

Energy metabolism of growing pigs during protein and energy deficiency and subsequent realimentation

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ABSTRACT

The energy metabolism of pigs, which initially differed in energy reserve in the body and size of internal organs, was measured using the comparative slaughter method on 90 Polish Landrace gilts kept individually and grown from 15 to 70 kg. During a restriction period from 15 to 25 kg, the pigs of group P consumed 40% less protein daily, while the pigs of group E 40% less feed as compared with the C pigs (control). During subsequent realimentation from 25 to 70 kg, all of the pigs were fed *ad libitum* (A), or at two *restricted feeding levels*: 85 (R85) or 60% (R60) of *ad libitum* intake, diets with low (12.4 MJ ME - L) or high (13.2 MJ ME - H) energy density. Thus, pigs were fed at five feeding levels: A_H, A_L, R_{85H}, R_{85L}, R_{60H}. The animals were slaughtered successively at 15 (n=4), 25 (n=12, four from the C, P and E groups) and 70 kg body weight (n=74). After slaughter, the protein and fat content in the body was estimated. Energy metabolism was measured according to a two-step model as recommended by ARC (1981), using the following equations: (1) $MEI = ME_m + (1/k_g) \times RE$; (2) $(ME - ME_m) = (1/k_p) \times \Delta P + (1/k_f) \times \Delta F$. During the restriction period the maintenance requirement (ME_m) amounted to 647 kJ/kg^{0.75}, utilization of ME energy for growth, 62% ($k_g = 0.62$), and coefficients k_p and k_f 0.48 and 0.71, respectively. During realimentation the maintenance requirement (ME_m) amounted on average to 591 kJ/kg^{0.75}. Utilization of ME energy for growth came to 56% ($k_g = 0.56$), and for protein and fat, 36 ($k_p = 0.36$) and 74% ($k_f = 0.74$), respectively. Younger animals utilized ME energy for growth more efficiently than older ones due to better utilization of ME energy for protein deposition.

KEY WORDS: pig, growth, energy metabolism

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INTRODUCTION

Results of previous work on compensatory growth (Skiba et al., 2001) showed that the kind of underfeeding applied during the restriction period influenced fat storage in the body as well as the size of internal organs. At the end of the restriction period, animals underfed with protein increased, whereas those underfed for feed, decreased fat reserves in their body. Additionally pigs underfed with feed had smaller internal organs. Thus, the physiological and energy status of pigs underfed in two ways was completely different at the start of the subsequent realimentation period.

Based on scarce literature data (e.g., Close et al., 1983) it could be assumed that during compensatory growth: 1. pigs that had greater adiposity of their body would be able to utilize some part of body fat as an energy source to compensate protein gain during subsequent realimentation, 2. pigs that had smaller internal organs would have lower maintenance requirements (Noblet et al., 1997) so a larger part of the energy consumed with feed could be assigned to cover their growth requirement. In both cases utilization of ME could be better than in pigs continuously fed at a "normal" level, and the energy metabolism processes of these two different groups of pigs would proceed in different pathways.

MATERIAL AND METHODS

The study was carried out on 90 Polish Landrace gilts. During a restriction period from 15 to 25 kg the pigs of group P (n=27) consumed 40% less protein, while the pigs of group E (n=31) 40% less feed as compared with the C animals (control, n=32). During subsequent realimentation from 25 to 70 kg the pigs were fed *ad libitum* (A), or at two *restricted feeding levels*: 85 (R85) or 60% (R60) of *ad libitum* intake, diets with low (12.4 MJ ME - L) or high (13.2 MJ ME - H) energy density. Thus, pigs were fed at five feeding levels: A_H , A_L , R_{85H} , R_{85L} , R_{60H} . A detailed description of feed values and experimental design was given in a previous paper (Skiba et al., 2001). The lower *level of restricted feeding* (R_{60H} - 60% of *ad libitum* intake) was applied to diversify energy consumption by animals, which is an essential factor for studying energy metabolism by the comparative technique. Pigs were slaughtered successively at 15 (n=4), 25 (n=12, four from the C, E and P groups), and 70 kg body weight (n=74). After slaughter the protein and fat contents were estimated in the body (AOAC, 1994). Protein and fat gain in the body was calculated from the difference between the final and initial content of these components (25 and 15 kg and 70 and 25 kg, respectively during restriction and realimentation). The energy content in the body was calculated based on protein and fat contents as the main body's energy components using coefficients of 23.9 and 39.8 kJ/g, respectively. For metabolic body mass (kg) calculation, the

exponent of 0.75 was applied. The ME content of the diets was calculated based on digestible energy (DE) using a correction for protein content according to Noblet et al. (1989). Heat production (HP) was expressed as the difference between intake of metabolizable energy (MEI) and energy retained in the body (RE).

Energy metabolism was measured in a two-step model according to the equation recommended by ARC (1981). First, maintenance requirements and utilization of ME for growth were calculated (Equation 1):

$$\text{MEI} = \text{ME}_m + (1/k_g) \times \text{RE} \quad (1)$$

where: MEI = intake of metabolizable energy, kJ/kg^{0.75}

ME_m = ME for maintenance

RE = energy retained in the body

k_g = utilization of ME for growth (protein and fat deposition).

Second, utilization of ME for growth (k_g) was partitioned among protein and fat deposition based on metabolizable energy intake by pigs, decreased their maintenance requirement, established according to Equation 1 (Equation 2):

$$(\text{ME} - \text{ME}_m) = (1/k_p) \times \Delta P + (1/k_f) \times \Delta F \quad (2)$$

were: k_p = utilization of ME for protein deposition

k_f = utilization of ME for fat deposition

ΔP = protein deposition, g/day

ΔF = fat deposition, g/day.

Statistical analyses were performed by Statgraphics 6.0 software using analysis of variance ANOVA and regression analysis.

RESULTS

Restriction period (15-25 kg)

Daily energy retention in the body during the restriction period in the pigs of groups P and C was similar but greater ($P < 0.01$) than in the animals of group E (493 and 468 vs 151 kJ/kg^{0.75}, respectively), (Table 1). Both underfed groups of pigs deposited a similar amount of energy as protein but less ($P < 0.01$) than the C pigs, (97 and 95 vs 166 kJ/kg^{0.75}, respectively for the P and E and C pigs). The E pigs were characterized by greater ($P < 0.01$) heat losses as compared with the P and C pigs (82.9 vs 63.3 and 67.9, respectively).

TABLE 1

Daily energy balance during restriction period (15-25 kg), kJ/kg^{0.75}

Item	Group			S.E.
	P n=4	C n=4	E n=4	
Energy intake (MEI)	1389 ^B	1457 ^B	881 ^A	11.81
Energy retained (RE)	493 ^B	468 ^B	151 ^A	0.01
Energy retained as protein (RE _p)	97 ^A	166 ^B	95 ^A	2.44
Energy retained as fat (RE _f)	396 ^C	302 ^B	56 ^A	6.65
Heat production (HP)*, %	63.3 ^A	67.9 ^A	82.9 ^B	0.02

* , HP = ((MEI-RE)/MEI) x 100

^{A, B, C}P < 0.01

It was not possible to calculate the maintenance requirements separately for particular groups of pigs. The maintenance requirement established for all pigs amounted 647 kJ/kg^{0.75} (Equation 3). Utilization of ME energy for growth amounted 62% (1/1.61; $k_g = 0.62$), and coefficients k_p and k_f 0.48 (1/2.10) and 0.71 (1/1.41), respectively (Equation 4).

$$\text{MEI} = 647 (\pm 51) \text{ME}_m + 1.61 (\pm 0.13) \times \text{RE} \quad (3)$$

$$R^2 = 0.93, \text{ s.e.} = 69, n = 12$$

$$(\text{MEI} - \text{ME}_m) = 2.10 (\pm 0.29) \times \Delta P + 1.41 (\pm 0.12) \times \Delta F \quad (4)$$

$$R^2 = 0.93, \text{ s.e.} = 61, n = 12$$

Realimentation period (25-70 kg)

Daily energy deposition in the pigs' body during realimentation depended ($P < 0.01$) on feeding intensity (Table 2) and ranged from 363 (level R_{60H}) up to 634 kJ/kg^{0.75} (level A_H). Pigs deposited from 141 to 202 kJ/kg^{0.75} energy as protein and from 222 to 432 kJ/kg^{0.75} as fat. The amount of energy consumed daily did not influence body heat losses (on average 65%) except in pigs on the lowest feeding intensity (level R_{60H}). This group of pigs had greater ($P < 0.01$) heat losses (71%) as compared with the animals of the remaining groups.

The total amount of energy deposited in the body did not differ between the C, P and L groups of pigs (Table 2). However, the P pigs deposited the largest amount of energy as protein daily (180 kJ/kg^{0.75}), but lowest as fat (345 kJ/kg^{0.75}), ($P < 0.01$). The L pigs deposited the same amount of energy as protein daily as compared with the C pigs (167 vs 167 kJ/kg^{0.75}) and slightly more as fat (395 vs 361 kJ/kg^{0.75}). Daily heat losses did not differ between groups of pigs (on average 65.7%).

TABLE 2

Daily energy balance during realimentation period (25-70 kg), kJ/kg^{0.75}

Energy	Group	Feeding level					Mean ± s.e.
		R _{60H} n=14	R _{85L} n=15	R _{85H} n=15	A _L n=15	A _H n=15	
Intaked MEI	P	1246	1467	1583	1624	1865	1557
	C	1243	1491	1537	1604	1814	1538
	E	1265	1473	1598	1749	1817	1580
	Mean	1252 ^A	1477 ^B	1573 ^C	1659 ^D	1832 ^E	1558 ± 11.9
Retained RE	P	369	480	567	577	632	525
	C	356	508	566	600	623	528
	E	365	545	552	703	646	562
	Mean	363 ^A	511 ^B	562 ^C	627 ^D	634 ^D	538 ± 9.0
Retained as protein RE _p	P	153	168	195	173	211	180 ^B
	C	138	149	170	169	211	167 ^A
	E	131	168	174	177	183	167 ^A
	Mean	141 ^A	162 ^B	179 ^C	173 ^{BC}	202 ^D	171 ± 2.18
Retained as fat RE _f	P	216	312	372	404	421	345 ^A
	C	218	359	396	431	412	361 ^{AB}
	E	234	377	378	526	463	395 ^B
	Mean	222 ^A	349 ^B	382 ^{BC}	454 ^D	432 ^{CD}	367 ± 8.21
Heat production HP*	P	70.4	67.3	64.1	64.4	65.8	66.4
	C	71.4	65.9	63.9	62.7	65.7	65.9
	E	71.1	63.0	65.4	59.8	65.0	64.9
	Mean	71.0 ^A	65.2 ^A	64.5 ^A	62.3 ^A	65.5 ^A	65.7 ± 0.46

*, HP= ((MEI-RE)/MEI) x 100

A, B, C, D, E P<0.01

Maintenance requirements established for all pigs amounted on average to 591 kJ/kg^{0.75} and utilization of ME energy for growth 56% ($k_g = 0.56$; Equation 5). Utilization of ME for protein amounted to 36% ($k_p = 0.36$) and for fat 74% ($k_f = 0.74$; Equation 6).

$$\text{MEI} = 591 (\pm 96) \text{ME}_m + 1.80 (\pm 0.17) \times \text{RE} \quad (5)$$

$$R^2 = 0.88, \text{ s.e.} = 70, n = 76$$

$$(\text{MEI} - \text{ME}_m) = 2.76 (\pm 0.54) \times \Delta P + 1.35 (\pm 0.25) \times \Delta F \quad (6)$$

$$R^2 = 0.93, \text{ s.e.} = 63, n = 76$$

In the study presented here, an attempt to estimate the energy balance according to the classical equation (Kielanowski, 1965) was also made (Equation 7). The

maintenance requirement (ME_m) amounted to 567 kJ/kg^{0.75}, utilization of ME for protein, 29 % ($k_p = 0.29$), and for fat, 91 % ($k_f = 0.91$), respectively.

$$MEI = 567(\pm 81) ME_m + 3.47 (\pm 0.53) \times \Delta P + 1.08 (\pm 0.14) \times \Delta F \quad (7)$$

$$R^2 = 0.72, \text{ s.e.} = 108; n = 76.$$

DISCUSSION

The greater, though insignificant, heat losses during the restriction period of the control pigs (group C) as compared with the pigs underfed with protein intake (group P) resulted from the difference in the proportion between energy retained as protein and fat, which amounted to 0.55 and 0.24, respectively, since utilization of ME for fat deposition is much more efficient than for protein deposition. The very high heat loss of the pigs underfed with feed intake (group L) was caused by the very low feeding level of this group of pigs.

Utilization of ME for protein deposition ($k_p = 0.48$) during the restriction period was comparable to the results given by other authors (e.g., Noblet et al., 1988). The coefficient of energy utilization for fat deposition ($k_f = 0.71$) is close to the theoretical value given by Schiemann et al. (1971) for diets similar to the mixture used in our study.

The maintenance requirement (ME_m) according to the terminology in animal and human energy metabolism (Venk et al., 2001) is described as a situation where the energy intake equals the energy output and hence no energy will be retained (i.e. as growth, milk, eggs). Although ME_m is clearly defined, it is very difficult to measure, especially in producing animals, as energy accretion or production are "normal" physiological processes of young organisms. The situation becomes even more complicated as ME_m is often defined to include "normal activity". In young animals at least 1/3 of the maintenance requirement is used to cover their requirements connected with physical activity. Thus, separation of ME_m maintenance requirements is virtually impossible and seems to have no physiological meaning in this group of animals. A more common opinion is that utilization of ME energy for protein deposition and maintenance requirement should be considered together. However, in our study we tried to partition the energy in the pigs' body according to the "classic" way separating maintenance requirement (ME_m), utilization of ME for protein (k_p), as well as for fat deposition (k_f). The estimated ME_m was high, but still in the upper range of values obtained earlier (e.g., Fernandez et al., 1985). The high value of ME_m was probably caused by the physical activity of the pigs due to freedom of movement in the pen as opposed to restricted movements in metabolic cages. In most studies on energy metabolism, pigs were kept in metabolic cages and had restricted mobility. The impossibility of deter-

mining ME_m separately for particular groups of pigs does not mean that it could not differ between groups. When assuming that utilization of ME for protein and fat during the restriction period was similar for all groups (48 and 71%, respectively), the maintenance requirement should amount to 681 kJ/kg^{0.75} (group C), 627 kJ/kg^{0.75} (group P), and 603 kJ/kg^{0.75} (group E), and was significantly different ($P < 0.05$) between the control (C) and the pigs restricted with feed (the E pigs). So, the calculated values of ME_m indicated that at the start of realimentation, pigs underfed with feed could differ from those fed at standard intensity. This could be explained by smaller organ size (Skiba et al., 2001), since organ size is responsible for fasting heat production to a large degree (Noblet et al., 1997).

During the realimentation period the feeding level did not influence body heat losses except for pigs on the lowest feeding intensity (level R_{60H}), which is characteristic of the situation when the maintenance requirement predominates the needs of growth. ME_m during realimentation was high, partly due to the housing system, which closely resembled the situation in practice (pigs kept without bedding in large pens permitting free movement). The value of the maintenance requirement presented here is similar to earlier data obtained using the same method (Kielanowski, 1965; Fandrejewski, 1992). The remaining components of the Equation 6: $k_p = 0.36$ and $k_f = 0.74$ are comparable to the values given by other authors (Ewan, 1983). In the pigs that deposited approximately 130 g protein/day (similarly to animals used in this study) utilization of ME for protein deposition (k_p) should not be lower than 0.35 (Fandrejewski, 1992).

This study showed that coefficient k_g was greater in young pigs (growing from 15 to 25 kg) than in older animals (growing from 25 to 70 kg). It means that utilization of ME for growth is more efficient in young animals. Considering that utilization of ME for fat deposition (k_f coefficients) was similar in both groups of pigs, and close to data shown in literature (ARC, 1981) better utilization of ME for growth in younger animals must have resulted from better utilization of ME for protein deposition since the k_p coefficient was 12% higher in the younger than in the older pigs.

The energy metabolism established using the Kielanowski (1965) formula (Equation 7) indicated that the value of the maintenance requirement is slightly lower than when it is established according to Equation 6. However, the value of coefficient k_p was extremely low (0.29) and the efficiency of ME for fat was very high ($k_f = 0.91$). Both values are very difficult to accept and coefficient k_f even exceeded the theoretical value for *in vitro* study (Schiemann et al., 1971).

Unfortunately, in the present study we did not manage to establish maintenance requirements, as well as efficiency of ME for protein (k_p) and fat (k_f) deposition separately for groups of animals differing in energy storage (group E) and maintenance requirements (group E) at the beginning of the realimentation period. It seems that both systems: classical (Kielanowski, 1965 - multiple regression with

three independent variables) and the two-step model recommended by ARC (1981) include into body energy metabolism only energy consumed with feed and not energy that could be mobilized from the pig's stored body fat. Evidence for the existence of this relationship was the highly significant correlation ($r = 0.33$) between fat stores at the beginning of the realimentation period and daily protein deposition. Test relationships between daily protein deposition, fat stores and energy intake using multiple regression analysis (Equation 8) also made it possible to confirm that body fat stores of pigs assisted in protein metabolism.

$$\Delta P = -0.04 (\pm 0.1) + 4.1 (\pm 0.44) \times \text{MEI} + 5.4 (\pm 1.8) \times F_{25} \quad (8)$$

$$R^2 = 0.54, \text{ s.e.} = 13.4, n = 76$$

where: ΔP = daily protein deposition
 MEI = daily metabolizable energy intake, MJ
 F_{25} = fat content at 25 kg body weight.

When analysing this equation it could be concluded that increasing initial body fat stores at 25 kg by 1 kg caused an increase in daily protein deposition by 5.4 g. Because in this study the difference between pigs underfed with protein and those underfed with feed amounted to over 2 kg (Skiba et al., 2001) this factor could be attributed to a difference in protein deposition of at least 60%. As no other studies have been performed to elucidate this relationship, a discussion must await further detailed work to be conducted.

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STRESZCZENIE

Przemiana energii u rosnących świń w okresie niedoboru białka lub energii oraz w okresie realimentacji

Przemianę energii u świń różniących się zawartością energii w ciele oraz masą narządów wewnętrznych oznaczano metodą ubojową na 90 świnich (loszkach) rasy pbz od 15 do 70 kg m.c. W okresie niedoborowym, od 15 do 25 kg, świnie grupy P pobierały dziennie o 40% mniej białka, a zwierzęta grupy E o 40% mniej paszy w porównaniu ze świniami grupy kontrolnej (C). W okresie realimentacji, od 25 do 70 kg, świnie żywiono z różną intensywnością: A_H , A_L , R_{85H} , R_{85L} , R_{60H} paszą o większej (13,2 MJ EM) lub mniejszej (12,4 MJ EM) zawartości energii. Zwierzęta ubito przy masie ciała 15 (n=4), 25 (n=12, po cztery z grup P, E, C) i przy 70 kg (n=74). Po uboju oznaczono zawartość białka i tłuszczu w ciele świń. Przemianę energii badano w dwóch etapach (ARC, 1981) posługując się następującymi równaniami regresji: (1) $MEI = ME_m + (1/k_g) \times RE$; (2) $(ME - ME_m) = (1/k_p) \times \Delta P + (1/k_f) \times \Delta F$. W okresie niedoborowym zapotrzebowanie bytowe oszacowano na 647 kJ/kg^{0.75}, wykorzystanie energii na wzrost wynosiło 62% ($k_g = 0.62$), wykorzystanie energii na odłożenie białka 48, a na odłożenie tłuszczu 71% ($k_p = 0.48$; $k_f = 0.71$). W okresie realimentacji zapotrzebowanie bytowe świń wynosiło średnio 591 kJ/kg^{0.75}, wykorzystanie energii na wzrost 56% ($k_g = 0.56$), a oddzielnie na odłożenie białka i tłuszczu odpowiednio 36 ($k_p = 0.36$) i 74% ($k_f = 0.74$). Zwierzęta młodsze (od 15 do 25 kg) wykorzystywały energię na wzrost lepiej niż starsze (od 25 do 70 kg) przede wszystkim dzięki lepszemu wykorzystaniu energii na odłożenie białka.