was, however, greater in layers. The improvements in average AA digestibility of broilers, pullets and layers were 4.9, 6.4 and 17.5%, respectively.

The main effects of fiber content and bird type were significant ($P < 0.001$) for the digestibility of Asp and Lys, and there were no interactions ($P > 0.05$). The digestibility of these AA increased with increasing fiber content. Broilers had the highest and layer the lowest AA digestibilities, with pullets being intermediate.

The effects of dietary fiber content and bird type on the CAID of minerals are summarized in Table 4. Fiber content had no effect ($P > 0.05$) on the digestibility of Ca and there was no interaction ($P > 0.05$) between the

Table 3. Influence of fiber content and bird type on the coefficient of apparent ileal digestibility of nitrogen (N) and amino acids.¹

Fiber content	Bird type	N	AA ²	Asp	Ser	Glu	Pro	Gly	Ala	Cys	Ile	Leu	Phe	His	Lys	Arg	Val	Met	Thr	
Low fiber	Broiler	0.798 ^b	0.818 ^{b,c}	0.806	0.806 ^b	0.865 ^{b,c}	0.808 ^b	0.771 ^b	0.808 ^b	0.752 ^{a,b}	0.822 ^b	0.837 ^b	0.854 ^b	0.834 ^{b,c}	0.834	0.889 ^b	0.803 ^{b,c}	0.850 ^b	0.743 ^b	
	Pullet	0.754 ^e	0.783 ^d	0.757	0.769 ^c	0.852 ^c	0.769 ^c	0.696 ^c	0.802 ^b	0.645 ^c	0.808 ^b	0.837 ^b	0.848 ^b	0.801 ^d	0.808	0.859 ^c	0.764 ^d	0.846 ^b	0.662 ^c	
	Layer	0.673 ^d	0.679 ^e	0.712	0.647 ^d	0.780 ^d	0.628 ^d	0.628 ^d	0.613 ^d	0.693 ^c	0.381 ^d	0.720 ^c	0.722 ^c	0.765 ^c	0.693 ^e	0.773	0.826 ^d	0.660 ^e	0.729 ^c	0.526 ^d
High fiber	Broiler	0.835 ^a	0.858 ^a	0.839	0.846 ^a	0.892 ^a	0.847 ^a	0.813 ^a	0.864 ^a	0.797 ^a	0.866 ^a	0.882 ^a	0.895 ^a	0.871 ^a	0.867	0.907 ^a	0.849 ^a	0.896 ^a	0.797 ^a	
	Pullet	0.803 ^b	0.833 ^{a,b}	0.805	0.812 ^b	0.878 ^{a,b}	0.814 ^{a,b}	0.770 ^b	0.857 ^a	0.724 ^b	0.858 ^a	0.880 ^a	0.890 ^a	0.847 ^{a,b}	0.850	0.886 ^b	0.826 ^{a,b}	0.886 ^a	0.746 ^b	
	Layer	0.784 ^b	0.798 ^{c,d}	0.791	0.780 ^{b,c}	0.856 ^c	0.782 ^{b,c}	0.741 ^b	0.818 ^b	0.631 ^c	0.826 ^b	0.845 ^b	0.864 ^b	0.812 ^{c,d}	0.827	0.875 ^{b,c}	0.787 ^{c,d}	0.846 ^b	0.690 ^c	
Pooled SEM		0.010	0.010	0.010	0.012	0.007	0.011	0.012	0.009	0.022	0.009	0.009	0.008	0.01	0.008	0.006	0.011	0.009	0.016	
Main effects																				
<i>Fiber content</i>																				
Low fiber		0.742	0.760	0.758 ^b	0.741	0.833	0.735	0.693	0.768	0.593	0.784	0.799	0.822	0.776	0.805 ^b	0.858	0.743	0.808	0.644	
High fiber		0.807	0.830	0.812 ^a	0.813	0.875	0.814	0.775	0.846	0.717	0.850	0.869	0.883	0.843	0.848 ^a	0.889	0.820	0.876	0.744	
<i>Bird type</i>																				
Broiler		0.817	0.838	0.823 ^a	0.826	0.878	0.828	0.792	0.836	0.775	0.844	0.860	0.875	0.852	0.851 ^a	0.898	0.826	0.873	0.77	
Pullet		0.779	0.808	0.781 ^b	0.791	0.865	0.792	0.733	0.829	0.684	0.833	0.858	0.869	0.824	0.829 ^b	0.872	0.795	0.866	0.704	
Layer		0.728	0.739	0.752 ^c	0.714	0.818	0.705	0.677	0.755	0.506	0.773	0.783	0.815	0.753	0.800 ^c	0.851	0.723	0.787	0.608	
Probabilities, P ≤																				
Fiber content		0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	
Bird type		0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	
Fiber content × Bird type		0.01	0.001	0.07	0.001	0.01	0.001	0.001	0.001	0.001	0.01	0.001	0.001	0.001	0.435	0.05	0.001	0.001	0.001	

Means in a column not sharing a common letter are significantly different ($P < 0.05$).

¹Each value represents the mean of 6 replicates (8 birds per replicate), measured after 7 d on treatment diets.

²Average digestibility of 16 amino acids.

Table 4. Influence of fiber content and bird type on the coefficient of apparent ileal digestibility of minerals.¹

Fiber content type	Bird type	Ca	P	Mg	K	Na	Cu	Mn	Zn
Low fiber	Broiler	0.235	0.322 ^{c,d}	0.123	0.851 ^{b,c}	-0.347 ^c	-0.460	-0.199	-0.488
	Pullet	0.226	0.262 ^d	-0.076	0.828 ^c	-0.967 ^b	-0.530	0.031	-0.450
	Layer	0.780	0.696 ^a	0.234	0.890 ^a	-1.740 ^a	-0.240	0.035	-0.547
High fiber	Broiler	0.261	0.422 ^b	0.176	0.825 ^c	-0.312 ^c	0.404	-0.054	-0.263
	Pullet	0.159	0.381 ^{b,c}	0.108	0.853 ^{b,c}	-0.823 ^b	0.360	0.017	-0.191
	Layer	0.758	0.679 ^a	0.240	0.863 ^{a,b}	-0.815 ^b	0.451	0.020	-0.446
SEM		0.033	0.029	0.041	0.012	0.137	0.056	0.037	0.080
Main effects									
Fiber content									
	Low fiber	0.414	0.427	0.094 ^b	0.856	-1.018	-0.410 ^b	-0.044	-0.495 ^a
	High fiber	0.393	0.494	0.175 ^a	0.847	-0.650	0.405 ^a	-0.006	-0.300 ^b
Bird type									
	Broiler	0.248 ^b	0.372	0.150 ^b	0.838	-0.330	-0.028 ^b	-0.126 ^b	-0.376 ^b
	Pullet	0.192 ^b	0.321	0.016 ^c	0.841	-0.895	-0.085 ^b	0.024 ^a	-0.321 ^b
	Layer	0.769 ^a	0.688	0.237 ^a	0.877	-1.277	0.106 ^a	0.028 ^a	-0.497 ^a
Probabilities, $P \leq$									
Fiber content									
		0.439	0.007	0.021	0.335	0.003	0.001	0.211	0.006
Bird type									
		0.001	0.001	0.001	0.004	0.001	0.006	0.001	0.097
Fiber content x Bird type									
		0.380	0.050	0.092	0.048	0.005	0.169	0.060	0.588

Means in a column not sharing a common letter are significantly different ($P < 0.05$).

¹Each value represents the mean of 6 replicates (8 birds per replicate), measured after 7 d on treatment diets.

fiber content and bird type. The main effect of bird type was significant ($P < 0.05$) for Ca digestibility, with layers showing considerably higher digestibility compared to pullets and broilers. Calcium digestibility in pullets and broilers was similar ($P > 0.05$). Phosphorus digestibility differed among bird types, but the extent of responses to increased fiber content varied causing a significant ($P < 0.05$) interaction. Similar to Ca digestibility, P digestibility was markedly higher in the layers and was not affected by increased fiber content. In broilers and pullets, P digestibility increased in high fiber diets. The main effects of fiber content and bird type were significant ($P > 0.05$) for apparent ileal Mg digestibility. The digestibility was higher in birds fed the high fiber diet than those fed the low fiber diet. The digestibility was higher ($P < 0.05$) in layers compared to pullets and broilers, and was higher ($P < 0.05$) in broilers compared to pullets.

An interaction ($P < 0.05$) was observed for K digestibility, with digestibility increasing numerically in the high fiber diet for pullets, but the opposite was observed for broilers and layers. High fiber content enhanced Na digestibility only in layers, resulting in a significant ($P < 0.01$) fiber content by bird type interaction. The digestibility of Cu and Zn was higher ($P < 0.05$) in birds fed the high fiber diet, and layers digested these minerals more efficiently than broilers and pullets ($P < 0.05$). The main effect of bird type was significant ($P < 0.001$) for Mn digestibility, with higher digestibility in layers and pullets than the broilers.

DISCUSSION

The objective of this study was to examine the influence of diet and bird type on CAID of nutrients and

energy utilization. The results demonstrated that the CAID of DM, starch, fat, NDF and GE were influenced by dietary fiber content. The responses to the increased dietary fiber content, however, differed among bird types with pronounced improvements in layers compared with broilers and pullets. The increases due to increased fiber content in the CAID of DM, starch, fat and GE in layers was 27.0, 25.0, 62.0 and 25.0%, respectively. The corresponding increases in broilers and pullets were 3.0, 3.0, 35.0 and 0.3%, and 4.0, 1.3, 27.0 and 7.7%, respectively. Similar comparative studies reporting the interaction between fiber content and bird type are not available in the literature. The low nutrient digestibility values observed for layers fed low fibre diet were unexpected and difficult to explain. However, in a recent study (Mtei et al. 2019), examining the interaction between bird type (broilers vs layers) with corn particle size (fine, medium and coarse) using the same low fibre diet as the current study, similar low ileal digestibility values were observed for DM (0.497), starch (0.769), GE (0.498) and N (0.559) in layers offered finely ground corn diet. Feeding coarse diets increased the CAID of DM by 31.0% (from 0.497 to 0.651), starch by 21.2% (from 0.769 to 0.932) and GE by 29.5% (from 0.498 to 0.645), respectively, over the fine diet. Limited secretion of digestive enzymes and villus absorptive capacity may be potential constraints to nutrient utilization in laying hens and pullets compared to broilers (Zavarize et al., 2012; Kimiaetalab et al., 2017, 2018). Moreover, it has been documented that texturizing the poultry feed either by increasing the particle size (Dahlke et al., 2003; Röhe et al., 2014) or whole wheat inclusion (Gabriel et al., 2008) can increase the villus surface and enhance the intestinal absorptive capacity. Therefore, it is reasonable to assume that any feeding strategy that may improve diet texture,

such as inclusion of fibrous ingredients in the current study, would favor nutrient utilization to a greater extent in layers than broilers. The striking digestibility responses in layers lends support to this thesis and may suggest that the function of upper digestive tract in layers is more sensitive to fiber and feed structure than the broilers and pullets (Moran and Evans, 1977). Studies have shown that birds fed diets with moderate inclusions of fiber increased the musculature, size and weight of the gizzard (Abdollahi et al., 2018), stimulated the gizzard activity, retained the digesta longer in the gizzard, thus increasing nutrient digestibility. Layers fed diets with 10 g/kg wood shavings (Hetland et al., 2003), 40 g/kg OH (Hetland and Svihus, 2001) and 30 g/kg wood shavings (Hetland and Svihus., 2007) increased gizzard weights by 50, 60 and 70%, respectively, than those fed the control diets.

Variable responses in nutrient digestibility to increased dietary fiber content by different bird types have been reported in the literature. Broilers fed diets containing 0, 10, 20 and 30 g/kg high-fiber sunflower meal showed reductions in DM digestibility, from 0.77 to 0.70, 0.66 and 0.61, respectively, with increasing sunflower meal inclusions (Kalmendal et al., 2011). Increasing the inclusion of oat bran from 187 to 375 g/kg in broiler diets reduced the starch digestibility from 0.97 to 0.94 (Jorgensen et al., 1996). In contrast, starch digestibility in layers fed a whole wheat diet with 10 g/kg wood shavings was increased from 0.95 to 0.98 (Hetland et al., 2003). These differences in responses in nutrient digestibility among broilers and layers may be partly reflective of age effects. Layers are mature birds, whereas pullets and broilers are growing birds. Older birds fed high fiber diets retain the digesta longer in the gizzard compared to young birds (Shires et al., 1987), which may explain the pronounced digestibility responses in layers fed the high fiber diet in the current study.

In the low fiber diet, the CAID of fat was highest in pullets, followed by broilers and lowest in layers; however, these differences evened out in the high fiber diet. In all bird types, fat digestion increased at high dietary fiber content. It is noteworthy that most of the dietary fat in the low fiber diet originated from intact fat within the corn grain, whereas over half the fat in the high fiber diet was in the form of supplemental soybean oil. Supplemental soybean oil has been shown to be more digestible than the lipids encapsulated within the cell wall matrix (González-Alvarado et al., 2007; Kil et al., 2010). Cell walls become a physical barrier to digestive enzymes and this may explain the lower fat digestibility in all bird types fed the low fiber diet. It is also reasonable to suggest that a better developed gizzard in birds fed the high dietary fiber diet may enhance gastrointestinal refluxes and remixing with bile causing greater solubilization and increase fat digestion.

The available literature generally highlight dietary fiber as an antinutrient and diluent in poultry diets, and it is universally assumed that poultry do not have the

capacity to digest fiber. Fiber digestibility estimates determined in pullets and layers fed the low fiber diet were determined to be negative suggesting that the fiber was not digested. In contrast, some NDF digestion occurred in broilers fed the low fiber diet. Increasing the dietary fiber content had no effect on the NDF digestibility in broilers, but it was increased in the pullets and layers. In the high fiber diet, NDF digestibility was not different among the bird types. These findings were unexpected, but provide evidence for the capacity of poultry to digest some fiber components. Walugembe et al. (2014) similarly reported a higher ileal NDF digestibility in a high dietary fiber diet (0.25; 80 g/kg dried distillers grains with solubles and wheat bran) than a low dietary fiber diet (0.18; 60 g/kg dried distillers grains with solubles and wheat bran). In their study, broilers and layers showed similar ileal NDF digestibility in both diet types.

Ileal GE digestibility was highest in broilers compared to other two bird types and was not influenced by the dietary fiber content. On the other hand, pullets and layers responded to the increased fiber content with increases in GE digestibility of 7.7 and 25.0%, respectively. In the present study, the AMEn was unaffected by the dietary fiber content, but differed among bird types at both fiber contents. Walugembe et al. (2014) reported similar AMEn between layer and broiler chicks fed diets containing 60 or 80 g/kg dried distillers grains with solubles and wheat bran. Inclusion of 30 g/kg sunflower hulls vs. no sunflower hull inclusion has been reported to increase the AMEn from 3040 to 3080 kcal/kg by Kimiaetalab et al. (2017) and from 2872 to 2911 kcal/kg by Kimiaetalab et al. (2018). In these studies, the responses of broilers and pullets to the increased fiber content were similar. The inclusion of OH in broiler diets up to 50 g/kg increased AMEn values in a study reported by Jiménez-Moreno et al. (2013), but further increase to 75 g/kg reduced the AMEn.

Despite the fact that the ileal GE digestibility was based on a single point measurement at the time of euthanasia and dependent on the recovery of marker, whereas the AMEn represents balance of energy measured over a 4-d period, the effect of bird type on these 2 parameters followed the same pattern. However, the difference between IDE and AMEn was greater in laying hens (738 kcal/kg DM) compared to broilers (330 kcal/kg DM) and this could be attributed to the higher cecal fermentation capacity of the former.

The CAID of N and AA increased with the increased dietary fiber content in all bird types, but the responses were greater in layers than in broilers and pullets. Feeding of the high fiber diet increased the CAID of N and average AA in layers by 16.5 and 17.5%, respectively, compared to broilers (4.6 and 4.9%, respectively) and pullets (6.5 and 6.4%, respectively). These findings further demonstrate that layers require higher fiber content in their diets for efficient protein digestion. It is recognized that the layers can tolerate relatively high

inclusions of fibrous feed ingredients compared to broilers (Matterson et al., 1966; Ravindran and Blair, 1991; Roberson et al., 2005; Walugembe et al., 2014). However, improvements in N and AA digestibility with increased dietary fiber in all bird types may be due to the enhanced development and functionality of the upper digestive tract.

Regardless of the dietary fiber content, CAID of N and AA were highest in broilers, intermediate in pullets and the lowest in layers. Several factors may be responsible for the observed differences among the bird types, including age, gender and genotype. The influence of age on nutrient digestibility in well recognized (Batal and Parsons, 2002; Huang et al., 2005; Thomas et al., 2008). Nutrient digestibility of poultry is compromised at the time of hatch, but increases with advancing age (Uni et al., 1995). The digestion and uptake of AA in growing broilers reported to be higher compared to older birds (Batal and Parsons 2002; Huang et al., 2006). Batal and Parsons (2002) reported that the total tract digestibility of Lys, Arg, Thr and Cys in broilers increased from 0.78, 0.88, 0.69 and 0.62 at the age of 2 d to 0.89, 0.94, 0.85 and 0.81 at the age of 21 d, respectively. The rate of growth is proportional to the rate of nutrient supply to the growing tissues (Wakita et al., 1970) and the increased intestinal absorption of nutrients in growing birds may be associated with the need to supply nutrients for their rapid growth rate (Uni et al., 1995). Huang et al. (2005) reported that the digestibility of most AA in canola meal, soybean meal, and meat and bone meal for broilers were higher at 28 and 42 d than at 14 d of age.

Published data on the influence of gender on AA digestibility are contradictory. Wakita et al. (1970) found higher intestinal absorption of Glu and Met in male than in female chickens. A study by Zuprizal et al. (1992) reported higher AA digestibility of rapeseed meal in male (0.77) than female (0.70) broilers. In contrast, ten Doeschate et al. (1993) observed 3.0% higher digestibility of protein and AA in female broilers.

Similar to the present findings, Kimiaetalab et al. (2017) reported higher total tract N retention in birds fed a diet containing 30 g/kg sunflower hulls than that containing no sunflower hulls (0.61 vs. 0.59) and higher retention in broilers compared to pullets (0.64 vs. 0.55). It was suggested that the pullets require less N for growth compared to broilers and therefore the lower retention of N in pullets was to be expected. Ravindran et al. (1999b) reported a significant strain effect on AA digestibility and energy utilization in broilers and attributed this to genetic variation in the nutrient utilization among genotypes. In their study, average AA digestibility coefficient in the three broiler strains varied between 0.79 and 0.86. Al-Marzooqi et al. (2010) found that the average AA digestibility of 4 barley varieties varied between 0.66 and 0.77 for modern broilers and between 0.50 and 0.66 for slow-growing native meat birds. Huang et al. (2006) reported that the digestibility of AA in corn, wheat and sorghum was higher

in broiler chickens than layers. Huang et al. (2007) reported higher digestibility of most AA in corn in broilers than in layers, but the AA digestibility of wheat middlings, a fibrous ingredient, was higher in layers.

It is likely that part of the differences in apparent AA digestibility among bird types may be attributed to differences in endogenous AA losses (Ravindran and Hendriks 2004; Adedokun et al., 2007; Huang et al., 2007). In particular, given that bird types differ in their tolerance to handle fiber, these effects may be exacerbated in the high fiber diet (Ravindran, 2016).

With the exception of Ca and P, published data on the CAID of minerals for poultry are scant. For all minerals, there are no published reports examining the influence of bird type or fiber on CAID. In the current study, the effects of fiber content and bird type differed for the different minerals. Ileal digestibility of Ca was unaffected by the dietary fiber content. However, there were differences among bird types, with layers showing markedly higher CAID of Ca compared to pullets and broilers. The average Ca digestibility coefficients in broilers, pullets and layers were 0.248, 0.192 and 0.769, respectively. Ileal P digestibility was also similarly higher in the layers. The average P digestibility coefficients in broilers, pullets and layers were 0.372, 0.321 and 0.688, respectively. The CAID of Ca and P determined for broilers are comparable to those reported in the literature for corn-soy diets not supplemented with phytase for 21 d broilers (Ravindran et al., 2006; 2008). The present data showed that the CAID of these two minerals were similar for pullets and broilers.

The markedly better digestion of Ca and P in layers was not unexpected because of the high metabolic requirements for Ca and P for bone resorption and eggshell formation (Etches, 1987), and the fact that hens were laying eggs during the 7 d on treatment diets. Nevertheless, the difference of layers compared to broilers and pullets was pronounced, presumably due largely to the low Ca content of the experimental diets (8.5 g/kg) compared to the recommendations for layers (40 g/kg; Hy-Line Brown, 2016). A Ca-deficient diet would result in a negative Ca balance in the body and increase the efficiency of Ca absorption. Several studies have demonstrated that Ca retention in layers is markedly increased under conditions of negative balance (Hurwitz and Bar, 1969; Rao and Roland, 1990). Low dietary Ca contents may increase Ca-binding proteins in the intestinal epithelial cells resulting in an increased Ca absorption (Bar and Wasserman, 1973). Moreover, although not measured in the present study, a recent work from our laboratory showed a higher relative gizzard weight and lower gizzard pH values in layers than in broilers (Mtei et al., 2019). Gizzard pH plays a critical role in the solubilization of Ca and P. A lower gizzard pH promotes the solubility of mineral salts and reduces the formation of mineral-phytate complexes (Champagne, 1988; Selle et al., 2000), and consequently could increase the absorption of these minerals.

Phosphorus digestibility and absorption is also known to be influenced by dietary Ca contents (Hurwitz and Bar, 1965; van der Klis et al., 1993). The high P digestibility in layers in the current study may therefore be explained by the low Ca level in the diet. Phosphorus digestibility in layers was not influenced by increased fiber content. Phytate is a major determinant of P digestibility (Selle and Ravindran, 2007). In the current study, however, phytate P concentration of the two diets were similar. In broilers and pullets, P digestibility was increased in the high fiber diet. Similar improvements in digestibility in the high fiber diet was noted for Mg and Cu. It is tempting to speculate that the high dietary fiber through its effects on gizzard functionality increased the secretion of hydrochloric acid (González-Alvarado et al., 2010), thus reducing digesta pH and increasing the solubility and absorption of minerals (Shafey et al., 1991).

The trends in the digestibility of the two electrolyte minerals were distinctly different, with K being well digested and Na having a negative digestibility. The negative CAID of Na has been previously reported (Ravindran et al., 2008; Selle et al., 2009). The negative Na digestibility reflects the secretion of large amounts of endogenous Na into the small intestine, mainly in the form of sodium bicarbonate. Another noteworthy observation in the current study was the lack of absorption of the trace minerals, Cu (in the low fiber diet), Mn (in broilers, regardless of fiber content) and Zn. Given the biological significance of trace minerals in growth, metabolism and health, the present data emphasize the need to improve their utilization in poultry.

Although the current design had some limitations, the results nevertheless have implications to the understanding of differences in nutrient digestion among bird types. First, the diets were based on different ingredients (soybean meal vs. soybean meal + palm kernel meal + canola meal) and part of the differences observed in nutrient digestibility may reflect differences in nutrient composition. Second, soybean oil was included to increase the energy in the diet containing fibrous sources, which may have resulted in a confounded lipid effect especially on the utilization of fat and energy. The inclusion of added oil, however, was limited to 38.2 g/kg to reduce possible lipid effect resulting in a difference of 100 kcal/kg in ME contents. It must be noted that some evidence suggests that a difference of 100 kcal/kg will not have any effect on nutrient digestibility (Rabie et al., 2017). Furthermore, the focus of the study was nutrient utilization, and not the performance. The primary objective was therefore to establish diets with different fiber contents rather than diets equivalent in energy contents, and no attempt was made to adjust the energy density in the low and high fibre diets. Third, comparison of nutrient digestibility among different bird types is complicated because of the array of confounding interacting factors (strain, age, nutrient requirements and gender) involved. In the current work,

for the purpose of simplicity, same diets were offered to all bird types. The consequence of this approach was that the dietary content of nutrients does not meet the recommendations for the specific bird type. An example was dietary Ca content; the Ca was adequate for broilers and pullets, but exceedingly deficient for layers. Notwithstanding this limitation, we believe that the study design provided valid comparisons of digestibility among the bird types.

The present study was designed to test the hypothesis that layers are more tolerant of fibrous diets and will digest nutrients in high fiber diets more efficiently than broilers and pullets. While acknowledging the significant interaction between fiber content and bird type for all nutrients and AME_n, the current findings do not support the null hypothesis that the efficiency of nutrient digestion is greater in layers than broilers. In general, broilers showed higher nutrient digestibility and energy utilization than layers, with pronounced differences in the low fiber diet. However, the greatest responses to increased dietary fiber content were observed in layers. It is worth noting that the measured parameters, except AME_n, were lower in the low fiber diet for all bird types, possibly due to poor upper digestive tract development. Broilers exhibited no responses (DM, starch, NDF and GE) or minimal responses (N and AA) to increased dietary fiber content compared to pullets and layers. Some studies have suggested that broilers require a minimal amount of fiber in their diet to optimize digestive tract functionality and nutrient digestibility (Hetland et al., 2003; Amerah et al., 2009).

Although the current design had some limitations, the findings nevertheless have implications to the understanding of differences in nutrient digestion among bird types. Taken together, the current results demonstrate that the digestibility of nutrients was influenced by bird type regardless of dietary fiber content, with higher digestibility in broilers compared to pullets and layers. Bird types showed varying magnitudes of digestibility response to the inclusion of fibrous feed ingredients. Nutrient digestibility and AME_n were lower in layers fed the low fiber diet, but most of these reductions were restored in the diet with fibrous sources. Nutrient digestibility responses to dietary fiber content were greater in layers than in broilers and pullets, which may be a reflection of sensitivity of layers to fiber and better development of upper digestive tract. Overall, these findings indicate that laying hens require higher dietary fiber contents to efficiently digest and utilize the nutrients and energy. The interactions observed between the fiber content and bird type also suggest that the data on the dietary inclusion level of fiber sources and nutrient digestibility for one type of bird may not be applicable to other bird types. Further investigations are warranted to investigate the optimum fiber content in diets for different bird types to optimize nutrient digestibility, but this may differ for different fiber sources.

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