The respiratory quotient in relation to fat deposition in fattening–growing pigs

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The relationship between non-protein respiratory quotient (RQ_{np}) and total fat retention (RFAT) or fat retained from synthesized carbohydrates (RFAT(CHO)) was evaluated from experiments with fattening–growing pigs in the live weight (LW) range from 45 to 120 kg. A commercial feed compound (31 g fat/kg) was fed at low (LI) or high (HI) feed intake in Expt 1, while a semi-purified diet (9·5 g fat/kg) was given without (LO) or with (HO) supplement of 90 g soya-bean oil/kg in Expt 2. RQ_{np} was calculated from 24 h measurements of the gas exchange, RFAT from 7 d N and C balances and RFAT(CHO) from differences between RFAT and digested fat. The measurements showed that about 85% of the total gas exchange was caused by oxidation of non-protein nutrients and the RQ_{np} varied from 1·00 to 1·34. In Expt 1 RFAT increased with LW from 46 to 141 and from 199 to 335 g/d on LI and HI respectively, whilst in Expt 2 RFAT increased from 191 to 377 and from 267 to 511 g/d on LO and HO respectively. A pronounced linearity was found between RQ_{np} and RFAT for all diets, but the curve for Expt 2 on HO had a lower position than the common curve for the other diets. By relating RQ_{np} to RFAT(CHO) a common linear curve and regression equation could be established in spite of the great variation in dietary composition, intake of fat and fat deposition.

24 h gas exchange: Respiratory quotient: Fat retention: Lipogenesis: Pigs

In recent papers the theoretical basis of indirect calorimetry in research with humans in health and disease has been discussed (Elia & Livesey, 1988; Ferrannini, 1988; Livesey & Elia, 1988). By indirect calorimetry the heat production (HE) can be calculated either by the respiratory quotient (RQ) method (HE, RQ) or by the C–N-balance method (HE, CN). Both methods are reliable and can be carried out with high accuracy, as discussed by Christensen *et al.* (1988).

The RQ method is based on measurements of O_2 consumption, CO_2 and CH_4 production and the amount of N excreted in the urine. The HE from oxidation of non-protein materials (glucose and triacylglycerol) is based on their respective RQ values ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) and the heat released during complete oxidation. The validity of indirect calorimetry when RQ is above 1·0, associated with lipogenesis, has been demonstrated by Elia & Livesey (1988). In humans RQ values above 1·0 have been obtained during infusion of glucose (Askanazi *et al.* 1980) and intake of high-carbohydrate meals (Acheson *et al.* 1984). In animals RQ values above 1·0 were measured in dogs by overfeeding with glucose over a 4 h period (Lusk, 1928) and in geese by overfeeding with carbohydrates (Benedict & Lee, 1937). In growing–fattening pigs on high feed intake RQ values, measured in 24 h periods, were constantly above 1·0 (Thorbek *et al.* 1984; Christensen, 1985).

HE, CN is calculated as the difference between metabolizable energy (ME) and energy retained in fat + protein (RE), measured by C–N balances. In measuring the C–N balances

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the amount of total fat retention can be calculated directly (Christensen *et al.* 1988), while fat retention by the RQ method is calculated indirectly as the difference between retained energy (determined as RE = ME–HE, RQ) and energy retained in protein.

Both methods are used in our laboratory. We observed that the non-protein RQ (RQ_{np}) was linearly related to the amount of fat retention measured by the C–N balances, but also that a high intake of fat depressed the RQ values in spite of a high fat retention. As the fat intake is high in human diets compared with conventional swine diets, we thought that our observations on pigs receiving different amounts of dietary fat might contribute to further discussion about the relationship between RQ_{np} and fat retention caused by directly deposited dietary fat and fat synthesized from carbohydrates.

The results from measurements of 24 h gas exchange in fattening–growing pigs in relation to fat deposition will be presented in the present paper.

MATERIALS AND METHODS

Animals and diets

The findings examined were taken from publications concerning measurements of energy metabolism by indirect calorimetry in growing pigs (Thorbek *et al.* 1984; Christensen, 1985). The material included twenty-two castrated male Danish Landrace pigs in the growing–fattening period from 45 to 120 kg live weight (LW) in which the RQ values were above 1·0.

A commercial pelleted feed compound was fed at low (LI) and high (HI) feed intake to fourteen pigs in Expt 1 (Thorbek *et al.* 1984), while a semi-purified basal diet was given to eight pigs in Expt 2 (Christensen, 1985). In this experiment four pigs received a basal diet (LO) and four were given a supplement of 90 g soya-bean oil/kg (HO).

The components applied in the different diets are shown in Table 1 together with the mean values for the chemical composition determined for eight samples from each diet during the two experiments. Minerals and vitamins were included according to Danish standards. The fat content was 31 g fat/kg in the commercial diet (Expt 1), while it was 9·5 and 99·5 g fat/kg in Expt 2 on LO and HO respectively.

The total duration of Expts 1 and 2 was 110 and 56 d respectively.

Experimental procedure

Digestibility, C–N balances and gas exchange were measured individually in four LW ranges from 50 to 120 kg in Expt 1 and from 45 to 95 kg in Expt 2. All measurements were carried out with a 7 d preliminary period with the pigs in individual pens followed by a 7 d period of collection in metabolism crates, including a 24 h measurement of gas exchange in the middle of the period. An open-air-circuit respiration unit with two chambers (Thorbek, 1969) was used for determination of O_2 consumption and CO_2 production. The temperature in the pens, as in the respiration unit, was kept at 18°. All pigs were fed twice daily and received water *ad lib.*

The pigs in Expt 1 were kept in their pens and fed on the commercial diet on high feed intake until they reached the LW range planned for the balance experiments. Each pig was assessed on LI and HI, and no pigs were assessed in more than two consecutive LW ranges. The distribution of pigs in the different groups is demonstrated in Table 2. A total of fifty balance periods was planned, but four periods were omitted for the reasons indicated. A total of thirty-two balance periods was planned in Expt 2, but only twenty-nine were completed due to the death of one pig on treatment HO.

The fat analyses in feed and faeces were carried out with HCl-hydrolysis before diethyl ether extraction in accordance with the Stoldt (1952) method. C in feed, faeces and urine

Table 1. *Expts 1 and 2. Composition of experimental diets (g/kg)*

Expt 1		Expt 2 (Basal diet)*	
Components		Components	
Barley	770	Maize starch	292
Oats	50	Cassava meal	185
Soya-bean meal	140	Glucose	65
Meat-and-bone meal	20	Sucrose	65
Mineral and vitamin mix	20	Cellulose	33
Analysis		Skim-milk powder	160
Dry matter	892	Soya-bean meal	80
Crude protein (N × 6·25)	165	Casein	80
Crude fat	31	Mineral and vitamin mix	40
NFE	627	Analysis	
Gross energy (MJ/kg)	16·5	Dry matter	900
		Crude protein	183
		Crude fat	9·5
		NFE	614
		Gross energy (MJ/kg)	15·8

NFE, N-free extracts.
* Basal diet (LO) and diet supplemented with 90 g soya-bean oil/kg (HO).

Table 2. *Distribution of animals on balance experiments in different live-weight (LW) ranges on low (LI) and high (HI) feed intake*

LW range (kg)...	50–60		60–80		80–100		100–120	
Feed intake...	LI	HI	LI	HI	LI	HI	LI	HI
Animal no.								
1, 4, 6, 7	·	·	·	·	×	×*	×	×
13, 14, 15, 16	×	×	×†	×	·	·	·	·
21, 23, 24	×	×	·	·	·	·	·	·
25, 27, 28	·	·	·	·	×	×	×†	×*

* Pigs nos. 1 and 28 omitted; feed residuals.
† Pigs nos. 15 and 28 omitted; technical errors.

was measured by means of a Carmograph (Wösthoff, Bochum, Germany), working with high precision on the electric conductivity principle (Neergaard *et al.* 1969). The standard procedure for balance experiments at this Institute, as described by Thorbek (1975) and Christensen (1985), was followed.

Calculations

The proportion of gaseous exchange resulting from the oxidation of protein was calculated from the N excretion in the urine (UN) as: CO_2 (l/g protein) = UN(g) × 6·25 × 0·774 and O_2 (l/g protein) = UN(g) × 6·25 × 0·957, using the factors given by Brouwer (1965). By subtracting these values from the measured total gas exchange the non-protein gas exchanges ($CO_{2(np)}$ and $O_{2(np)}$) and the values of RQ_{np} were calculated.

From the N balances (NBAL), calculated by subtracting N excreted in faeces and urine from N intake, the amount of C retained in protein (C_n) was calculated as: C_n (g) = NBAL (g) × 6·25 × 0·52, assuming that protein contains 520 mmol C/mol (Brouwer, 1965).

The total C balance (CBAL) was calculated from C intake in feed minus C lost in faeces,

urine, CO_2 and CH_4. By subtracting C_n from the total CBAL the amount of C retained in non-protein material (C_{np}) was calculated. Assuming that the glycogen depots in the body are fairly constant during short-term measurements, the values of C_{np} can be considered as C stored in fat. Then the amount of retained fat (RFAT) can be calculated as: RFAT (g) $= C_{np} \times 100/76{\cdot}7$ assuming that fat contains an average of 767 mmol C/mol (Brouwer, 1965).

The amount of RFAT consists partly of digested dietary fat (lipid) stored directly in the body (RFAT(L)) and partly of fat being synthesized *de novo* from carbohydrates (RFAT(CHO)). Assuming that all digested fat (DFAT) is stored directly in the body as RFAT(L), the amount of RFAT(CHO) was calculated as the difference between RFAT and DFAT.

Regression analyses were performed with RFAT and RFAT(CHO) as independent variables and RQ_{np} as the dependent variable using GLM procedures of SAS as described by Freund & Littell (1981).

RESULTS

N metabolism

N balances were measured individually in 7 d balance periods in the different LW groups in Expts 1 and 2 and the results are shown in Tables 3 and 4 together with the mean LW of the pigs. The mean LW achieved in the different LW ranges in Expt 1 was approximately the same on LI and HI, whilst in Expt 2 mean LW for HO was about 1·1 that for LO, probably due to the higher energy intake.

The mean apparent digestibility coefficients for protein were 0·81 and 0·92 respectively in Expts 1 and 2, reflecting the different protein sources used. In both experiments the coefficient of variation (CV) for digested N (DN) in different LW ranges was less than 5%.

The mean retention of N (RN), calculated from the individual measurements, was 14·5 (SE 1·22) and 27·1 (SE 1·10) g/d in Expt 1 on LI and HI respectively and 27·1 (SE 0·61) and 24·4 (SE 0·59) g/d in Expt 2 on LO and HO respectively.

Gas exchange

The respiration unit was calibrated frequently with CO_2 test gas during the experimental time and showed errors below 0·5%. The gas exchange was measured individually for 24 h in all balance periods and the mean values for O_2 consumption and CO_2 production in the different LW groups are shown in Tables 5 and 6. No feed residuals occurred in the respiration chambers. The gas exchange measured for 24 h is supposed to be a representative mean value for the 7 d balance period.

N excreted in urine was measured in the 7 d balance periods and used for calculation of gas exchange from oxidation of protein. By subtracting these values from the total gas exchange the non-protein (np) gas exchange and RQ_{np} were calculated as shown in Tables 5 and 6. The measurements showed that about 85% of the total gas exchange resulted from oxidation of non-protein nutrients. The maximal range in RQ_{np} measured individually was from 1·00 to 1·34.

The intake of energy and loss of energy in faeces and urine were measured individually in the 7 d balance periods for determination of metabolizable energy (ME). The mean intake of ME in relation to metabolic LW (kg $LW^{0{\cdot}75}$) during all periods was 738 (SE 16) and 1207 (SE 14) kJ/kg $LW^{0{\cdot}75}$ on LI and HI respectively in Expt 1, while it was 1341 (SE 8) and 1420 (SE 5) kJ/kg $LW^{0{\cdot}75}$ on LO and HO respectively in Expt 2.

Fat metabolism

The amount of DFAT was measured individually in 7 d periods in the different LW groups in Expt 2. In Expt 1 the values were not measured directly but calculated for each group

Table 3. *Expt 1. Intake of N (IN), digested N (DN), N in urine (UN) and retained N (RN) in fattening–growing pigs fed on low and high feed intakes**

(Mean values with their standard errors)

LW range (kg)...	50–60		60–80		80–100		100–120	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Low feed intake								
n	7		3		7		6	
LW (kg)	53·9	1·73	67·7	2·30	94·6	2·25	110·8	2·59
IN (g/d)	31·6	0·26	39·3	0·57	39·7	0·34	53·1	0·46
DN (g/d)	25·5	0·44	31·9	0·90	33·1	0·41	43·3	0·85
UN (g/d)	11·9	0·77	12·8	1·12	21·4	1·19	26·6	1·74
RN (g/d)	13·6	0·67	19·1	0·55	11·7	1·25	16·7	2·16
High feed intake								
n	7		4		6		6	
LW (kg)	57·4	1·44	70·8	2·91	98·1	1·59	110·6	2·65
IN (g/d)	52·5	0·44	60·6	0·75	79·6	0·70	79·1	0·74
DN (g/d)	41·2	0·58	49·0	1·23	63·8	0·89	62·9	1·46
UN (g/d)	17·6	0·73	17·0	0·71	39·7	2·65	31·9	1·70
RN (g/d)	23·6	0·60	32·0	1·91	24·1	2·48	31·0	1·23

* For details of diets and procedures, see Table 1 and pp. 334–335.

Table 4. *Expt 2. Intake of N (IN), digested N (DN), N in urine (UN) and retained N (RN) in fattening–growing pigs fed on low and high oil intakes**

(Mean values with their standard errors)

LW range (kg)...	45–55		55–65		65–80		80–95	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Low oil intake								
n	4		4		4		4	
LW (kg)	47·6	0·78	57·4	0·71	68·9	1·09	81·1	1·07
IN (g/d)	49·6	0·0	58·4	0·0	51·3	0·0	58·0	0·0
DN (g/d)	46·1	0·26	53·9	0·15	46·4	0·33	52·3	0·41
UN (g/d)	19·0	0·57	24·5	0·62	20·3	0·83	26·8	1·51
RN (g/d)	27·1	0·75	29·5	0·68	26·1	0·94	25·5	1·57
High oil intake								
n	4		3		3		3	
LW (kg)	51·9	0·15	64·5	0·29	77·0	0·70	89·7	1·87
IN (g/d)	49·0	0·0	57·6	0·0	51·5	0·0	58·2	0·0
DN (g/d)	45·8	0·84	53·4	0·38	47·0	0·71	53·2	0·76
UN (g/d)	21·0	0·46	27·4	0·64	24·0	1·42	28·8	1·20
RN (g/d)	24·4	0·60	26·0	0·92	22·9	2·02	24·4	1·00

* For details of diets and procedures, see Table 1 and pp. 334–335.

using values for digestibility of fat in the commercial feed compound measured in a previous, not published, experiment.

The total amount of RFAT was calculated from the C–N balances measured individually in 7 d periods including 24 h measurements of the CO_2 production. The amount of fat retention from lipogenesis (RFAT(CHO)) was calculated as differences between RFAT and DFAT, and the results are shown in Tables 7 and 8.

Table 5. *Expt 1. Gas exchange total value and from oxidation of non-protein nutrients (np) in fattening–growing pigs fed on low and high feed intakes**

(Mean values with their standard errors)

LW range (kg)...		50–60		60–80		80–100		100–120	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Low feed intake									
n		7		3		7		6	
$CO_{2(total)}$	(l/d)	564	4·3	669	17·0	732	14·5	886	9·9
$O_{2(total)}$	(l/d)	564	8·3	661	27·1	740	17·2	844	15·0
$CO_{2(np)}$	(l/d)	506	4·5	607	15·1	628	16·3	757	10·6
$O_{2(np)}$	(l/d)	493	9·7	584	25·6	612	19·5	685	15·1
$RQ_{(np)}$		1·029	0·013	1·041	0·020	1·028	0·007	1·107	0·010
High feed intake									
n		7		4		6		6	
$CO_{2(total)}$	(l/d)	750	16·2	871	19·3	1075	22·1	1110	17·5
$O_{2(total)}$	(l/d)	658	14·4	766	20·8	929	22·4	977	21·6
$CO_{2(np)}$	(l/d)	665	16·0	789	22·4	883	27·9	956	20·0
$O_{2(np)}$	(l/d)	554	15·5	664	24·3	692	27·2	786	27·6
$RQ_{(np)}$		1·203	0·015	1·189	0·013	1·279	0·015	1·219	0·020

* For details of diets and procedures, see Table 1 and pp. 334–335.

Table 6. *Expt 2. Gas exchange total value and from oxidation of non-protein nutrients (np) in fattening–growing pigs fed on low and high oil intakes**

(Mean values with their standard errors)

LW range (kg)...		45–55		55–65		65–80		80–95	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Low oil intake									
n		4		4		4		4	
$CO_{2(total)}$	(l/d)	692	7·6	788	14·4	896	14·7	1021	27·0
$O_{2(total)}$	(l/d)	642	11·1	707	21·0	756	17·8	872	37·8
$CO_{2(np)}$	(l/d)	601	8·7	670	15·4	798	14·7	892	23·4
$O_{2(np)}$	(l/d)	528	14·0	561	23·5	635	19·3	712	33·5
$RQ_{(np)}$		1·139	0·023	1·197	0·026	1·258	0·020	1·257	0·026
High oil intake									
n		4		3		3		3	
$CO_{2(total)}$	(l/d)	686	7·2	794	14·2	901	5·7	956	16·0
$O_{2(total)}$	(l/d)	692	12·9	751	12·8	817	11·9	872	2·7
$CO_{2(np)}$	(l/d)	584	8·4	662	13·7	785	5·3	817	19·9
$O_{2(np)}$	(l/d)	565	15·3	588	13·1	673	18·2	700	6·4
$RQ_{(np)}$		1·033	0·015	1·126	0·007	1·167	0·025	1·166	0·019

* For details of diets and procedures, see Table 1 and pp. 334–335.

The amount of RFAT in Expt 1 on LI increased from 46 to 141 g daily, while on HI in Expt 2 it increased by more, from 191 to 403 g daily. The highest retention was obtained in Expt 2 on HO, with values increasing from 267 to 511 g/d. The highest values of RFAT (CHO) were obtained in Expt 2 on LO, increasing from 180 to 366 g daily.

The range of values obtained in RQ_{np} in relation to RFAT or RFAT(CHO) is given in Figs. 1 and 2 respectively.

Table 7. *Expt 1. Digested fat (DFAT), total retained fat (RFAT) and fat retained from carbohydrate RFAT(CHO) in fattening–growing pigs fed on low and high feed intakes**

(Mean values with their standard errors)

LW range (kg)...		50–60		60–80		80–100		100–120	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Low feed intake									
n		7		3		7		6	
DFAT	(g/d)	22		28		28		37	
RFAT	(g/d)	46	6·5	72	10·5	65	13·2	141	4·1
RFAT(CHO)	(g/d)	24		44		37		104	
High feed intake									
n		7		4		6		6	
DFAT	(g/d)	37		43		56		56	
RFAT	(g/d)	199	14·0	227	8·4	403	20·5	335	14·7
RFAT(CHO)	(g/d)	162		184		347		279	

* For details of diets and procedures, see Table 1 and p. 334–335.

Table 8. *Expt 2. Digested fat (DFAT), total retained fat (RFAT) and fat retained from carbohydrate RFAT(CHO) in fattening–growing pigs fed on low and high oil intakes**

(Mean values with their standard errors)

LW range (kg)...		45–55		55–65		65–80		80–95	
		Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Low oil intake									
n		4		4		4		4	
DFAT	(g/d)	11	0·3	13	0·2	9	0·2	11	0·7
RFAT	(g/d)	191	6·7	257	14·6	328	10·9	377	22·6
RFAT(CHO)	(g/d)	80	6·5	244	14·6	319	10·8	366	22·2
High oil intake									
n		4		3		3		3	
DFAT	(g/d)	148	0·7	173	1·5	201	1·3	228	2·7
RFAT	(g/d)	267	6·1	335	9·6	402	2·3	511	22·4
RFAT(CHO)	(g/d)	119	5·6	162	9·3	201	1·5	283	20·0

* For details of diets and procedures, see Table 1 and pp. 334–335.

Regression analyses showed that the values from Expt 1 on LI and HI could be pooled with the values from Expt 2 on LO and the following equations were obtained:

Expt 1 (LI + HI) + Expt 2 (LO) *n* 62

$$RQ_{np} = 1{\cdot}005 + 0{\cdot}714 \times \text{RFAT (kg)}, \quad (1)$$

(SE 0·009) (SE 0·038)

residual SD (RSD) 0·038, CV 3·3%, R^2 0·85.

Expt 2 (HO) *n* 13

$$RQ_{np} = 0{\cdot}930 + 0{\cdot}505 \times \text{RFAT (kg)}, \quad (2)$$

(SE 0·051) (SE 0·133)

RSD 0·045, CV 4·0%, R^2 0·57.

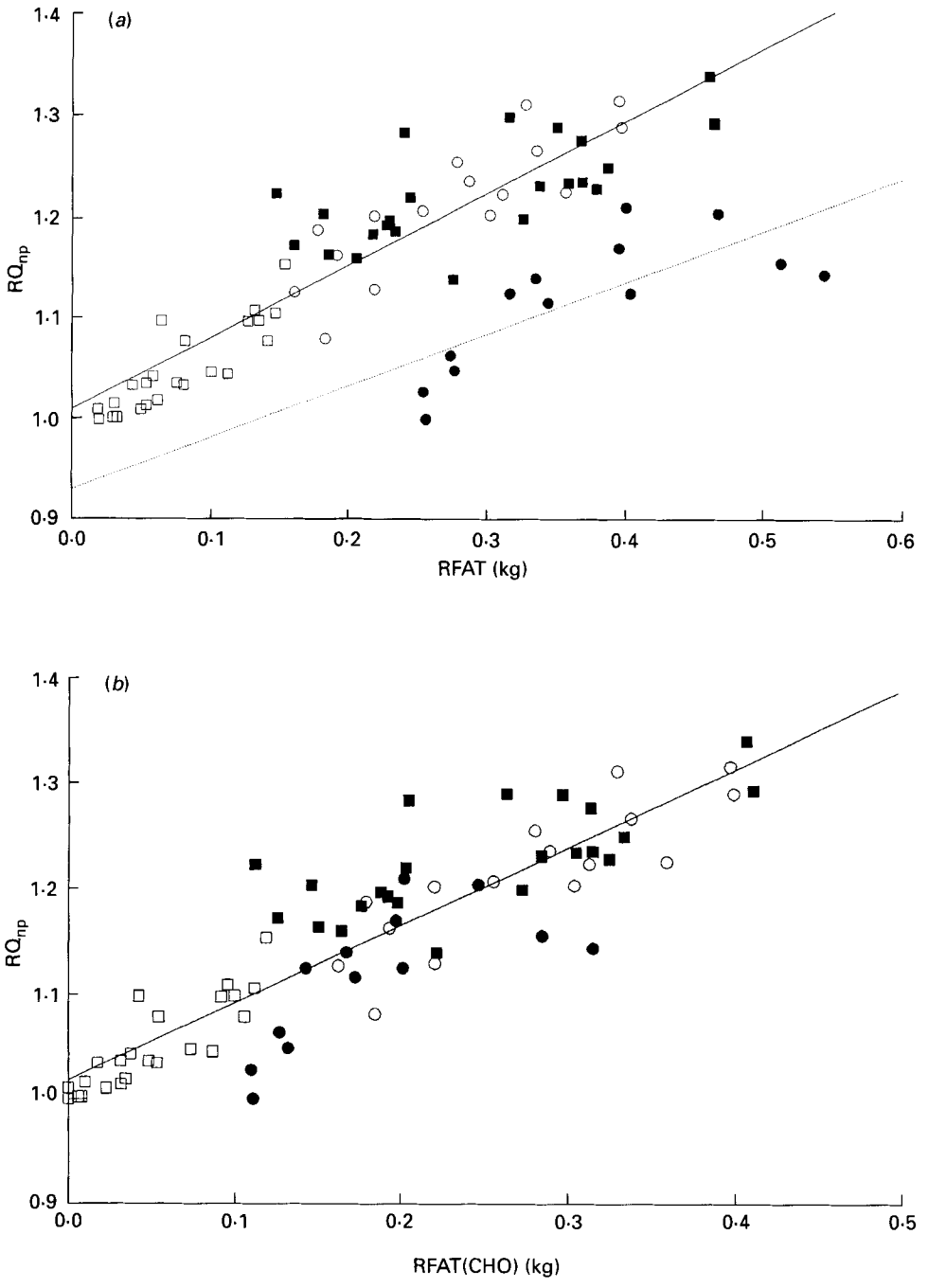

Fig. 1 (*a*) Non-protein respiratory quotient (RQ_{np}) *v.* total retained fat (RFAT) in pigs fed on low (□) or high (○) feed level of a commercial diet and on a semi-purified diet without (■) or with (●) supplement of soya-bean oil (*n* 62 (except (●), *n* 13)). (*b*) Non-protein respiratory quotient (RQ_{np}) *v.* retained fat synthesized from carbohydrate (RFAT(CHO)) in pigs fed on low (□) or high (○) feed level of a commercial diet and on a semi-purified diet without (■) or with (●) supplement of soya-bean oil (*n* 75).

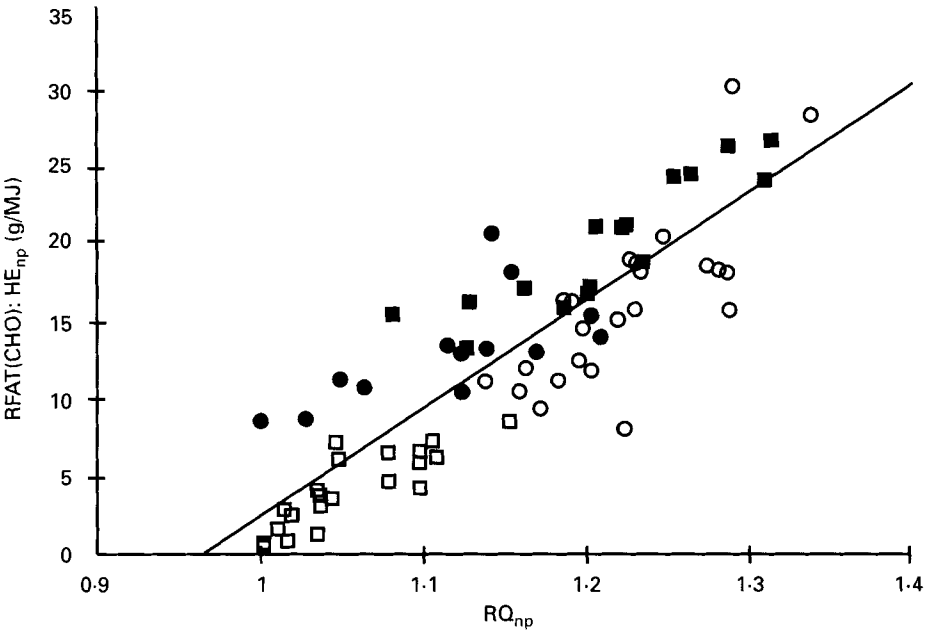

Fig. 2. Fat synthesized *de novo* from carbohydrate (RFAT(CHO)) per unit non-protein heat production (HE_{np}) *v.* non-protein respiratory quotient (RQ_{np}) in pigs fed on low (□) or high (○) feed level of a commercial diet and on a semi-purified diet without (■) or with (●) supplement of soya-bean oil, (*n* 73).

By relating RQ_{np} to RFAT(CHO) as shown in Fig. 2 a common linear relationship for all values could be established with the following regression equation:

Expt 1 + Expt 2 *n* 75

$$RQ_{np} = 1{\cdot}017 + 0{\cdot}729 \times \text{RFAT(CHO) (kg)} \quad (3)$$

(SE 0·009) (SE 0·044)

RSD 0·043, CV 3·7%, R^2 0·79.

DISCUSSION

Theoretically RQ_{np} values above 1·0 are associated with lipogenesis, as shown by Elia & Livesey (1988). Only few values, however, are available to test this relationship. The present paper demonstrates the relationship in growing pigs. In order to be able to generalize we chose a material representing a relatively big variation with respect to animals (twenty-two pigs), LW range (45–120 kg), feed type (commercial feed and semi-purified, virtually fat-free diets without (LI, HI and LO) and with (HO) the inclusion of oil), different energy intakes (738, 1207, 1341, 1420 kJ ME/kg $LW^{0·75}$ on LI, HI, LO and HO respectively), and different fat intakes ranging from 11 to 13 g DFAT daily on LO, 22–37 g on LI, 37–56 g on HI and 148–228 g on HO.

Our methods do not allow direct measurements of lipogenesis. On the basis of the measured 7 d C–N balances we have calculated the daily fat deposition (RFAT). We have measured the daily amounts of digested fat (DFAT) and have calculated the minimum amount of fat which could be deposited from lipogenesis (RFAT(CHO)) by subtracting DFAT from RFAT. Thereby we have anticipated that all DFAT has been deposited. From

a dynamic point of view this anticipation is not correct since fat is turned over constantly. However, taken over 24 h the pigs are in a positive energy balance with a hormonal status favouring lipogenesis and fat deposition. Thus, more fat may have been synthesized than deposited, so our values for RFAT(CHO) may be lower than the true lipogenic rates.

Our results shown in Fig. 1 demonstrate that there is no general linear relationship between RQ_{np} and RFAT for the present diets. Only in the case of virtually fat-free diets, as used on LI, HI and LO, is there a common regression line, because RFAT in this case is almost identical to RFAT(CHO). When oil (HO) is included in the diet the difference between RFAT and RFAT(CHO) becomes greater because more dietary fat is deposited and less fat is synthesized. This would be the case for human diets where 30–40% of energy intake is from fat.

However, a generalization could be established between RQ_{np} and RFAT(CHO) as shown in Fig. 2 which supports the theoretical considerations made by Elia & Livesey (1988). The range of RQ_{np} was between 1·00 and 1·34.

In the present studies the protein allowances were close to the requirement for maximal N retention. Thus, protein oxidation was relatively low, averaging 15% of total heat production in all experiments. Hence, protein has contributed little to overall lipogenesis in these studies. It is interesting to note that this contribution is similar to that observed in humans (Thorbek *et al.* 1991). Normally, protein is fed in much greater amounts to pigs than in the present studies, whereby much more protein is oxidized and excreted in urine.

In the pig, studies of *de novo* lipid synthesis *in vitro* (O'Hea & Leveille, 1968; Christensen & Goel, 1972) and *in vivo* (Christensen, 1969; Hood & Allen, 1973) have shown that glucose is the major precursor and adipose tissue the major site of lipogenesis. Dietary fatty acids, notably linoleic and linolenic acid, are, however, readily absorbed and deposited both in adipose tissue (Christensen, 1973) and in structural lipids (Christensen, 1974). Thus, it may be calculated that the pigs on LO deposited a total of 14 kg fat of which at least 13 kg was synthesized from carbohydrates. The pigs on HO deposited 19 kg fat of which up to 17 kg may have originated from dietary fat with at least 2 kg from carbohydrate.

The lipogenic capacity in man is not quite clear. *De novo* fatty acid synthesis from carbohydrates in adipose tissue is not of quantitative significance in man (Arner, 1990). In individuals ingesting hyperenergetic, high-carbohydrate diets, glycogen storage seemed to be the principal metabolic fate of ingested carbohydrates (Acheson *et al.* 1984). However, the latter studies were performed over short intervals. During a 14 d study patients receiving energy (glucose and amino acids), parenterally at 1·5 times their resting metabolic expenditure showed a net fat gain with RQ values in the range 1·03–1·28 (King *et al.* 1984).

If the high fat content in human diets is ingested above maintenance level, it is likely that the same situation would occur as in the pigs receiving the high-fat (HO) diet in the present study. During the high fat intakes at maintenance level RQ_{np} would probably not exceed unity in humans. This may be one reason why only theoretical considerations on RQ_{np} above 1·0 in humans are found. Another reason may be that most studies on ingestion of carbohydrates in relation to fat deposition in man have been carried out over a short time-interval often with depleted glycogen depots, in which case it is not surprising that none or only little lipogenic activity occurs. Even if species differences may occur between pigs and humans concerning site and rate of lipogenesis, our findings strongly indicate that if pigs were fed with the same high amounts of fat as the Western human population receives in their diet the pigs would deposit most of the fat from dietary fat and only synthesize a small amount of fat if any from carbohydrates. Thus, RQ_{np} is only highly correlated with fat deposition if fat is being synthesized from carbohydrates.

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