animal

Effects of fermentable starch and straw-enriched housing on energy partitioning of growing pigs

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Both dietary fermentable carbohydrates and the availability of straw bedding potentially affect activity patterns and energy utilisation in pigs. The present study aimed to investigate the combined effects of straw bedding and fermentable carbohydrates (native potato starch) on energy partitioning in growing pigs. In a 2 × 2 factorial arrangement, 16 groups of 12 pigs (approximately 25 kg) were assigned to either barren housing or housing on straw bedding, and to native or pregelatinised potato starch included in the diet. Pigs were fed at approximately 2.5 times maintenance. Nitrogen and energy balances were measured per group during a 7-day experimental period, which was preceded by a 30-day adaptation period. Heat production and physical activity were measured during 9-min intervals. The availability of straw bedding increased both metabolisable energy (ME) intake and total heat production (P < 0.001). Housing conditions did not affect total energy retention, but pigs on straw bedding retained more energy as protein (P < 0.01) and less as fat (P < 0.05) than barren-housed pigs. Average daily gain (P < 0.001), ME intake (P < 0.001) and energy retention (P < 0.01) were lower in pigs on the native potato starch diet compared to those on the pregelatinised potato starch diet. Pigs on the pregelatinised potato starch diet showed larger fluctuations in heat production and respiration quotient over the 24-h cycle than pigs on the native potato starch diet, and a higher activity-related energy expenditure. The effect of dietary starch type on activity-related heat production depended, however, on housing type (P < 0.05). In barren housing, activity-related heat production was less affected by starch type (16.1% and 13.7% of total heat production on the pregelatinised and native potato starch diet, respectively) than in straw-enriched housing (21.1% and 15.0% of the total heat production on the pregelatinised and native potato starch diet, respectively). In conclusion, the present study shows that the availability both of straw bedding and of dietary starch type, fermentable or digestible, affects energy utilisation and physical activity of pigs. The effects of housing condition on protein and fat deposition suggest that environmental enrichment with long straw may result in leaner pigs. The lower energy expenditure on the physical activity of pigs on the native potato starch diet, which was the most obvious in straw-housed pigs, likely reflects a decrease in foraging behaviour related to a more gradual supply of energy from fermentation processes.

Keywords: energy metabolism, environmental enrichment, resistant starch, satiety, straw bedding

Introduction

Dietary fermentable carbohydrates, such as non-starch poly-saccharides (NSP) and resistant starch (RS), have been shown to reduce energy expenditure on physical activity in restrictively fed growing pigs, likely due to enhanced fermentation in the gastrointestinal tract (Schrama *et al.*, 1998; Schrama and Bakker, 1999). This reduced activity partly compensates for the low NE value of fermentable carbohydrates (Schrama

et al., 1998). Reduced activity following NSP or RS intake has been suggested to reflect increased satiety, and therefore fermentable carbohydrates may improve welfare in restrictedly fed pigs (Gerrits *et al.*, 2003; De Leeuw *et al.*, 2005). It is unknown, however, which behavioural activities are affected by adding fermentable carbohydrates to the diet of growing pigs.

Behavioural effects of fermentable carbohydrates may be studied most easily under housing conditions that allow for the performance of a broad behavioural repertoire. Environmental enrichment by providing 'rooting material', such as

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straw bedding, strongly influences behaviour of pigs. Straw serves as an outlet for the motivation to perform foraging behaviours, such as chewing, rooting and digging, and in this way profoundly improves welfare (Fraser *et al.*, 1991; Beattie *et al.*, 1995; Tuyttens, 2005). The effects of straw bedding on energy partitioning in group-housed, growing pigs have not been studied so far. Straw bedding could affect energy partitioning in different ways. Besides the influence of straw intake on energy utilisation, straw bedding may increase energy expenditure on activity, because pigs supplied with rooting material are generally more active than barren-housed pigs (Fraser *et al.*, 1991; Beattie *et al.*, 1995; Bolhuis *et al.*, 2006). It is unknown whether and how these effects of straw bedding on activity and energy partitioning of pigs interact with the effects of dietary fermentable carbohydrates.

The aim of this study was to investigate (1) the quantitative impact of straw bedding on energy partitioning in pigs; (2) the effects of fermentable carbohydrates (native potato starch (NS)) on behaviour in group-housed pigs; and (3) the interaction of both factors, straw bedding and fermentable carbohydrates, on energy partitioning and behaviour in pigs. The effects of provision of straw bedding and fermentable carbohydrates on energy metabolism are reported in the current paper. The effects on behaviour, straw intake and intestinal weight are reported elsewhere (Bolhuis *et al.*, 2007; Staals *et al.*, 2007; Bolhuis *et al.*, in preparation).

Material and methods

Animals and housing
Effects of housing (enriched with straw bedding, S, or barren, B) and type of potato starch in the diet (pregelatinised (PS) or NS) on energy partitioning of growing pigs were assessed, using a 2×2 factorial arrangement. The experiment was carried out in eight successive batches. Each batch consisted of a 30-day adaptation period, of which the last 7 days were spent in climate respiration chambers, followed by a 7-day experimental period in these chambers. Two treatment combinations were tested per batch, resulting in four groups (of 12 pigs each) per treatment combination.

Per batch, 32 growing [Pietrain $\times$ (Yorkshire $\times$ Finnish Landrace)] gilts of 25 ± 2 kg were assigned to either B or S housing. During the first 23 days of the adaptation period, gilts were group-housed ($n = 8$ per group) in 10.6 m^2 pens. B pens consisted of 5.8 m^2 slatted and 4.8 m^2 solid concrete floor. In S pens, 5.4 m^2 of the floor was covered with rubber mats and a bedding of long wheat straw (approximately 8 kg per pen at the start), which was separated from the rest of the pen by a barrier ($3.00 \times 0.05 \times 0.20$ m) that could easily be crossed by the piglets. Pens had one nipple drinker and a feed trough ($3.60 \times 0.31 \times 0.17$ m), which could be closed. Room temperature was set at 20°C.

After the first 23 days of the adaptation period, six selected pigs (based on body weight) from each pen were transported to one of two identical climate respiration chambers (Verstegen *et al.*, 1987). Pigs were habituated to the climate respiration chambers and the smaller group sizes for 7 days before measurements started. Each chamber contained two 8.9 m^2 pens, and two groups of six pigs, with the same treatment combination, were housed per chamber. B pens consisted of 1.5 m^2 slatted and 7.4 m^2 solid floor. In S pens, 5.3 m^2 of the floor surface was covered with straw (9 kg at the start of each week); this part was separated from the rest of the floor by a barrier ($3.00 \times 0.05 \times 0.20$ m). Pens contained two drinking nipples and a feed trough, which could be closed. Temperature was kept constant at 20 °C. Relative humidity was maintained at 65%.

Throughout the experiment, all pens were cleaned in the morning. Soiled straw was removed from the S pens and replaced with fresh straw (2.3 and 3.0 kg per pen per day during the adaptation and climate respiration period, respectively). During the 7-day experimental period, soiled straw was stored until the end of this period. Animals were exposed to 12 h of light (0600 h to 1800 h) and 12 h of dimness. The Animal Use and Care Committee of Wageningen University approved the experimental protocols.

Diets and feeding
Pigs were gradually adapted, in 4 days, to the experimental diets and to restricted access to the feed troughs. They were fed a diet with either PS or NS. Except for the type of potato starch, raw materials of both diets were identical (Table 1). In the PS diet 35% potato starch was included, whereas in the NS diet 39.2% was included to compensate for a lower dry matter (DM) content of the NS. Consequently, the feeding level (in kg) of the NS-fed pigs was 4.2% higher than that of the PS-fed pigs. Diatomaceous shell powder (3%) was included in both diets, because acid-insoluble ash was used as an indigestible marker. The analysed nutrient composition of both diets and the wheat straw supplied is given in Table 2.

Pigs were fed at 2.5 times the energy for maintenance (MEm = 450 kJ/kg$^{0.75}$ per day; ARC, 1981). The amount of feed was adjusted daily, based on animal weight and expected daily gain. Diets were fed twice a day in mash form (water: feed = 2.8:1) in the feed troughs, which were open until 30 min after feeding. During the adaptation period, pigs were fed at 0700 h and 1600 h. In the climate respiration chambers, pigs were fed at 0630 h and 1530 h. Water was available *ad libitum*.

Measurements
Body weights of individual pigs were determined weekly. Exchange of O_2, CO_2 and CH_4 was measured in 9-min intervals as described by Verstegen *et al.* (1987). Physical activity was monitored continuously by two radar devices per chamber (Verstegen *et al.*, 1987). Changes in the frequency of the reflected radar waves due to movement of the animals (Doppler effect) were converted into electrical pulses and recorded in the same 9-min intervals.

Table 1 *Composition of the experimental diets*

Ingredient	Pregelatinised	Native
Soy oil	3.00	3.00
Wheat fibre (Xylo-Gold, Meneba, Weert, The Netherlands)	4.00	4.00
Sugar beet pulp (<100 g/kg sugar)	5.00	5.00
Barley	10.00	10.00
Wheat	16.24	16.24
Wheat gluten	9.00	9.00
Potato protein (Protastar)	9.40	9.40
Pregelatinised potato starch[1]	35.00	
Native potato starch (Paselli WA 4)[1]		39.20
Vitamin mineral premix[2]	0.50	0.50
Limestone	1.20	1.20
Monocalcium phosphate	1.30	1.30
L-Lysine HCl	0.29	0.29
DL-Methionine	0.02	0.02
Magnesium oxide (80%)	0.05	0.05
KCl	0.50	0.50
NaHCO$_3$	1.50	1.50
Indigestible marker (acid insoluble ash)	3.00	3.00
Total	100.00	104.20

[1]Except for potato starch type, raw materials of both diets were identical. To compensate for the lower dry matter (DM) content of the native potato starch, 35% potato starch was included in the PS diet and 39.2% in the NS diet. Consequently, the feeding level of the NS-fed pigs was 4.2% higher than that of the PS-fed pigs.

[2]Provided the following per kg of feed (of the P diet): vitamin A: 10 000 IU, vitamin B$_{12}$: 20 μg; vitamin D$_3$: 2000 IU; vitamin E: 30 mg; vitamin K$_3$: 1.5 mg; D-panthothenic acid: 12 mg; niacin: 20 mg; folic acid: 0.2 mg; riboflavin: 4 mg; choline chloride: 150 mg; Fe: 100 mg (FeSO$_4$.H$_2$O); Cu: 20 mg (CuSO$_4$.5H$_2$O); Zn: 70 mg (ZnSO$_4$.H$_2$O); Mn: 30 mg (MnO); Co: 0.15 mg (CoSO$_4$.7H$_2$O); I: 0.75 mg (KI); Se: 0.20 mg (Na$_2$SeO$_3$).

Table 2 *Analysed nutrient composition of the experimental diets and straw (g/kg dry matter, unless indicated otherwise)*

	Pregelatinised	Native	Straw
Dry matter (g/kg product)	907	879	900
Energy (MJ/kg)	18.1	18.1	17.0
Crude protein	203	202	41
Crude fat	29	32	9
Crude ash	80	81	125
Starch	509	518	8
ADF	45	47	451
Sugars	11	11	1

Manure was collected quantitatively. In the S chambers, manure and soiled straw were collected as two separate fractions, homogenised and sampled. In order to increase homogeneity and to allow for representative sampling, visible faeces were removed from the soiled straw by washing. Faeces and washing water were added to the manure fraction. After weighing, the washed soiled straw was spread out over an area of approximately 8 m^2 and sampled for energy and N analysis at six different spots. To evaluate this sampling procedure of the soiled straw fraction, in one batch the six different samples were analysed separately; coefficients of variation of air DM in soiled straw, DM in air dry samples, DM and N in fresh material were 2.6%, 0.6%, 2.4% and 2.8%, respectively.

Aerial NH$_3$ was quantitatively trapped in 4.5 M sulphuric acid and in water that condensed on the heat exchanger (Verstegen *et al.*, 1987). Feed and fresh straw were sampled during each experimental period. DM content in feed, manure, and fresh and soiled straw was determined according to ISO 6496 (1998b). Kjeldahl N content was determined according to ISO 5983 (1997) in feed, manure, and fresh and soiled straw and in NH$_4^+$-containing sulphuric acid and water that condensed on the heat exchanger. Crude fat and crude ash content in feed and fresh straw were analysed according to ISO 6492 (1999)

and ISO 5984 (2002), respectively. The starch and sugar content in feed and fresh straw was determined as described previously (Rijnen *et al.*, 2001). ADF was analysed according to ISO 13906 (2006). Gross energy (GE) content in feed, manure, and fresh and soiled straw was analysed using adiabatic bomb calorimetry (IKA-calorimeter C7000, Staufen, Germany) according to ISO 9831 (1998a).

To assess heat production and CH$_4$ emission of manure and manure with straw, gaseous exchanges were measured during 1 day after departure of one batch of experimental pigs. Heat production of manure and manure with straw was estimated to be 7 (approximately 1% of H_{tot}) and 20 kJ/kg$^{0.75}$ per day (approximately 2.5% of H_{tot}), respectively. CH$_4$ emission of manure and manure with straw were estimated to be 0.04 kJ/kg$^{0.75}$ per day (approximately 1.5% of total CH$_4$ emission) and 0.02 kJ/kg$^{0.75}$ per day (approximately 1.7% of total CH$_4$ emission), respectively. H_{tot} and CH$_4$ data given in the results section are uncorrected for heat production and CH$_4$ emission of manure.

Calculations
Energy and nitrogen (N) balances were assessed per chamber over the 7-day experimental period. Metabolisable energy (ME) intake was calculated by subtracting the energy content of manure, soiled straw and methane outputs from that of feed and fresh straw inputs. Total heat production (H_{tot}) during the last 6 day of the experimental period was calculated from the gaseous exchanges according to Brouwer's equation (1965). Estimated regression coefficients of H_{tot} and activity counts were used to calculate the heat production related to activity (H_{act}) as described by Heetkamp *et al.* (1995). The heat production not related to physical activity (H_{cor}) was calculated by subtracting H_{act} from H_{tot}.

Energy retention (ER) was calculated by subtracting H_{tot} from ME intake. Retention of N was calculated from N in feed, fresh straw, soiled straw and manure. Aerial NH$_3$ and NH$_4^+$ of water that condensed on the heat exchanger were included in the N excretion from manure. Crude protein content was calculated as $6.25 \times$ N. ER as protein (ER$_p$) was calculated as $23.8 \times$ N retention, assuming 23.8 kJ/g of protein. ER as fat was calculated by subtraction of ER$_p$ from ER. The respiration quotient (RQ) was calculated from the ratio of CO$_2$ production to O$_2$ consumption. Means over the

whole experimental period were calculated for all variables and hourly means were calculated for H_{tot}, H_{act}, H_{cor} and RQ.

Statistical analyses

The experimental unit for all measurements was the group of 12 pigs, i.e. two pens of six pigs each, in a chamber. Effects of housing, starch type and their interaction on average daily gain (ADG) and energy partitioning were assessed by analysis of variance using the GLM procedure in SAS (v. 9.1, SAS Institute Inc., Cary, NC, USA). In addition, the hourly means of RQ, H_{tot}, H_{act} and H_{cor} were analysed using the same model.

Results

One pig on the PS diet in barren (B) housing was removed from the chamber before the start of the experimental period, because of an unhealthy appearance and lack of growth. None of the feed offered was refused during the experimental period. Effects of housing and starch type on growth rate and energy partitioning are given in Table 3. At the start of the experimental period, BWs were similar for the four treatment groups. ADG over the 7-day experimental period was higher ($P < 0.001$) in pigs fed the PS diet (758 g) than in pigs fed the NS diet (659 g, s.e. = 16), and was unaffected by housing.

Energy partitioning

GE supply as straw was 646 kJ/kg$^{0.75}$ per day in the pigs on straw bedding. ME intake was 81 kJ/kg$^{0.75}$ per day higher ($P < 0.001$) in S-housed than in B-housed pigs. S-housed pigs also showed a higher heat production (H_{tot}, $+86$ kJ/kg$^{0.75}$ per

day) than B-housed pigs ($P < 0.001$). Total ER was not affected by housing. S-housed pigs retained, however, more energy as protein ($+24$ kJ/kg$^{0.75}$ per day; $P < 0.01$) and less as fat (-28 kJ/kg$^{0.75}$ per day; $P < 0.05$) than B-housed pigs. Straw bedding reduced fat retention in pigs on the PS diet with -48 kJ/kg$^{0.75}$ per day and in pigs on the NS diet with -12 kJ/kg$^{0.75}$ per day, but the housing $\times$ starch type interaction was not significant ($P = 0.13$).

GE intake was slightly ($+17$ kJ/kg$^{0.75}$ per day) higher in NS-fed pigs than in PS-fed pigs ($P < 0.05$), whereas ME intake was 85 kJ/kg$^{0.75}$ per day lower in NS-fed pigs ($P < 0.001$). In B housing, metabolisability (ME/GE) was lower in the NS-fed pigs (75.3%) than in the PS-fed pigs (83.0%, $P < 0.001$). Metabolisability was not calculated for the S-housed pigs because of an unknown GE intake from straw. H_{tot} was not affected by starch type. The lower total ER in NS-fed pigs (-84 kJ/kg$^{0.75}$ per day; $P < 0.01$) was reflected both in a lower protein (-24 kJ/kg$^{0.75}$ per day; $P < 0.001$) and in a lower fat retention (-60 kJ/kg$^{0.75}$ per day; $P < 0.001$) as compared to PS-fed pigs.

The effect of starch type on CH$_4$ production depended on housing (housing $\times$ starch type interaction, $P < 0.01$), with highest levels in the B-housed/PS-fed pigs (0.28% of GE) and lowest in the S-housed/NS-fed pigs (0.03% of GE).

When the differences in ME intake between treatments were considered and energy expenditure was expressed as a proportion of ME intake, ER/ME was lower in S-housed than in B-housed pigs ($P < 0.01$). Effects of housing and starch type on (ER as protein)/ME were not significant ($P = 0.15$ and $P = 0.16$, respectively), although when expressed as a proportion of total ER/ME they were ($P < 0.001$ and $P < 0.01$, respectively). Contrary to effects on absolute levels, H_{tot}/ME

Table 3 *Effect of housing (enriched with straw bedding v. barren) and type of starch (pregelatinised v. native) on growth rate and energy partitioning (in kJ.kg$^{0.75}$/day, unless indicated otherwise) in group-housed growing pigs*

| Housing | Straw bedding | | Barren | | | P value[2] | | |
Starch type	Pregelatinised	Native	Pregelatinised	Native	s.e.[1]	H	S	H $\times$ S
No of groups	4	4	4	4				
No of pigs	48	48	47	48				
Initial BW (kg)	43.6	43.1	44.4	43.1	0.9	NS	NS	NS
ADG (g/day)	747	683	769	636	22	NS	***	NS
GE intake (feed)	1320	1340	1320	1334	7	NS	***	NS
GE supply (straw)	643	649	–	–	–	–	–	–
CH$_4$	1.6	0.6	3.7	1.3	0.16	***	***	**
ME intake	1171	1092	1096	1004	12.1	***	***	NS
H_{tot}	782	776	689	696	7	***	NS	NS
H_{act}	165	117	111	95	6	***	***	*
H_{cor}	617	659	578	600	6	***	***	NS
ER	388	316	406	309	11	NS	***	NS
ER as protein	209	179	179	160	8	**	**	NS
ER as fat	179	137	227	149	11	*	***	NS
RQ	0.992	0.980	1.017	0.991	0.003	***	***	*

ADG = average daily gain; GE = gross energy; ME = metabolisable energy; ER = energy retention; RQ = respiration quotient.
[1]Pooled standard error of the LSMeans.
[2]Statistical significance of effects of housing (H), starch type (S) and their interaction (H $\times$ S) is indicated: NS = non-significant; $^\dagger P < 0.10$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

was higher in NS-fed than in PS-fed pigs ($P < 0.001$). All other effects on H_{tot}, ER, ER as protein and ER as fat, expressed as a proportion of ME intake were similar to the effects as presented in Table 3.

Heat production and RQ
Circadian patterns in heat production and RQ are shown in Figure 1a–d. The higher H_{tot} in S-housed pigs was partly due to a higher heat production corrected for activity (H_{cor}, $+49$ kJ/kg$^{0.75}$ per day, $P < 0.001$). Starch type did not affect H_{tot}, but NS-fed pigs had a higher H_{cor} ($+46$ kJ/kg$^{0.75}$ per day) than PS-fed pigs ($P < 0.001$). Effects of starch type on H_{act} depended on housing (housing $\times$ starch type interaction, $P < 0.05$): in B-housed pigs, H_{act} was hardly affected by starch type (16.1% of H_{tot} in B-housed/PS-fed pigs and 13.7% of H_{tot} in B-housed/NS-fed pigs), whereas in S-housed pigs a profound difference between pigs on the P (21.1% of H_{tot}) and N (15.0% of H_{tot}) diets was found

(Figure 1b). Both H_{tot} and H_{act} varied more over the 24-h cycle in PS-fed pigs than in NS-fed pigs (Figure 1a and b).

When energy expenditure was expressed as a proportion of ME intake, the effect of housing on H_{cor}/ME was not significant, whereas the effect of starch type remained ($P < 0.001$). Effects of housing and starch type on H_{act}/ME ($P < 0.001$ and $P < 0.01$, respectively) were similar to effects on absolute levels as presented in Table 3.

Both RQ and fluctuations in RQ over the 24-h cycle were higher in PS-fed than in NS-fed pigs, but these effects of starch type were larger in B housing than in S housing (housing $\times$ starch type interaction, $P < 0.05$). During the postprandial periods, PS-fed pigs in B housing showed a rapid increase in RQ, whereas in the other groups, RQ increased less (PS-fed/S-housed pigs) or not at all (NS-fed pigs) after meals. In the hours before the first meal, RQ was lower in PS-fed pigs than in NS-fed pigs, and lower in B-housed pigs than in S-housed pigs (Figure 1d).
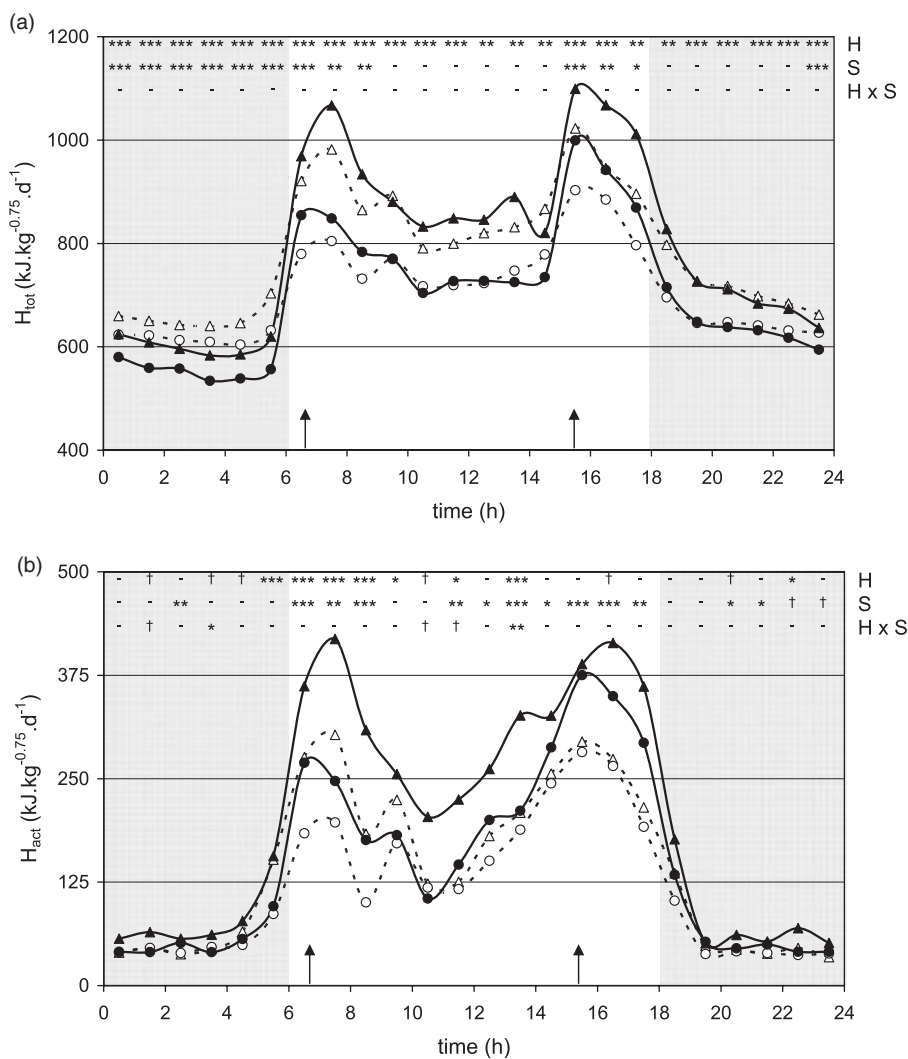

Figure 1 (a) Hourly means of total heat production (H_{tot}, s.e.m. = 13), (b) activity-related heat production (H_{act}, s.e.m. = 13), (c) heat production corrected for activity (H_{cor}, s.e.m. = 7), and (d) respiration quotient (RQ, s.e.m. = 0.003) of pigs in barren housing (circles) or on straw bedding (triangles) fed a pregelatinised (solid lines, closed symbols) or native (dotted lines, open symbols) potato starch diet. Arrows indicate time of feeding. The dark period is indicated by a shaded background. Statistical significance of effects of housing (H), starch type (S) and their interaction (H $\times$ S) is indicated: †$P < 0.10$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
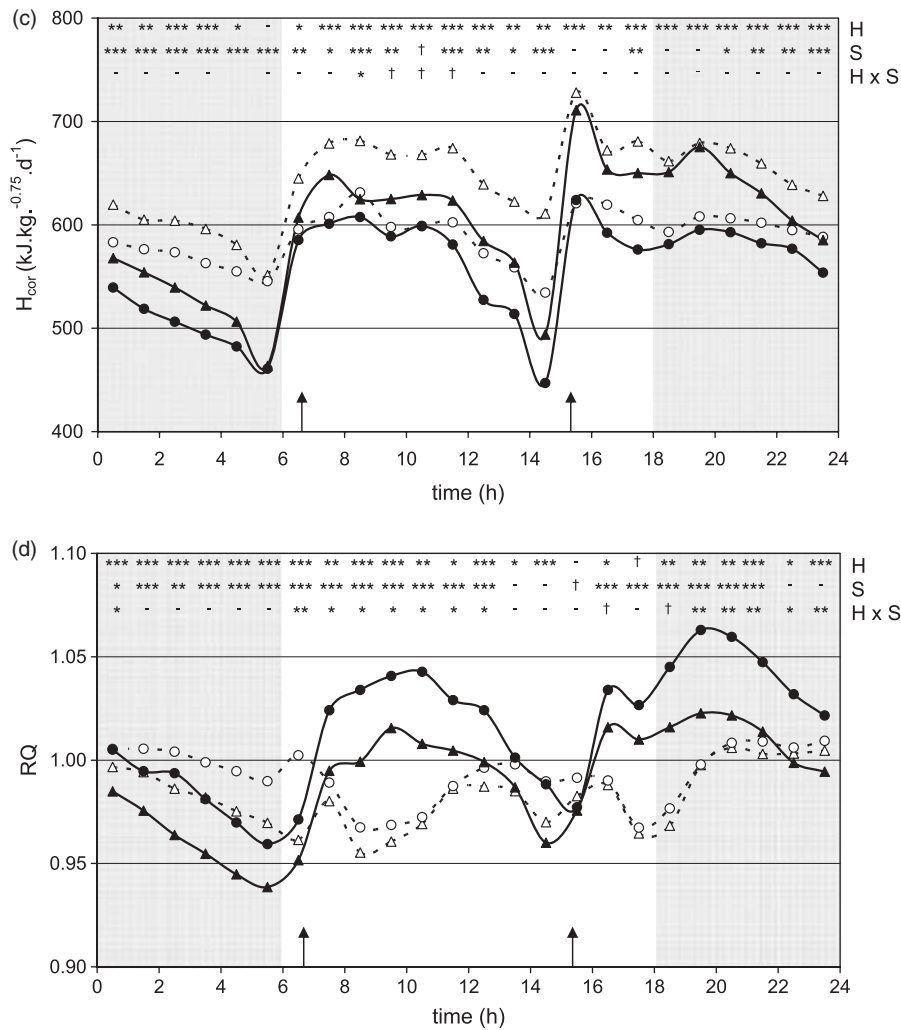
Figure 1 Continued

Discussion

In the present study, energy partitioning of pigs fed either PS or NS in the diet was studied in two different housing environments, barren (B) or enriched with straw bedding (S).

Effects of housing

By supplying pigs with straw bedding, not only a different housing condition was provided compared to the barren environment but also the possibility for unrestricted intake of straw. Based on two different methods, straw intake in this study was estimated to be between 143 and 234 g DM/ day in the PS-fed pigs, and between 96 and 156 g DM/day in the NS-fed pigs (Staals *et al.*, 2007), indicating that substantial amounts of the bedding were ingested. Several studies reported that the digestibility and/or metabolisability of straw, which contains high lignin and cellulose levels, are zero or even negative for growing pigs (Shi and Noblet, 1993; Schrama and Bakker, 1999; Noblet and Le Goff, 2001; De Lange *et al.*, 2006). In contrast, in the present study, straw ingestion resulted in an increased ME intake. Pigs in our study were, however, habituated to the experimental conditions for 30 days prior to the assessment of energy partitioning, which is much longer than the adaptation period used in other studies (e.g. 12 days in Shi and Noblet, 1993; Schrama and Bakker, 1999 and 10 days in De Lange *et al.*, 2006). As it has been found that volatile fatty acid (VFA) absorption increased up to 21 to 28 days following intake of a high-cellulose diet in growing pigs (Giusi-Perier *et al.*, 1989), the difference in length of the adaptation period could partly explain the discrepancy between the current and other studies in ME resulting from straw intake. In addition, effects of straw intake on the utilisation of other dietary components cannot be excluded (see Staals *et al.*, 2007). The manner and form in which the straw was provided may be important in this respect. In our study long, unchopped straw was provided as bedding material, whereas in other studies straw was mostly milled and included in the diet.

The increased ME intake related to straw ingestion compensated for the higher heat loss in straw-housed pigs. Consequently, total ER did not differ from that of pigs in barren housing.

Surprisingly, ER as protein was higher in pigs on straw bedding than in B-housed pigs, at the expense of a lower

fat retention, suggesting that enrichment of pens with long, unchopped straw may result in leaner pigs. Apparent faecal nitrogen digestibility was, however, much lower in S-housed pigs than in B-housed pigs in the present study (Staals *et al.*, 2007). This likely results from a shift from excretion of nitrogen from urine to faeces due to an increased amount of fermentable substrate in the colon (Heijnen and Beynen, 1997; Canh *et al.*, 1998), and may therefore not be present at the ileal level.

It is unknown whether the effect of straw bedding on protein and fat retention should be attributed to an influence of straw as rooting material, increasing the activity levels of the animals, or to an influence of straw intake. Both activity patterns and straw ingestion potentially influence nutrient utilisation via effects on transit time (Filer *et al.*, 1986; Latymer *et al.*, 1990). Other studies (Schrama and Bakker, 1999; De Lange *et al.*, 2006), however, reported no changes in protein or fat deposition in growing pigs that were offered milled or chopped wheat straw in the diet. It is therefore more likely that the lower fat deposition in S-housed pigs as compared to B-housed pigs, reflected in a lower postprandial increase in RQ on the PS diet, is related to the higher postprandial activity levels of pigs on long straw bedding. In humans, postprandial (light) exercise has been shown to blunt the postprandial plasma glucose increase and fat synthesis (Høstmark *et al.*, 2006) and to increase fat oxidation (Matsuo and Suzuki, 1999). Further research will have to elucidate how the availability of straw, due to either its behavioural or its nutritional effects, alters fat and protein metabolism in growing pigs.

Straw provision also influenced fermentation processes of the two different diets, as indicated by the interactive effect of housing and starch type on methane emission. Several studies have reported a positive relationship between endogenous methane production and quantities of fermentable carbohydrates provided (Jensen and Jørgensen, 1994; Jensen, 1996; Schrama *et al.*, 1998). In the present study, however, methane production was highest in the B-housed/PS-fed pigs and lowest in the S-housed/NS-fed pigs. This effect could not be attributed to methane emission from manure or manure with straw, which accounted for less than 2% of the total methane emission. Others (De Lange *et al.*, 2006) also reported a decrease in methane losses in pigs following ingestion of straw, and suggested either that straw reduces fermentation by methanogenic bacteria or that some of the methane produced might be adsorbed by faecal material of the pigs. NS consumption did not increase methane emission as compared to PS, possibly due to a high production of propionic acid relative to other fermentable carbohydrates (Awati *et al.*, 2006).

Effects of starch type and its interaction with housing
ER was lower in NS-fed pigs than in PS-fed pigs, mainly due – at least in B-housed pigs – to a lower metabolisability of the NS diet. This low availability of energy from the NS diet is in line with studies reporting a low digestibility or metabolisability of raw potato (starch) (Hoffmann *et al.*, 1990; Van der

Meulen *et al.*, 1997; Martin *et al.*, 1998). NS-fed pigs also showed a higher energy loss as heat corrected for activity as compared to pigs fed enzymatically degradable starch, likely reflecting a less efficient utilisation of fermentative end-products (Shi and Noblet, 1994; Jørgensen *et al.*, 1996).

Part of the lower efficiency of the NS diet was, however, compensated for by a reduced energy expenditure on physical activity, in accordance with the results of Schrama and Bakker (1999). A similar reduction in activity-related heat production was observed in restrictedly fed growing pigs when sugar beet pulp was added to their diet (Schrama *et al.*, 1996 and 1998; Rijnen *et al.*, 2003). Notably, in the present study, the effect of starch type on activity-related heat production depended strongly on housing conditions. Activity-related heat production was remarkably high in S-housed, PS-fed pigs, much higher than in NS-fed pigs on straw bedding, whereas the effects of starch type were less obvious in barren housing. Effects of NSP and RS on activity-related energy expenditure have been attributed to fermentation processes (Schrama and Bakker, 1999). In contrast with the rapid digestion of enzymatically degradable starch, fermentation of RS may continue for many hours after feeding, resulting in a more gradual supply of energy (Asp *et al.*, 1996; Van der Meulen *et al.*, 1997). In our study, this was reflected in the distinct circadian patterns in RQ and heat production of pigs on the two different diets. In PS-fed pigs, RQ increased rapidly after feeding, exceeded 1 for a substantial period and remained relatively high for at least 6 h, suggesting the enhanced oxidation of carbohydrates and *de novo* fatty acid synthesis, which is expected in the absorptive period of a highly digestible diet (Jakobsen and Thorbek, 1993; Achour *et al.*, 1997; Wenk *et al.*, 2001). Pigs on the NS diet showed, in contrast, relatively small fluctuations in heat production and RQ within the 24 h cycle. RQ was rather high in these pigs during the nightly hours before the first meal, likely reflecting the oxidation of absorbed VFAs, and, particularly in barren housing, *de novo* fatty acid synthesis from VFA. The gradual and prolonged supply of energy from fermentation of RS potentially increases periods of satiety (Heijnen *et al.*, 1995; Achour *et al.*, 1997; Haralampu, 2000). As feeding motivation seems to increase the physical activity of pigs (Jensen *et al.*, 1993; De Leeuw *et al.*, 2005), fermentation processes could therefore be largely responsible for the reduced activity-related heat production in NS-fed pigs, apart from possible specific effects of fermentation products on activity patterns (Schrama and Bakker, 1999).

Pigs housed on straw bedding dedicate most of their active time to straw-directed foraging behaviours such as nosing, rooting and chewing (Beattie *et al.*, 2000; Bolhuis *et al.*, 2005). The high activity level of straw-housed pigs on the PS diet may therefore have reflected an increase in foraging behaviour, possibly due to decreased interprandial satiety as compared with straw-housed/NS-fed pigs. This is supported by the higher DM intake from straw in PS-fed pigs as compared to NS-fed pigs observed in this study (Staals *et al.*, 2007). Interprandial satiety in B-housed pigs

may also have been lower for animals on the PS diet compared to those on the NS diet. However, barren-housed pigs on the PS diet did not have an outlet for their increased motivation to display foraging behaviour, because a suitable substrate was lacking in the B pens. This might explain why effects of starch type on activity-related heat production were lower in B-housed pigs than in pigs on straw bedding.

In conclusion, the present study shows that the availability of both straw bedding and dietary starch type, fermentable or digestible, affects energy utilisation and the physical activity of restrictedly fed pigs. The effects of housing condition on protein and fat deposition suggest that enrichment of pens with long straw may result in leaner pigs. Moreover, the relative impact of starch type on activity-related heat production depends on housing conditions of the pigs under study. The lower energy expenditure on the physical activity of pigs on the NS diet, which was most obvious in straw-housed pigs, likely reflects a decrease in foraging behaviour related to a more gradual supply of energy from fermentation processes.

Acknowledgements

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