COMPENSATORY GROWTH OF ASHANTI BLACK WEANER PIGS: EFFECTS OF CONTINUOUS VERSUS RESTRICTIVE DIETARY INTAKE OF PROTEIN OR ENERGY

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ABSTRACT
An experiment was designed to determine the compensatory growth of pigs fed a nutrient-restricted diet and then re-alimented with an energy or protein diet. A total of 24 Ashanti Black weaner pigs (20.97 ± 0.49 kg) were either randomly assigned and fed continuously with a diet formulated to meet their requirements for growth (Standard) or with a restricted diet formulated to meet only 42% and 33% of their crude protein and metabolizable energy requirements, respectively (Restricted) for an entire 80-day period whereas a third and fourth group of pigs were fed the restricted diet for 40 days and then re-alimented with a protein (Re-protein) or energy (Re-Energy) diet for additional 40 days. Data on feed intake, growth performance and weights of body organs were analyzed by PROC GLIMMIX procedure of SAS (1991; SAS Inst. Inc., Cary, NC) in a completely randomized design. Feed intake did not differ (P=0.646) among all treatments during the first period of 40 days but average daily weight gain and feed efficiency of Restricted, Re-Protein and Re-Energy pigs were lower (P=0.001) than those fed the Standard diet continuously. Feed cost per intake for the entire 80-day period was expectedly higher (P=0.001) for pigs fed the Standard diet. Feed cost per intake for pigs fed the Standard diet was nearly twice that of pigs fed the Restricted diet. However, when the cost was expressed per ADG, the difference was not significant (P=0.212) among diets. These findings suggest that pig farmers could reduce the protein content of their diets and improve their profit margins during seasons of feed scarcity when most protein ingredients are expensive, by restricting dietary intake of protein and re-alimenting it later when proteinous ingredients become abundant, without affecting growth performance of their pigs.

Keywords: *Ashanti Black weaner pigs, compensatory growth performance, energy, protein.*

INTRODUCTION
As the human population in developing countries continues to outstrip food production, challenges with human food security and the cost of feeding pigs will continue to increase due to competition between man and pigs for staple cereal and legume grains that serve as food for humans and pigs.

Two strategies have successfully been employed to reduce feed cost without adverse effects on growth performance and meat quality of pigs; using agricultural by−products and inducing compensatory growth (Bussières *et al.,* 2014; Addah *et al*., 2016). Crop and animal by−products are usually of less human food value and are cheaper compared to the main cereal and legume grains; however, recent technological improvements in crop and livestock genotypes, the efficiency of production and processing, recycling, and extension education on post−harvest losses, have reduced food losses and wastage in sub−Saharan Africa and therefore the volume of crop and animal by−products generated in the food value chain (Golob, 2009; Sheahan and Barrett, 2017) that can be used as feed for pigs. Compensatory growth has been exploited in the swine (Heyer and Lebret, 2007) and ruminant (Ryan et al., 1993; Marais et al., 1991; Addah et al., 2017) industry even though the results have not been consistent across most studies to conclusively ascertain whether re−alimentation of energy or protein will elicit the needed significant compensatory growth after a period of restrictive nutrient intake. Growth rate was reduced during the growing period but increased during the finishing period when pigs were restricted up to 65% of their ad-libitum intake (Heyer and Lebret, 2007).

The Ashanti Black pig is the commonest breed of pig in West Africa. They are found in almost all the agro−ecological zones of Ghana (Barnes and Fleischer, 1998). The standard nutritional requirements of the Ashanti Black pig for rapid growth have been estimated at 17−18% crude protein (CP) and 13−14.0 MJ/kg DM metabolizable energy (ME), whereas to maintain their body weight, a dietary CP of 14.4 % and ME of 12.0 MJ/kg is required (Barnes and Fleischer, 1998; Addah et al., 2016). Instead of feeding a standard diet continuously from weaning to finishing, pigs could be fed a nutrient-restricted diet and then re−alimented with a protein or energy diet. Suppose pig farmers can increase and achieve market weights of pigs similar to those continuously fed a standard grower diet, by inducing compensatory growth through restrictive nutrient intake, they could reduce feed cost and improve their profit margins. Other benefits of inducing compensatory growth in pigs are improvements in the leanness and tenderness of meat (Kristensen et al., 2002). In most parts of West Africa and Ghana in particular, there is food insecurity during the planting season. This affects the nutrient quality of feed offered to pigs during this time. However, during the period of harvest, there tends to be a glut in crop residues from food harvesting and processing that can be used to meet the nutrient requirements of pigs. However, the question that arises is which nutrient (protein or energy) can be re-alimented to result in the greatest recovery or compensatory growth? In our previous studies, we compared re-alimentation of high protein or energy following restrictive intake on the growth performance of pigs (Addah et al., 2016) and sheep (Addah et al., 2017) and observed that when a maintenance diet was re-alimented with dietary protein, feed intake was increased by 18 % whereas daily growth rate and efficiency of feed utilization increased by twofold each compared to those re-alimented with energy. The design of these two previous studies was, however, confounded by the absence of a fourth treatment that would have allowed us to also compare the re-alimentation of the protein or energy diet with a regular standard grower diet fed throughout the experiment. This study was therefore designed to compare the re−alimentation of a high protein or energy diet with either a restricted diet or regular standard grower diet. The objective of the study was to determine whether increasing dietary protein or energy of Ashanti Black weaner pigs following a period of restrictive dietary intake will result in similar effects on growth performance compared to those fed a regular standard grower diet continuously.

MATERIALS AND METHODS

Animal Management

A total of 24 Ashanti Black weaner gilts with an initial average weight of 20.97 ± 0.49 kg were randomly assigned to twenty−four pigsties (3.8 × 2.8 m). The pens were then randomly assigned to four dietary feeding regimes in a completely randomized design. This resulted in six replicate pens per treatment. The pigs were weighed on two consecutive days each at the start and end of the experiment, and the average of each of the two consecutive weights used as initial and final weights, respectively (Addah et al., 2016; 2017). Subsequently, pigs were weighed every 14 days until the end of an 80−day feeding experiment. The pigs were offered on *ad libitum* basis, their experimental diets, once daily, in a concrete feeding trough (0.5 × 0.8 × m). Clean drinking water was offered twice daily. Each pen also contained a concrete wallow (1.5 × 0.75 m). Prior to the commencement of the study, the pigs were housed in the pens for a 14-day adaptation period. The pens and troughs were cleaned daily. The cost per kg of each feed ingredient and its level of inclusion in each diet was used to estimate the cost (GHS) per kg of each diet.

Feeding Regimen

The feeding regime in the first and second periods of the 80-day feeding experiment is shown in Table 1. In the first dietary feeding regimen, pigs were either fed a nutrient-restricted diet [11% CP and 8.6 ME (MJ/kg DM)] formulated to supply 43% and 33% of their requirements for CP and ME, respectively (Restricted) or a positive control diet formulated to supply 100% of their requirements for rapid maximum growth (Standard) for the entire 80−day period. For the third and fourth treatments, pigs were initially fed same restricted diet (11% CP and 8.6 ME (MJ/kg DM) for 40 days and then switched to a high energy (Re-Energy) or a high protein (Re-Protein) diet for the remaining 40 days. Pigs on Re-Protein and Re-Energy were offered the same diet (Restricted) for 40 days during the first period before being switched to their re-alimented diets (Re-Protein or Re-Energy) in the second period (Table 1).

Feed and ingredient samples were collected daily, frozen (−20oC), and then pooled every 14 days and subsampled for subsequent determination of DM and nutrient content. Measured quantities of feed were offered daily at 09:30 AM every morning after the leftovers of the previous day had been collected and weighed. Feed intake was calculated by subtracting the weight of the leftover feed (expressed on a DM basis) from the weight of the feed offered (expressed on a DM basis) the previous day. Tables 2 and 3 show the ingredient and nutrient composition of the diets, respectively. Feed intake and growth performance parameters (weight gains, ADG and feed efficiency) were estimated separately for the first 40 days (restricted period), the next 40 days (re−alimented period), and the entire 80−day period (overall period). Average daily gain (ADG) was estimated as the difference between the initial and final weights divided by the number of days in each period, whereas feed efficiency for each period was estimated as an ADG divided by average daily feed intake for each period.

Feed Cost and Economics of Compensatory Growth

The cost of each feed ingredient was used to estimate the cost per kg of each diet which was then used to estimate the economics of feeding the pigs; feed cost per intake and feed cost per ADG (Dritz, 2011). The cost per kg of each diet was used to calculate the daily cost of feed intake by dividing the cost per kg DM of each diet by daily kg feed intake per pig per day. The cost of daily feed intake per ADG was estimated by dividing the average daily cost of feed consumed by each pig by the ADG of each pig. Feed cost (Ghana cedis; GHS) was converted to United States Dollars (USD) at a prevailing market rate of 1.0 GHS to 4.5 USD prior to the estimation of each economic indice of feeding.

Organ Measurements and Backfat Thickness

At the end of the feeding trial, two pigs were randomly selected from each treatment. The pigs were weighed without any feeding in the morn-

Table 1: Feeding regime of pigs during the experiment

Treatment	First period (40 days)	Second period (40 days)
Standard	Pigs are fed a diet to meet their requirements for growth	Pigs are continuously fed the same Standard diet in the first period
Restricted	Pigs are fed a restricted diet (10.6% CP; 8.6 ME (MJ/kg DM) formulated to meet 42% and 33% of their CP and ME requirements respectively, compared to the Standard diet	Pigs are continuously fed the same Restricted diet fed in the first period
Re-Energy	Pigs are fed the Restricted diet	Pigs are re-alimented with a high energy (ME=11.2 MJ/kg DM) diet
Re-Protein	Pigs are fed the Restricted diet	Pigs are re-alimented with a high protein diet (CP=10.6% DM) diet

Table 2: Ingredient composition (% DM) **of Standard, Restricted and re-alimented diets offered to Ashanti Black weaner pigs**

Item	Standard[1]	Restricted[2]	Re-Energy[3]	Re-Protein[4]
Corn chaff	43.0	48.5	33.0	43.5
Millers' waste	30.0	35.0	49.5	31
Wheat bran	15.0	6.0	11.0	15
Fish meal	8.5	7.0	3.0	9.5
Oyster shell	1.0	1.0	1.0	1
Mineral−vitamin premix	2.5	2.5	2.5	2.5

[1]A standard diet formulated to meet the requirements of Ashanti Black pigs for maximum growth (Barnes and Fleischer, 1998; Addah et al., 2016). The diet was fed for the entire 80 days of the study.
[2]A nutrient-restricted diet formulated to supply only 42% and 33% of the CP and ME requirements of pigs compared to the Standard diet. The diet was fed for the entire 80 days of the study.
[3]A nutrient-restricted diet initially formulated to supply only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then then re-alimented with energy for additional 40 days.
[4]A nutrient-restricted diet initially formulated to supply only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then then re-alimented with protein for additional 40 days.

ing before being transported to the Meat Unit of the University for Development Studies, about 100 m away from the barn where the feeding trial took place. They were stunned by a direct blow to the skull and immediately bled by hoisting one of the rear legs and severing the carotid arteries and jugular veins with a sticking knife just above the breastbone at about 45° pointed toward the head (FAO, 1991). The bled carcass was then scalded in a horizontally-cut singeing barrel containing hot water (60−68°C). The carcass was dehaired by scrubbing with a knife and then singed with a gas flame before being eviscerated. The hot carcass weight (inclusive of the skin, head, and heart) was measured after the visceral organs were removed. The plucks (heart, liver, lungs, and trachea), visceral organs (liver, full and empty small and large intestines) and back fats (including skin) were also weighed individually.

The hot carcass was then halved and chilled (4° C) overnight. After 24 h, the subcutaneous backfat thickness of each halved carcass was measured at five areas using a Vernier calliper. The areas included the thickest point over the shoulder, the area between the last thoracic and first lumbar vertebrae, at three points on the sacrum: above the rostral edge of the sacrum, above the middle sacrum, and above the caudal edge of the gluteal muscle section (Jacyno *et al*., 2015). Measurements from each half were pooled and averaged for each pig. The average of the five measurements was then used to estimate backfat thickness.

Laboratory Analysis

Feed ingredients, diets, and left−overs subsampled during the feeding trial were analyzed for DM at 60°C for 48 h in a forced-air oven. The proximate composition of the diets was determined according to the official methods of analysis described by the Association of Official Analytical Chemists (AOAC, 2005). Feed samples were analyzed on DM basis for total nitrogen (CP was calculated as N × 6·25), ash, ether extract (EE), crude fibre (CF) and Nitrogen−free extract (NFE). Nitrogen−free extract was computed by the equations previously described by AAFCO (2012) and Asaro *et al* (2017) where total carbohydrate was approximated as NFE, and was calculated as: % NFE = 100−(%CP + % CF + %EE + %Ash). Metabolizable energy and Net energy of gain of diets were calculated from equations previously described by Atwater (1916) and Noblet *et al*. (1994). Metabolizable energy was estimated as ME (kcal/kg) = [4 × CP (%) + 4 × NFE (%) + 9 × crude fat (%)] × 10 whereas NEg was estimated from the equation of Noblet *et al*. (1994) modified as: NEg (MJ/kg DM) = 0.730 × ME − 0.0028 × CP + 0.0055 × EE − 0.0041 × CF + 0.0015 × NFE where NFE replaced starch (AAFCO, 2012; Asaro *et al*., 2017). Starch was not determined in the present study.

Statistical Analysis

Data on feed intake, weight gain, ADG, and feed efficiency were analyzed by Analysis of Variance using the PROC GLIMMIX procedure of SAS (1991; SAS Inst. Inc., Cary, NC) for the fixed effects in each treatment in a completely randomized design with each pigsty as the experimental unit. The data on feed intake and growth performance was adjusted for the effect of initial weight using initial weight as a covariate, whereas the data on organ weights were adjusted for the effect of final slaughter weight using slaughter weight as a covariate in the model (Kaps and Lamberson, 2009) as follows

$$y_{ij} = \mu + C_i + \beta(\chi_{ij}) + \varepsilon_{ij}$$

where y_{ijk} is the dependent variable (growth performance or weight of organs) measured in the ith treatment (ie Standard, Restricted, Re-Energy, Re-Protein) on j^{th} pig used in the growth performance and organ weight experiments; μ is the overall mean effect, β is the linear regression coefficient indicating the dependency of y_{ij} on χ_{ij}; Ci is the effect of the ith treatment (ie Standard, Restricted, Re-Energy, Re-Protein); χ_{ij} is the independent continuous variable (initial weight) used as a covariate to control error and adjust the least-square means of the dependent variable in the ith treatment; ε_{ij} is the random error. Data collected during the restricted and re-alimented periods were analyzed separately with the BY option of SAS for each period, and the 80−day period as a whole (Addah *et al*., 2016). The PDIFF option of LSMEANS was used to compare differences in least-square means using the Tukey adjustment option of SAS.

RESULTS

Effect of Re-alimentation on Dietary Nutrient Composition

The CP content of 10.6% and 13.0 in the Restricted and Re-Energy diets was lower than 16% and 15% observed in the Re-Protein and Standard diets, respectively (Table 3). Similarly, the ME concentration was reduced from 11.45 MJ/kg in the Standard diet to 8.6, 11.2 and 10.8 MJ/kg in the Restricted, Re-Energy and Re-Protein diets, respectively. Thus the nutrient restriction imposed, reduced the CP and ME concentration of the restricted diet by 42% and 33% respectively, compared to the Standard diet (Table 3).

Effect of Re-alimentation of Energy or Protein on Growth Performance and Feed Cost

The growth performance of pigs during the first and second 40-day periods, and the entire 80-day period are shown in Table 4. There was no statistical difference (P=0.646) in feed intake among pigs during the first 40 days when all the pigs except those on the Standard diet, were fed the Restricted diet. Consequently, the ADG and feed efficiencies of all treatments were similar (P>0.05) except for pigs fed the Standard diet, which had higher (P=0.001) ADG and feed efficiency than the other nutrient-restricted diets (Restricted, Re-Energy and Re-Protein).

The pattern of feed intake during the period of restriction and re-alimentation for the entire period is illustrated in Fig. 1. In the second period when protein and energy were re-alimented in Re-Protein and Re-Energy diets, respectively, feed intake was similar among pigs except that the intake of pigs on the Re-Energy diet was lower (P=0.034) than those on the Standard diet. The ADG of pigs fed Re-Protein and Standard diets were also similar (P= 0.781), whereas those fed the Re-Energy diet had higher (P=0.006) ADG than those fed the Restricted. The ADG of pigs on the Re-Energy diet did not however differ from pigs fed the Re-Protein (P=0.585) and Standard (P=0.152) diets.

Data on feed intake during the entire 80-day period indicated that feed intake was not affected (P=0.712) by restrictive dietary nutrient intake. However, consistent with our expectation, final and total weight gains of pigs fed the Restricted diet were lower (P=0.004) than the other treatments. Average daily weight gain (P=0.003) and feed efficiency (P=0.004) were higher for pigs offered the Standard diet than for the other treatments.

As expected, the daily cost per feed intake was

Table 3: Nutriet composition (% DM) of standard, restricted and re-alimented diets offered to Ashanti Black weaner pigs

Item	Req-100[1]	Restricted[2]	Re-Energy[3]	Re-Protein[4]
DM	93±0.86	93±1.0	94±0.01	93±1.0
Crude protein	15±0.1	10.6±0.39	13±0.1	16 ±1.75
Crude fat	7±0.22	8±0.50	5±0.01	2±0.02
Ash	10.±0.66	16±0.96	12±0.5	12±0.1
Crude fibre	8.7	24	9	10
NFE	60.1	41	62	60
ME (MJ/kg DM)[5]	11.45	8.6	11.2	10.8
NEg[6]	8.4	6.2	8.2	7.9

[1]Pigs were continuously fed a standard diet to meet approximately 100% of their requirements for growth for the entire 80 days of study
[2]Pigs were continuously fed a nutrient-restricted diet to meet approximately 50% of their requirements for growth for the entire 80 days of study
[3]Pigs were initially fed a nutrient-restricted diet to meet approximately 50% of their requirements for growth for the first 40 days and then re-alimented with energy for additional 40 days.
[4]Pigs were initially fed a nutrient-restricted diet to meet approximately 50% of their requirements for growth for the first 40 days and then re-alimented with a protein diet for additional 40 days.
[5]Metabolizable enrgy; ME (MJ/kg DM) = 0.31CP+0.12EE + 0.05CF+0.14NFE (Ellis, 1980).
[6]Net energy of gain; NEg was estimated from the equation of Noblet et al (1994) modified as NEg (MJ/kg DM) = 0.730ME−0.0028CP+0.0055EE−0.0041CF +0.0015NFE where starch was replaced with NFE (AAFCO, 2012; Asaro et al (2017) in the original equation.

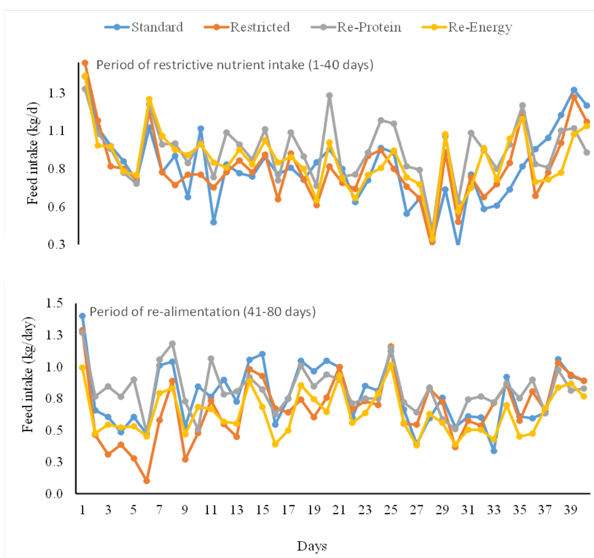

Fig. 1: Feed intake pattern of pigs during a 40-day period of nutrient-intake restriction and 40-day period of re-alimentation
Standard: Pigs were continuously fed a diet to meet their requirement for maximum growth for 80 days; Restricted: Pigs were continuously fed a nutrient-restricted diet to meet approximately only 42% and 33% of the CP and ME requirements of the Standard diet for the entire 80 days of study; Re-Energy: : Pigs were fed a nutrient-restricted diet initially formulated to meet only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then then re-alimented with energy for additional 40 days.
Re-Protein: Pigs were fed a nutrient-restricted diet initially formulated to supply only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then re-alimented with protein for additional 40 days.

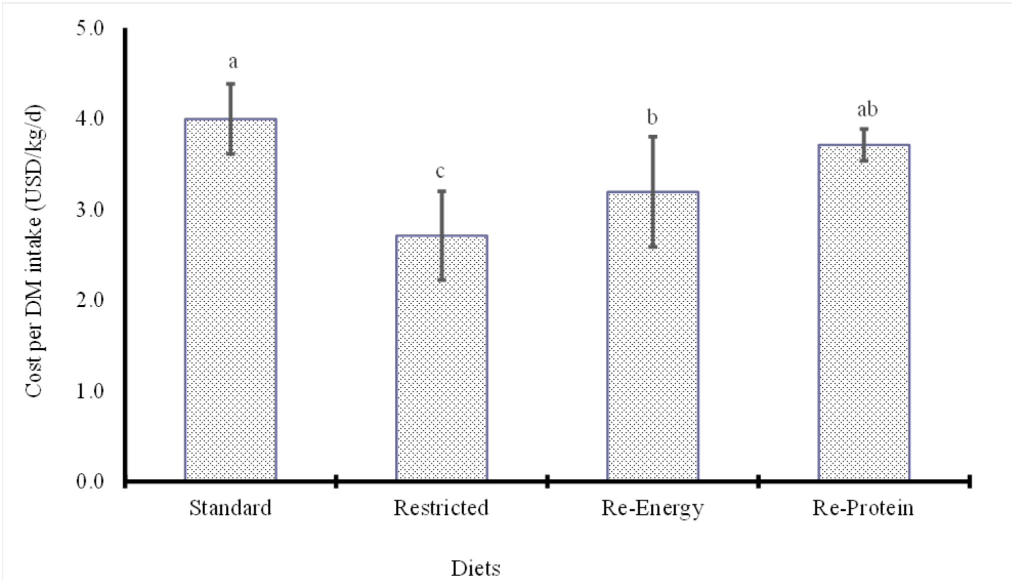

Figure 2: Effect of Realignmenting Energy or Protein on Feed Cost per Feed Intake of Ashanti Black Pigs Fed for 80 d.

Standard*: Pigs were continuously fed a diet to meet their requirement for maximum growth for 80 days; Restricted: Pigs were continuously fed a nutrient-restricted diet to meet approximately only 42% and 33% of the CP and ME requirements of the Standard diet for the entire 80 days of study; Re-Energy: Pigs were fed a nutrient-restricted diet initially formulated to meet only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then re-alimented with energy for additional 40 days; Re-Protein:-Pigs were fed a nutrient-restricted diet initially formulated to supply only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then re-alimented with protein for additional 40 days.*

higher (P=0.001) for pigs fed the Standard diet. Thus, the cost of feeding the Standard diet was nearly twice that of the Restricted diet (Fig. 2). However, it is worth noting that when the cost was expressed per daily weight gain, the difference among diets was not significant (P=0.212).

Effects of Re-alimentation on Carcass Weight and the Growth of Internal Organs

Feeding pigs continuously for the entire 80-day period with a diet formulated to achieve maximum growth (Standard) or with the nutrient-restricted diet (Restricted) did not result in significant differences in the growth of internal body organs except in the weight of the liver, belly fat, and small intestines (empty). Pigs fed the Standard diet had more belly fat than (p= 0.032) the Restricted and Re-Protein diets but similar to Re-Energy. Similarly, the weight of the small intestines (empty) was highest (P= 0.039) in pigs offered the Standard diet but lowest in pigs fed the Re-Protein diet.

DISCUSSION

The CP and ME concentrations of the Standardard diet were comparable to the requirements for growing Ashanti Black Pigs in this region (Barnes and Fleischer, 1998; Addah *et al*., 2016). Consistent with our expectation, the ADG and feed efficiency of pigs offered the nutrient-restricted diets during the first 40-day period (Restricted, Re-Energy and Re-Protein) were lower than those offered the Standard diet. This reduction could be attributed to the pigs not receiving enough of their energy and protein requirements for growth as the concentrations of ME and CP were 33% and 42% lower than the requirements for maximum growth. When pigs are fed below their standard requirements for growth, they increase the partitioning of ME for maintenance while increasing the retention of the greater part NEg as body protein rather than lipids (Hornick *et al*., 2000; Poullet *et al*., 2019). At the same time, the rates of protein synthesis and accretion are reduced while protein degradation is enhanced (Hornick *et al*., 2000). This often results in retarded growth during this period. In most parts of Ghana, the phenomenon of compensatory growth occurs naturally; there is usually human food insecurity at the beginning of the planting season, this reduces the quality of feed offered to pigs during this time because a higher degree of processing of staple cereals and legumes during periods of food scarcity extracts a greater proportion of soluble carbohydrates, lipids and proteins, thereby increasing the proportion of more fibrous and less digestible components in the left-over by-products fed to pigs in the lean dry season (Konlan *et al*., 2019). However, during the period of harvest, there

Table 4: Growth performance of pigs fed a standard diet or a nutrient-restricted diet and re-alimented with dietary high protein or energy

Item	Standard[1]	Restricted[2]	Re-Energy[3]	Re-Protein[4]	SEM	P value
First Period (1-40 days)						
Initial weight (kg)	20.96	22.10	20.21	19.92	1.264	0.589
Final weight (kg)	29.74[a]	25.80[b]	25.00[b]	26.03[b]	0.485	0.001
Weight gain (kg)	8.92	4.93	4.18	5.19	0.486	0.001
Feed intake (kg DM /d)	0.82	0.84	0.84	0.89	0.047	0.646
Average daily gain (kg/d)	0.22[a]	0.12[b]	0.10[b]	0.13[b]	0.012	0.001
Feed efficiency (ADG/feed intake)	0.28[a]	0.15[b]	0.12[b]	0.14[b]	0.018	0.001
Second Period (41-80 days)						
Initial weight (kg)	29.74[a]	25.80[b]	25.00[b]	26.03[b]	0.485	0.001
Final weight (kg)	40.11[a]	32.83[b]	39.77[a]	32.28[a]	1.323	0.004
Weight gain (kg)	10.38[ab]	7.08[b]	14.77[a]	12.24[ab]	1.437	0.010
Feed intake (kg DM /d)	0.77[a]	0.71[ab]	0.62[b]	0.73[ab]	0.035	0.034
Average daily gain (kg/d)	0.25[ab]	0.17[b]	0.35[a]	0.29[ab]	0.034	0.010
Feed efficiency (ADG/feed intake)	0.32[b]	0.204[b]	0.670[a]	0.431[ab]	0.063	0.004
Overall period (1-80 days)						
Initial live weight (kg)	20.96	22.21	20.21	19.92	1.264	0.589
Final live weight (kg)	40.81[a]	32.83[b]	39.77a	32.28[a]	1.323	0.004
Total live weight gain (kg)	19.29[a]	12.01[b]	18.95[a]	17.45[a]	1.317	0.040
Feed intake (kg DM /d)	0.79	0.78	0.79	0.81	0.034	0.712
Average daily gain (ADG; kg/d)	0.241[a]	0.150[b]	0.24[a]	0.218[a]	0.016	0.004
Feed efficiency (ADG/feed intake)	0.308[a]	0.182[b]	0.360[ab]	0.276[a]	0.027	0.003
Feed cost per weight gain (USD)	3.99	2.71	3.19	3.71	0.444	0.212

[1]Pigs were continuously fed a diet to meet their requirement for maximum growth for 80 days
[2]Pigs were continuously fed a nutrient-restricted diet to meet approximately 42% and 33% of the CP and ME requirements of the Standard diet, for the entire 80 days of study
[3]_Pigs were fed a nutrient-restricted diet initially formulated to meet only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then re-alimented with energy for additional 40 days.
[4]Pigs were fed a nutrient-restricted diet initially formulated to supply only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then re-alimented with protein for additional 40 days.
P-value indicates probability value
a-c Least square means with different superscripts differed ($P \leq 0.05$).
ADG: average daily weight gain.
SEM: pooled standard error of least square mean (n = 6).

Table 5: Effects of re-alimentation of protein or energy on the growth of body organs of Ashanti Black weaner pigs

Item (kg)	Standard[1]	Restricted[2]	Re-Energy[3]	Re-Protein[4]	SEM	P value
Hot carcass	38.58[a]	30.66[ab]	29.20[b]	33.32[ab]	1.224	0.049
Internal organs (offals)	5.88	6.80	6.43	6.38	1.356	0.978
Liver	1.60[a]	0.49[c]	0.59[c]	0.81[b]	0.031	0.001
Belly fat	1.85[a]	0.70[b]	1.26[ab]	0.76[b]	0.177	0.032
Stomach (full)	1.11	0.16	1.175	1.760	0.359	0.819
Stomach (empty)	0.33	0.32	0.28	0.32	0.065	0.933
Small intestines (full)	1.18	0.85	1.08	1.040	0.143	0.458
Small intestines (empty)	0.74[a]	0.53[ab]	0.51[ab]	0.45[b]	0.034	0.039
Large intestines (full)	1.89	2.03	2.16	1.58	0.364	0.720
Large intestines (empty)	0.80	0.64	0.77	0.76	0.150	0.892
Back fat (cm)	3.42	2.08	2.30	2.72	0.523	0.461

[1]Pigs were continuously fed a diet to meet their requirement for maximum growth for 80 days
[2]Pigs were continuously fed a nutrient-restricted diet to meet approximately 42% and 33% of the CP and ME requirements of the Standard diet, for the entire 80 days of study
[3] Pigs were fed a nutrient-restricted diet initially formulated to meet only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then re-alimented with energy for additional 40 days.
[4]Pigs were fed a nutrient-restricted diet initially formulated to supply only 42% and 33% of the CP and ME requirements of the Standard diet for 40 days and then re-alimented with protein for additional 40 days.
P-value indicates probability value
abc Least square means with different superscripts differed (P≤0.05)
SEM: pooled standard error of least square mean (n = 3)

tends to be a glut in cereal and legume grains and hence a lower extent of processing resulting in higher proportion of soluble nutrients being retained in the crop by-products after processing. For example, maize bran and brewers spent grains are major ingredients in pigs' diets in Ghana. However, Konlan *et al* (2019) observed a 2.3% reduction in the crude protein and an 8% reduction in the digestibility of maize bran between the harvest and dry seasons. They also observed a 10% reduction in the crude protein content of brewers' spent grain within the same period. These variations account for the compensatory growth patterns associated with a cyclic weight-gain-weight-loss phenomenon observed in rural pigs in Ghana. Compensatory growth is said to occur when the growth of an animal is retarded below its genetic potential due to nutrient/feed intake restrictions, but the growth is accelerated to a level equal or above those of animals of comparable genetic source fed continuously without nutrient/feed intake restrictions (Skiba, 2005).

The average reduction in ADG of pigs on the restricted-nutrient group (Restricted, Re-Protein and Re-Energy) during the first 40 days compared to the Standard was 54%. This reduction is greater than the 42% and 33% reduction in CP and ME concentration imposed in the Restricted compared to the Standard diet. Poullet *et al*. (2019) reported that the reduction in ADG due to dietary restriction was not proportional to the reduction in dietary nutrient intake imposed. Poullet *et al*. (2019) however indicated that when feed efficiency is similar between restricted and fully-fed pigs, the reduction in ADG may be less than the proportional reduction in feed/nutrient intake. In the present study, the feed efficiency of the pigs in the nutrient-restricted group was lower than those offered the Standard diet.

The concentration and quality of dietary protein and energy during the periods of restrictive intake and re-alimentation are important in the induction of compensatory growth in pigs. Increased feed intake during the period of re-alimentation has often been considered as one of the most important factors responsible for inducing compensatory growth in pigs (Hayer and Lebret, 2007; Addah *et al*., 2016) but in this study and in our previous studies with sheep (Addah *et al*., 2017), feed intake was not increased during the period of re-alimentation yet growth was only greater than animals fed the Restricted but did not differ among the other treatments. In the present study, it was also observed that the trajectory of feed intake during the re-alimentation period was quadratic for the first 28 days before gradually becoming linear towards the last 7 days (Fig. 1). It is worth noting that the intake of pigs previously underfed has a quadratic intake response during the re-alimentation period. The increased feed intake during re-alimentation gradually declines after 14 days of re-alimentation because of the reduced capacity of the gut caused by previous restrictive intake. However, after another 14 days, intake begins to increase again, stabilizing during the last 14 days of re-alimentation (Fig. 1; Skiba, 2005). As observed in Fig. 1, the intake of pigs which was restricted during the first period, stabilized after 27 days of re-feeding during the re-alimentation period. Consequently, Skiba (2005) has recommended a minimum of 3-4 weeks duration to adequately understand the intake pattern of growing pigs subjected to the restriction-alimentation regime. Rapid growth rate as a result of increased gut size during re-alimentation has been considered as the reason for compensatory growth though this explanation may only be true for species with higher capacity for intake, such as cattle (Lawrence *et al*., 1997). It thus appears that some important cues other than increased intake may be responsible for accelerated growth observed during re-alimentation. Compensatory growth in pigs following protein restriction-re-alimentation regime has also been attributed to enhanced protein digestion (Hornick *et al*., 2000), N retention (Tulils *et al*., 1986), and elevated levels of IGFF -1 and growth hormones (Hornick *et al*., 2000).

Feed cost per gain for pigs fed continuously for the entire 80 days was not different from the other feeding regimes. This indicates that farmers can achieve body weights similar to those fed continuously by restricting protein or energy intake for 40 days and then re-alimenting them for another 40 days rather than continuously feeding them for 80 days. In Ghana, the economic implication of these findings on pig farmers is significant, particularly because the cost of protein ingredients is the highest and affects farmers' profit margins.

Even though feed conversion efficiency is an important biological indicator of productivity, feed cost per gain is a more direct and practical indicator of economic returns as it measures the impact of feed efficiency on economic performance and herd profitability (Dritz, 2011). The fact that feed cost per intake and ADG are not statistically different between Re-Protein and the Standard diet suggest that pig farmers could reduce the protein content of their pig diets during the lean season when most protein ingredients are expensive and then increase the protein content later when proteinous ingredients become abundant without affecting overall ADG.

The components of gain (ADG) observed during compensatory growth are important. Suppose the growth of non-carcass components such as the head and viscera and skin are susceptible to malnutrition (Tullis *et al*., 1986), in that case, it seems likely that they will respond to induction of compensatory growth evidently than carcass components such as skeletal muscle. This will result in compensatory growth of body parts that have less economic value. In particular, when dietary energy is adequate, comparable to standard-fed pigs, and protein is the limiting nutrient to rapid growth, pigs tend to have higher fat deposition relative to protein deposition during re-alimentation (Skiba *et al*., 2001). The liver weight was lowest for pigs fed the Restricted and Re-Energy diets but as expected, highest for those fed the Standard, whereas those fed the Re-Protein diet had a medium liver weight. When the nutrient intake of pigs is reduced, metabolically active organs such as the liver are among the first to respond to nutritional stress. The physiological mechanisms by which the protein restriction-re-alimentation regime induces compensatory growth in pigs has previously been explained differently; the phenomenon affects the secretion of insulin-like growth factor-1 and glycolipid metabolism by promoting the growth and multiplication of skeletal tissue (Zhang *et al*., 2020). The involvement of the liver in these processes in response to protein restriction-re-alimentation possibly accounts for its increased weight as observed in this study for pigs re-alimented with protein compared to those fed the Restricted or Re-Energy diets. The liver appears to have an effect on the re-alimentation of protein on skeletal muscle growth and liver function. Consequently, pigs with higher liver weights correspondingly had heavier hot carcass weights (Table 5).

The greater belly fat weight observed for pigs on the Standard diet suggests that the weight gain observed may be due to more fatty tissues deposition than that observed in the Re-Protein diet. In our previous studies (Addah *et al*., 2016), we already hypothesized that the gain observed due to protein re-alimentation was largely attributed to protein accretion than fatty acids deposition.

CONCLUSION

Reducing the protein requirements of Ashanti Black grower pigs by 42% during periods of feed scarcity and then re-alimenting it during periods of feed abundance to meet their standard requirements can be employed to reduce feed cost and improve profit margins of pig farmers in Ghana without adverse effects on growth performance.

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Compliance with ethical standards: The pigs were cared for and managed in accordance with the ethical considerations for handling experimental animals according to the Research Ethics Policy of the University for Development Studies, Tamale, Ghana.

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