Chapter 20

Energy for pigs: Metabolism, requirement, utilisation and prediction of dietary content

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This chapter will provide insight into:

- The basic concepts of energy metabolism
- The partition of energy in the body
- Dietary, animal and environmental factors influencing energy metabolism in animals
- Energy requirements
- Energy utilisation and efficiencies
- Prediction of dietary energy content
- Methods to study energy metabolism and how to do the calculations
- Feeding strategies and practical implications

1. Introduction to bioenergetics

The concepts of energy are important to understand for nutritionists because it is the most important nutritional factor. Indeed, recommendations for dietary concentrations of for example amino acids, minerals and vitamins are expressed relative to energy in most countries. Energy can be defined as the capacity to perform work. There are two categories of energy: potential and kinetic. Potential energy is energy of position or bound energy which can be released to produce kinetic energy or to do work. Kinetic energy is energy of movement. In the living organism, the energy of random molecular motion is heat energy. Energy supplied to animals in chemical form can be transformed to heat when used for life processes, for instance when carbohydrates are oxidised for maintaining a constant body temperature. Energy may also be stored in chemical form as

in growth, transferred in chemical form to a second animal as in pregnancy or lactation, or transferred to surroundings as heat loss due to for example physical activity (work). When biomolecules are converted within an animal, for instance in anabolic or catabolic processes, some of the chemical bound energy is inevitably lost as heat because metabolic processes operate at efficiencies below 100%. Bioenergetics of animals and man is primarily based on the two laws of thermodynamics (for more details see Kleiber [47].

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1) **The first law of thermodynamics is the law of conservation of energy and states that energy can be transferred or transformed but neither created nor destroyed. In essence, the amount of energy (in our universe) is constant but can be converted from one form into another.**

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2) **The second law of thermodynamics states that all forms of energy are quantitatively convertible to heat, that heat is the lowest energy form and that the driving force of all energy transactions is the tendency to reach the lowest energy form.**

The second law can also be stated as the tendency for energy with a high degree of orderliness to be converted to energy with a lower degree of orderliness. The degree in which the total energy of a system is uniformly distributed (randomness), and thus unable to do work, is expressed by the term entropy. In any isolated system, entropy tends to increase whereby energy potentially available for work decreases because randomness is more probable than is orderliness. The more disordered or random a system becomes, the more entropy it has. Some molecules have a greater order than others, and consequently their entropy is lower. For example, proteins are highly ordered but upon denaturation they change to a much more random structure, hence the increase in entropy during denaturation is considerable. Generally speaking, solids are more ordered than liquids which again are more ordered than gases. According to the second law, any change in the total energy content of a system (e.g. the heat of combustion in a biological oxidation) results in a change in both free energy and in the entropy of the system. Since only the

former can be utilised to perform work of any kind, energy-yielding reactions inevitably have an efficiency below 100%.

It can also be stated that in accordance with the first law of thermodynamics, the total energy within the universe remains constant, and, in accordance with the second law, the entropy of the universe always increases. Both laws of thermodynamics emphasise that all forms of energy (in living organism) can be measured by complete oxidation of animals (or compartments like organs, milk, urine etc.), feed or feed ingredients at high pressure and abundant oxygen, and the energy content may be quantified as the energy liberated as heat from the complete oxidation. Therefore, determination of heat production following complete oxidation is both theoretically and practically a robust measure of energy metabolism.

Potential energy derived from the metabolism of foods is stored in living organisms as "high energy compounds" mainly as fat and protein. However, minor amounts of carbohydrates (in most cases less than 2% of the energy in the body) may also be stored as glycogen in the liver or in muscles. As an exception, the lactating mammary gland produces substantial amounts of carbohydrate in form of lactose (a disaccharide) which is secreted into milk [4] [13]. The breakdown of these compounds liberates free energy, which can accomplish work and heat energy (of which the latter is not able to do work). The heat loss is thus a measure of the energetic inefficiency of the reaction. If, for instance, energy is utilised by an animal for milk production with an efficiency of 78%, it means that 22% is lost as heat when milk is produced. The energy liberated by chemical reactions in the cell is used to drive other reactions. These require some methods for coupling the reactions that liberate energy with those that utilise energy, and the first step involves storing the energy derived from combustion of foodstuffs in certain high-energy compounds. The most important of the high-energy compounds is adenosine triphosphate (ATP). In a simple way, we may say that a cell is supplied with energy stored in ATP, while the energy derived from oxidation of nutrients is used to resynthesise ATP (Figure 20.1).

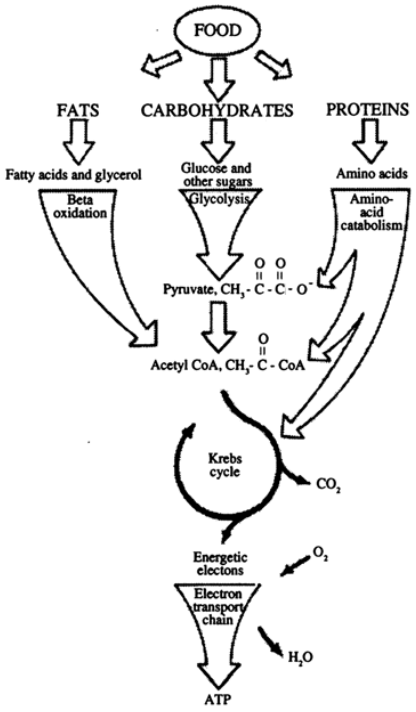


Figure 20.1. Model of ATP synthesis and hydrolysis.

The free energy released in the hydrolysis of ATP to ADP (adenosine diphosphate) under standard conditions is generally accepted to be about 30 kJ per mol. The standard free energy (ΔG) may be measured when 1 mol of reactant is converted to 1 mol of product at 37^o C and neutral pH (7.0). The standard ΔG of the reaction ADP->AMP (adenosine monophosphate) or AMP->phosphate is slightly lower, i.e. about 27 kJ/mol. However, under the conditions of physiological pH and temperature in the body, and because most of the ATP and ADP in intact cells are presented as Mg^{++} complex, which has the effect of shifting the equilibrium of ATP hydrolysis, which increases the standard free energy change of ATP hydrolysis. On average, the amount of energy that is available from the phosphate bond of ATP is 52 kJ/mol [13]. Therefore, the role of ATP is unique. In comparison with other phosphates, ATP is the only phosphate which serves as a carrier of chemical energy between donors and low-energy phosphate acceptors. ATP is a common intermediate in both energy-delivering and energy-requiring reactions of the cell, and it is the only form of chemical energy that can be converted into all others forms of energy used by living organisms.

2. Catabolism

The animals require energy for the maintenance of cellular function and for production (meat, milk, foetal growth). The energy is provided by degradation of the nutrients net absorbed from the feed. Under normal conditions, energy is produced by oxidation processes in the three main groups of nutrients *carbohydrates*, *fat* and *protein,* but the same dietary nutrients may also be used for biosynthesis (Figure 20.2).

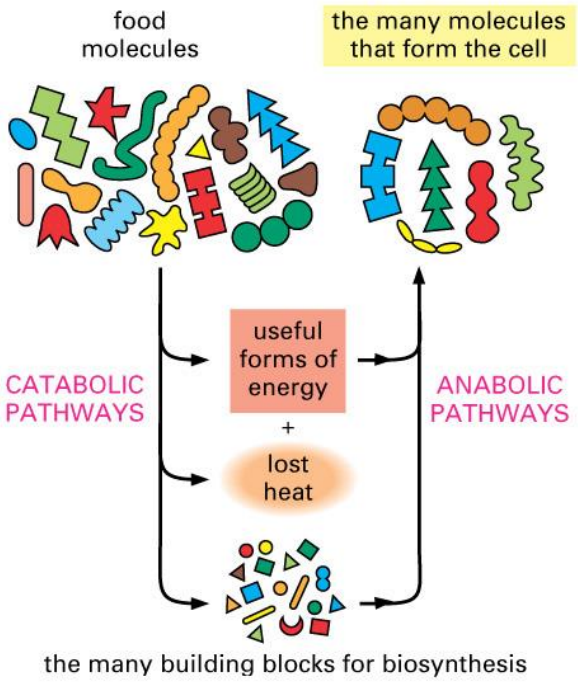


Figure 20.2. Model of catabolism and anabolism.

The oxidation proceeds through a series of processes in which the degradation from one stage to the next is catalysed by intercellular enzyme systems. The enzyme systems include for instance dehydrogenases, which liberate hydrogen, and oxidases, which activate oxygen. Part of the energy resulting from oxidation of the organic substances in the body is transferred to energy-rich phosphorus (mostly ATP) compounds from which they are later mobilised and utilised for syntheses and other life processes (mechanical work, intake and transport of food, net absorption of nutrients etc.). Oxidation of a typical carbohydrate, fat and protein is summarised in Table 20.1.

Table 20.1. Stoichiometric equations for oxidation of carbohydrate, fat and protein.

Glucose:
1 mol $C_6H_{12}O_6$ + 6 mol O_2 -> 6 mol CO_2 + 6 mol H_2O + Energy
180 g glucose[1] + 134.4 litre O_2 -> 134.4 litre CO_2 + 108 g H_2O + 2817 kJ
1 g glucose + 0.747 litre O_2 -> 0.747 litre CO_2 + 0.60g H_2O + 15.7 kJ
Fat (tripalmitate):
1 mol $C_{51}H_{98}O_6$ + 72.5 mol O_2 -> 51 mol CO_2 + 49 mol H_2O + Energy
807 g tripalmitate[1] + 1625 litre O_2 -> 1143 litre CO_2 + 883 g H_2O + 32130 kJ
1 g tripalmitate + 2.011 litre O_2 -> 1.416 litre CO_2 + 1.09 g H_2O + 39.8 kJ
Dietary, meat and milk protein:
1 g protein + 0.992 litre O_2 -> 0.848 litre CO_2 + 0.38 g H_2O + 0.332 g urea + 18.4 kJ*

[1]Note that 1 mol of gas (e.g. O_2 and CO_2) is equivalent to 22.4 L (standard temperature and pressure, dry air). This value is derived from the "gas-equation" P x V = n x R x T, where P = pressure, V = volume, n = number of mol gas, R is the gas constant (0.08205) and T is temperature in Kelvin (273).

[2]Note that the value of 18.4 kJ/g for protein oxidation is substantially lower than the combustion value of 23.9 kJ/g caused by formation and excretion of energy via urea when protein is oxidised in the animal body. Also note that protein consist of 20 different amino acids in various ratios and the presented stoichiometry for 1 g of protein represent an average amino acid composition.

When food molecules are converted into energy substrates, it is important to distinguish between glucogenic energy and ketogenic energy. Glucogenic energy can be converted into ketogenic energy, but in our body ketogenic energy cannot be converted into glucogenic energy, because Acetyl Co-A cannot be converted into pyruvate (Figure 20.3). A major part of energy from the diet is taken up as glucose which is metabolised in the glycolytic pathway and converted into pyruvate, and the entire glucolytic pathway is glucogenic substrates. However, when pyruvate is converted into acetyl co-A, CO_2 is lost and during this irreversible step, glucogenic energy is converted into ketogenic energy. The pool of acetyl Co-A can be used for oxidation, whereby 3 molecules of CO_2 is lost per molecule of pyruvate (the first carbon was lost when Acetyl CoA was formed, the two other CO_2 was formed in the Krebs cycle). A substantial part of the energy follows this route, because heat is constantly being produced. If energy become abundantly available (e.g. when growing pigs are fed ad libitum), then part of the Acetyl CoA pool is used for de novo fat synthesis. If the pigs are restricted considerably, i.e. insufficient amount of energy is consumed, then body fat is instead mobilised and converted into ketogenic energy (Acetyl CoA), i.e. the de novo fat synthesis route is reversed. When energy substrates are used as a fuel, heat is produced due to the chemical oxidation of energy in the Krebs cycle and O_2 is consumed in the oxidative phosphorylation, and ultimately, CO_2 and water is produced along with energy being bound in ATP. In Figure 20.3, the major routes of

metabolism of dietary energy in pigs are shown. Note that carbohydrates other than fibre are glucogenic energy substrates, dietary fat is ketogenic, short chain fatty acids originating from fibre fermentation are mainly ketogenic (Acetate and Butyrate) whereas approximately 25% is glucogenic (propionate). Finally, when amino acids are oxidised, most can enter as glucogenic energy whereas lysine and leucine are the only amino acids that are strict ketogenic, i.e, they enter the Krebs cycle through Acetyl Co-A.

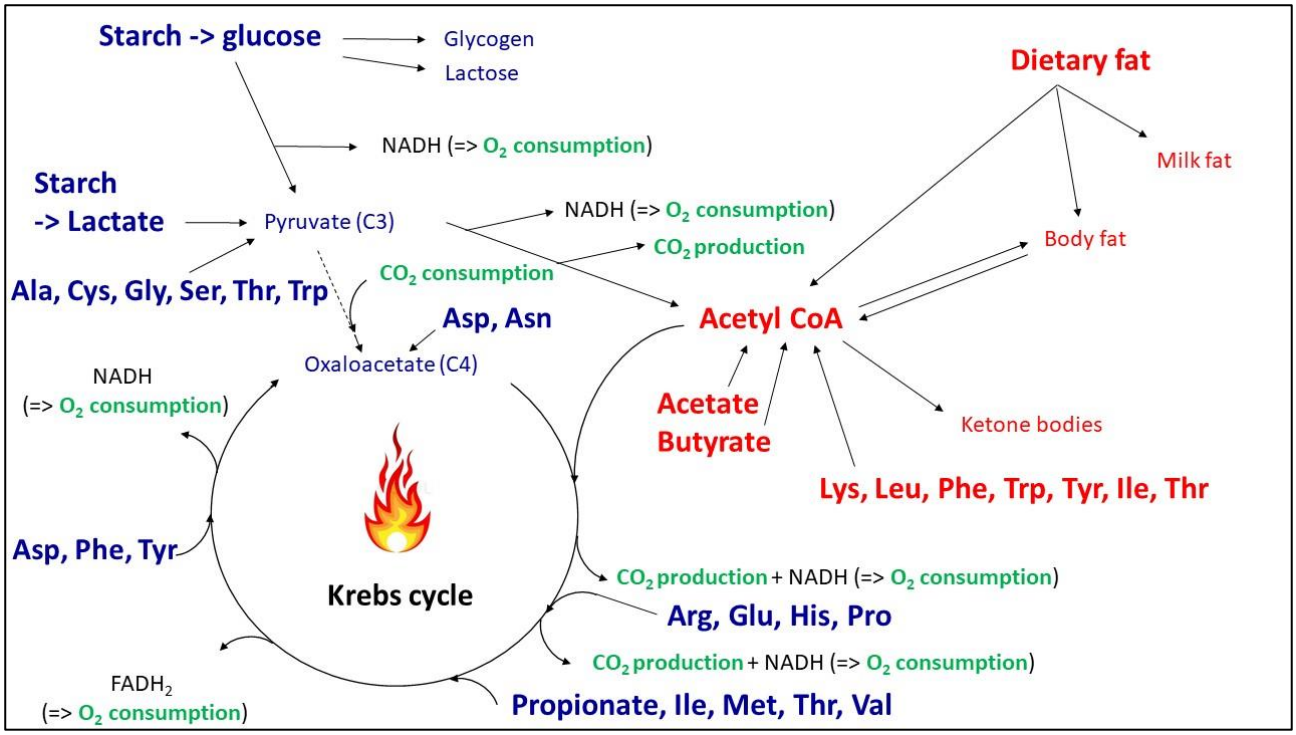


Figure 20.3. Overview of intermediary energy metabolism of dietary energy originating from starch, fat and protein, taken up to the blood as glucose, fat and amino acids, respectively. Glucogenic energy metabolites are shown in blue, ketogenic metabolites are shown in red, while exchange of O_2 and CO_2 are shown in green.

Carbohydrates are broken down by endogenous enzymes in the small intestine or by microbial fermentation in the large intestine [3]. These processes provide either monosaccharides, (mainly glucose) from the processes in the small intestine, lactate (produced mainly by lactobacilli in the stomach) and short-chain fatty acids (mainly acetate, propionate and butyrate) from fermentation processes in the hindgut (Figure 20.3). During the absorptive phase, glucose is net absorbed in excess of that used for oxidative processes, and the excess may be converted into glycogen. Under catabolic conditions, the glycogen that was previously stored, may be hydrolysed to CO_2 and H_2O, while O_2 is consumed. In the combustion of 1 mol of glucose, 6 mol of O_2 are used, 6 mol

CO_2 are produced, and 38 mol of ATP (adenosine triphosphate) are liberated which then act as energy donors for anabolic energy-consuming processes (Figure 20.4). Assuming that each mol of ATP contains 52 kJ, 1 mol of glucose will produce 38 × 52 = 1976 kJ in the body. Since the total energy content determined by combustion in a bomb calorimeter, i.e. outside the body, is 2817 kJ/mol, the amount of energy produced in the body equals an efficiency of 70%, (1976 kJ / 2817 kJ). Thus, only 70% of the total energy of the glucose is available for anabolic processes, while the rest is converted to heat.

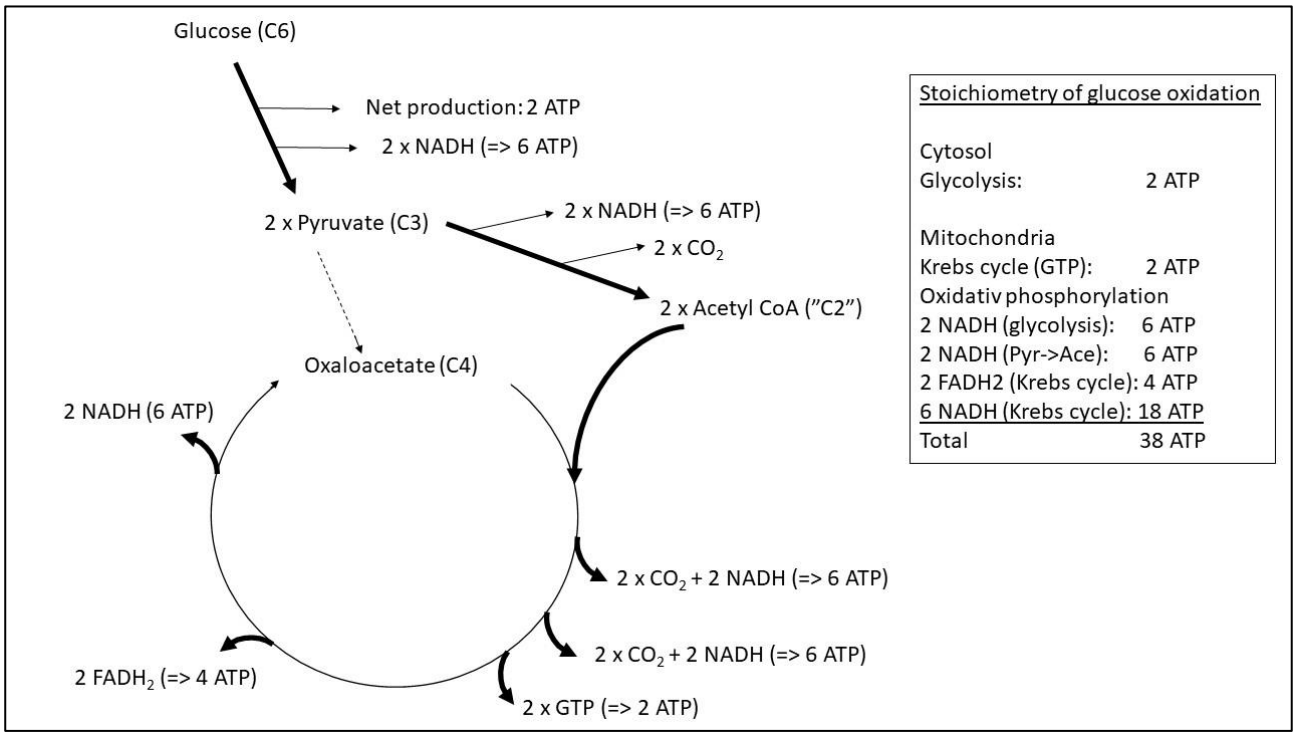


Figure 20.4. Stoichiometry of glucose oxidation. The pathway for glucose oxidation is shown with bold arrows. Energy metabolites are classified as glucogenic or ketogenic, and glucogenic energy can always be converted into ketogenic energy, which happens when pyruvate is converted into Acetyl CoA. In contrast, animals cannot convert ketogenic energy into glucogenic energy.

Not all tissues obtain energy from aerobic processes. Erythrocytes, white blood cells, kidney, tissue of eye and cancer cells gain most of their energy from the anaerobic conversion of glucose to lactate. According to the generally accepted view, metabolism is aerobic at rest and during moderate work. When the work load increases greatly, the O_2 supply will become insufficient and then energy will be supplied from anaerobic metabolism. Under anaerobic conditions, the formation of 2 mol of lactic acid from 1 mol of

glucose is associated with the net formation of only 2 mol of ATP. This is a fast way of obtaining energy, and lactate may then be released to the blood and later oxidised completely (by various tissues) when work load is less intense and O_2 again becomes abundantly supplied.

The majority of the body cells are able to oxidise and use fat/lipids as a source of energy as shown for tripalmitate (Table 20.1). The major part of the energy derived from fat is provided by the fatty acids. Fatty acids are made available from dietary lipids and lipids mobilised from body fat stores when glucose is unable to provide sufficient energy. The breakdown of dietary lipids starts by hydrolytic processes in the intestine where the fatty acids are split off from their ester-bounds to glycerol [49]. In catabolic metabolism, the net-absorbed glycerol is oxidised like a carbohydrate via the glycolysis and the tricarboxylic acid cycle in which 1 mol of glycerol yields 21 mol of ATP. The fatty acids are broken down to acetyl-CoA units and then completely oxidised into CO_2 and H_2O. For example, oxidation of 1 mol of tripalmitin yields 408 mol of ATP, thus providing 21 MJ stored in ATP. Since the total energy content determined by combustion in the bomb calorimeter is 32 MJ/mol, this will be equivalent to an efficiency of 65% (21/32), being almost similar to the efficiency of glucose oxidation.

The energy content per gram of protein, carbohydrate and fat is shown in Table 20.2. Note that if dietary protein is being retained, energy is being conserved, whereas protein is a bad energy substrate because a substantial amount of energy from the protein is being lost through urine, when protein is being oxidised.

Table 20.2. Gross energy content per gram of protein, carbohydrates and fat

	Diet, retention (body), milk	Oxidation (substrates used as fuel)
Protein	23.9	18.4
Carbohydrates[1]	17.6	17.6
Fat	39.8	39.8

[1]Note that carbohydrates are mainly polysaccharides. The energy concentration in starch is 10% higher per gram than in glucose (shown in Table 20.1), because molecular weight of glucose is 180 g/mol, whereas the molecular weight per glucose-unit in starch is 162 (remember that H_2O is released when polysaccharides are formed). Moreover, in the term "Carbohydrates", a minor amount of lignin is also included, which increases the gross energy concentration.

In pigs, under normal practical feeding conditions, about 5% of the energy available for anabolic processes originates from oxidation of short chain fatty acids, mainly acetate, propionate and butyrate. Acetate is converted to acetyl-CoA which is then oxidised via the tricarboxylic acid cycle to CO_2 and H_2O with a net yield of 10 mol of ATP per mol of acetate, corresponding to 10 × 52= 520 kJ/mol of acetate. The energy yield of acetate in the bomb calorimeter is 875 kJ/mol. The efficiency of the oxidation is then 520/875×100= 59%. Propionic acid can be converted to glucose and oxidised to CO_2 and H_2O with a net yield of 17 mol of ATP from each mol of propionate. The energy stored in ATP (884 kJ/mol propionate) is oxidised in the body. The energy yield of propionate in the bomb calorimeter is 1527 kJ/mol, and, consequently, the efficiency of the oxidation is then 884/1527×100= 58%. Small amounts of propionate are present in the peripheral blood supply; such propionate can be oxidised directly via succinyl-CoA with a net yield per mol propionate of 18 mol of ATP. Butyric acid can be decomposed to two acetyl-CoA units, then to CO_2 and H_2O yielding 25 mol of ATP, which is equivalent to 1300 kJ (25 mol of ATP × 52 kJ/mol). The energy yield of butyrate in the bomb calorimeter is 2184 kJ/mol. The efficiency of butyrate oxidation is therefore 60% (=1300/2184×100). If the oxidation pathway takes place via succinyl-CoA, additional 2 mol of ATP are generated, and the net yield per mol of butyrate is 27 mol of ATP.

Table 20.3. The enthalpies of combustion (ΔHc), yield of ATP upon complete oxidation, energy required for formation of 1 mol of ATP (ΔHc/ATP)[1] and the efficiency of oxidation in the animal.

Energy source	ΔHc kJ/mol	ATP Mol	Energy bound in ATP[2], kJ	Efficiency[3] %
Glucose (C6)	2817	38	2817	70
Lactate (C3)	1368	17	1368	65
Glycogen (c-polymer)	2839	39	2839	71
Starch (c-polymer)	2839	39	2839	71
Acetate (C2)	875	10	875	59
Propionate (C3)	1527	18	1527	61
Butyrate (C4)	2184	27	2184	64
Glycerol (C3)	1655	20	1655	63
Palmitate (C16)	9981	129	9981	67
Stearate (C18)	11285	146	11285	67
Tripalmitate (C51)	31606	407	31606	67
Amino acids[4]				
Alanine (N1, C3)	1623	16	1623	51
Arginine (N4, C6)	3738	29	3738	40
Asparagine (N2, C4)	1929	15	1929	40
Aspartate (N1, C4)	1568	17	1568	56
Cysteine (N1, C3)	2248	16	2248	37
Glutamate (N1, C5)	2266	26	2266	60
Glutamine (N2, C5)	2570	24	2570	49
Glycine (N1, C2)	974	7	974	37
Histidine (N3, C6)	3181	21	3181	34
Isoleucine (N1, C6)	3581	41	3581	60
Leucine (N1, C6)	3581	40	3581	58
Lysine (N2, C6)	3682	35	3682	49
Methionine (N 1, C5)	3176	18	3176	29
Phenylalanine (N1, C9)	4651	39	4651	44
Proline (N1, C5)	2739	29	2739	55

Serine (N1, C3)	1448	13	1448	47
Threonine (N1, C4)	2100	21	2100	53
Tryptophan (N2, C11)	5565	48	5565	44
Tyrosine (N1, C9)	4478	42	4478	49
Valine (N1, C5)	2930	33	2930	59

[1] On average 90 kJ is required for formation of 1 mol of ATP, and this value is often used as the mean enthalpy for mixed substrates.

[2] The net value of energy available from ATP hydrolysis is 52 kJ/mol ATP when oxidised in the intact organism.

[3] Calculated as Energy bound in ATP x 100 / total enthalpy (ΔHc).

[4] Enthalpies of amino acids oxidation include the enthalpy of synthesis of urea.

Food proteins are hydrolysed to amino acids in the intestine where they are net absorbed and used to build up proteins or become oxidised (Figure 20.2). Amino acids not used for synthesis (anabolic processes) are deaminated, resulting in the liberation of ammonia, and the amino acids are converted into the corresponding keto acids. These carbon skeletons can be used for glucose synthesis, lipogenesis or become oxidised to yield energy as ATP, and the energy content in a molecule is to a great extent determined by the number of carbon molecules (Figure 20.5).

The final product of amino acid degradation is acetyl-CoA and, depending on the nature of amino acids, glucose (from glucogenic amino acids) or ketone bodies (from ketogenic amino acids). The major glucogenic amino acids are alanine, glutamate and valine, while leucine and lysine are the only two amino acids that are strictly ketogenic. The other amino acids may be both glucogenic and ketogenic, depending on where they enter the citric acid cycle. The acetyl-CoA from amino acid degradation may be produced directly (from tryptophan and leucine), via pyruvat (from alanine, glycine, serine, threonine, cysteine) or via intermediates like oxalacetate, fumarate and succinyl-CoA.

All amino acids have a lower energy efficiency than carbohydrates and short chain fatty acids, because it cost energy to synthesise urea, and it is therefore inefficient to use protein (amino acids) as an energy source (oxidation of amino acids occur after each meal is consumed because the amino acid profile in a diet is never optimal for the animal performance). The efficiency when oxidising amino acids depends on the nitrogen:carbon ratio (Figure 20.6), where more nitrogen relative to carbon reduces the efficiency. Moreover, aromatic amino acids (tryptophane, tyrosine and phenylalanine) are even less

efficiently utilised than expected based on their nitrogen:carbon ratio, because they have to undergo substantial metabolic conversion before the metabolites can enter Krebs cycle. Sulphur-containing amino acids (methionine and cysteine) are also less efficiently utilised than expected based on their nitrogen:carbon ratio, whereas arginine is more efficiently utilised than expected based on their nitrogen:carbon ratio (arginine has 4 N per molecule, which is higher than any of the other amino acids). Then, acetyl-CoA is processed via the citric acid cycle to yield energy in the form of ATP, while CO_2 concomitantly is produced, and O_2 is consumed. Most of the ammonia arising from the degradation of amino acids is excreted as urea. Urea formation requires energy; a total of 4 mol of ATP are needed per 1 mol of urea formed. Further, about 1 mol of ATP is used during the excretion of urea. Therefore, in assessing the efficiency of amino acid oxidation, the energy required for urea synthesis must be considered in the calculations.

The high energy requirement for urea synthesis and excretion may be one of the main reasons for the great heat increment observed in animals consuming dietary protein in excess of their protein requirement. Taking aspartate as an example of amino acid oxidation, the heat of combustion (ΔHc) is 1568 kJ/mol, the net yield of ATP is 17 mol ATP per mol aspartate, and the ΔHc per mol of ATP can then be calculated as 1568/17 = 92 kJ/mol of ATP. The efficiency may now be calculated as 52/92 = 0.53, representing an efficiency of aspartate oxidation being 53% (the 52 kJ is the net value of energy from ATP hydrolysis when oxidised in an intact organism). The ΔHc may be found in Weast et al. [87], whereas the number of ATP may be derived from the energetic pathways of energy metabolism within animals, i.e. glycolysis, conversion of pyruvate to acetyl CoA, oxidation in Krebs cycle, and oxidative phosphorylation, as reported by Stryer [70]. The data in Table 20.3 summarise the estimates of heat energy equivalents of high energy phosphate bonds (ATP) formed during the oxidation of several major energy sources/metabolites relevant for pigs.

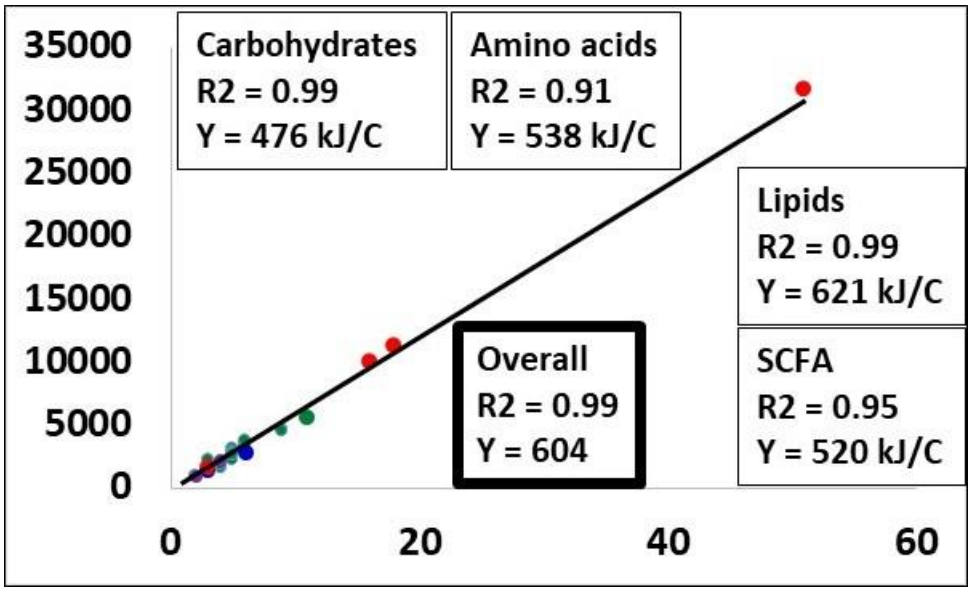


Figure 20.5. Relationship between number of carbon atoms and energy content in amino acids (green), glucogenic metabolites from carbohydrates (glucose, lactate, and glycerol; blue), short chain fatty acids (SCFA) from fibre fermentation (purple), and lipid molecules (red). The slope of the tendency line (604 kJ/C) represents the overall energy content per carbon molecule, and the boxes show the individual tendency lines for the 4 classes of metabolites (carbohydrate derived molecules, amino acids, short chain fatty acids, and lipids).

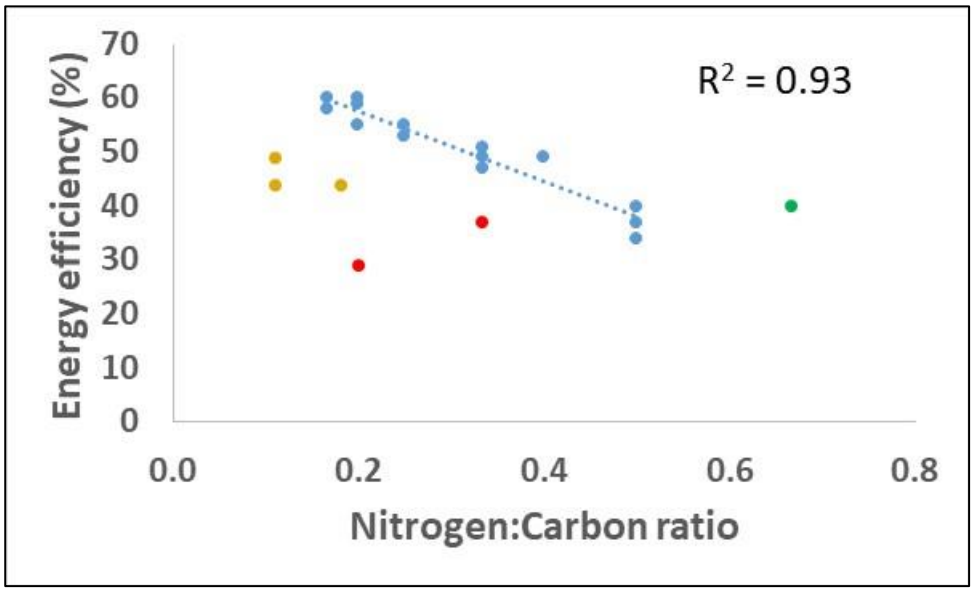


Figure 20.6: Relationship between nitrogen to carbon ratio in amino acids and the energetic efficiency (Regression line, R^2 = 0.93, represent 14 amino acids. Aromatic AA (yellow) and sulphur-containing AA (red) are even less efficient while arginine (green) are more efficient than expected based on the nitrogen to carbon ratio.

3. Anabolism

Most of the energy transferred to ATP via the oxidative processes is liberated and used in anabolic processes. Quantitatively, the anabolism mainly concerns the formation of carbohydrate (glycogen in the liver and the muscles; lactose in milk), fat (tissue and milk) and protein (enzymes, hormones, antibodies, colostrum, milk and growth of foetuses, placenta, uterus, mammary glands and muscles). Genetically, the urge of forming protein is quantitatively much more dominating than that of forming fat. In young growing pigs, the body gain may comprise 25% protein, 70% water and 5% fat where most of that fat is structural fat. As animals approach maturity, the preference towards protein retention decreases and that towards fat accretion increases. The chemical composition of pigs from birth to maturity is described in detail by Danfær and Strathe [14].

Glucose is a precursor for glycogen and lactose synthesis. Apart from net-absorbed glucose, glucose is synthesised from gluconeogenic substances as lactate (lactic acid), amino acids, propionate and glycerol. Glycogen is a complex polysaccharide made up of glucose residues and has the ability to add on further glucose units. It is a readily mobilised storage form of glucose. The formation of glycogen is a fairly cheap process, totally, as slightly more than 1 mol ATP per mol glucose 1-phosphate is used for the storage of glucose units in glycogen. Hence, 1 mol ATP is used to phosphorylate glucose to 1 mol of glucose 1-phosphate and one high-energy phosphate bond (ATP) is spent when incorporating glucose 6-phosphate into glycogen (also known as glycogenesis).

Fatty acids synthesised in the body and fatty acids absorbed from the intestine are involved in the esterification of fatty acids to triglycerides and certain phosphatides in depot fat. There are two systems of fatty acid synthesis: The first is a cytoplasmic system resulting in the production of palmitic acid from acetyl-CoA. The second is a mitochondrial system resulting in the elongation of the existing fatty acids by two-carbon addition (chain elongation) by means of acetyl-CoA units. Most unsaturated fatty acids are formed by dehydration of the corresponding saturated fatty acids, except the essential fatty acids which cannot be produced by the animal but must be supplied with the feed. Three mol of fatty acid and 1 mol of glycerol are used for complete synthesis of a triglyceride. The glycerol part is formed from glucose by reduction of dihydroxyacetone phosphate to glycerol.

In the first step of protein synthesis, the amino acids are linked to form peptides in a genetically determined order. Then the peptides are polymerised and folded to protein by means of different linkages. During all stages of protein synthesis, energy is provided by hydrolysis of ATP and guanosine triphosphate (GTP); the total number of mol of ATP and GTP needed to synthesise one peptide bond is 4. The 4 mol per peptide bond explain why lean growth is associated with substantial loss of energy due to increased heat production associated with re-generation of ATP from ADP (or GTP from GDP).

Table 20.4. Theoretical stoichiometric energy efficiencies for selected energy metabolites in plasma when employed during anabolism (only selected fates/products are shown).

Substrate	Product	Efficiency pct.	Heat increment pct.
Glucose	Body glycogen	95	5
	Body fat	81	19
	Milk lactose	94	6
Lipid	Body fat	96	4
Protein	Body protein	87	13
	Body fat	66	34
	Milk protein	86	14
Propionate	Milk lactose	78	22
Acetate	Milk fat	76	24

The data in Table 20.4 summarise the estimates of theoretical biochemical efficiencies for deposition of protein, fat and carbohydrate calculated as enthalpy of combustion of the product divided with enthalpy of combustion of the substrate + energy for synthesis from ATP.

4. Definitions of energetic terms

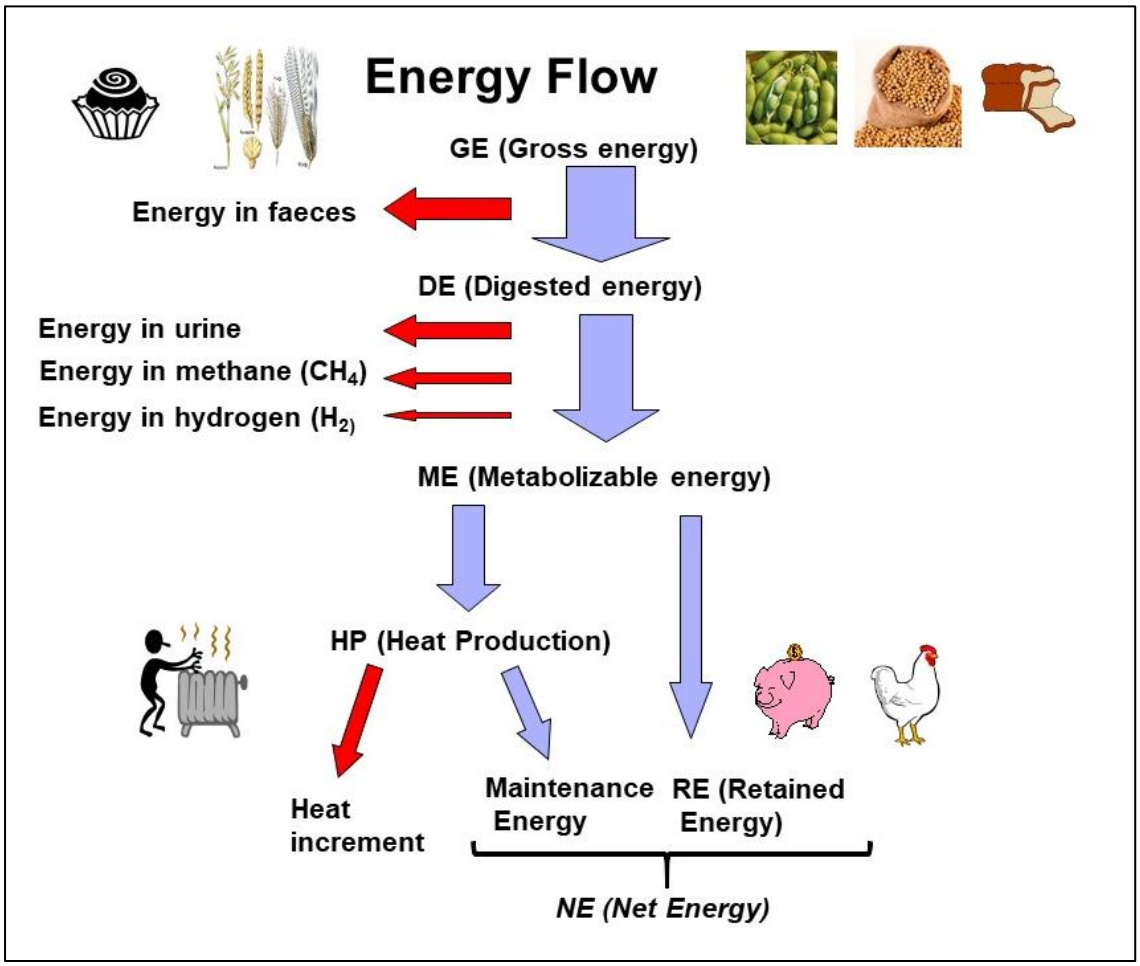


Figure 20.7. Schematic overview of energy terms used.

In animal nutrition, energy is interesting from four perspectives:

1) Energy metabolism (what is the fate of ingested energy within the pig?)
2) Energy expenditure (how much energy do pigs require?)
3) Energy utilisation (how efficient is dietary energy utilised?)
4) Prediction of dietary energy (how can we predict energy concentrations of diets based on dietary ingredients or dietary analyses?).

The first two aspects (energy metabolism and energy expenditure) are important from an animal perspective, whereas the latter two aspects (energy utilization and prediction of dietary energy) are important from the feed perspective. Especially the last aspect, prediction of dietary energy, is used every day worldwide when formulating feed

and optimising the dietary content of essential nutrients relative to dietary energy. The four different aspects of energy are described in detail in sections 5, 6, 7 and 8 in this chapter. Here, it is important to stress that energy metabolism, energy requirement, energy utilisation and prediction of dietary energy may all deal with energy at different levels, including gross energy, digestible energy, metabolisable energy and net energy (Figure 20.7). Note that the units used to denote the amount of gross energy, digestible energy, metabolisable energy or net energy are the same, namely kJ or MJ. Previously, kcal was used, and this unit is still widely applied especially within human nutrition. It is important to stress that energy metabolism and energy requirement refer to the amount of energy per unit of time (for example MJ/d), whereas energy utilisation is given in per cent (or a fraction, i.e. MJ/MJ), and prediction of dietary energy concentration in feed evaluation refers to the amount of energy per unit of feed (for example MJ NE/kg feed or MJ NE/kg DM). Since the energy requirement (in MJ/d) and energy concentration in feed (in MJ/kg) may represent four different energy levels, it is crucial always to specify which energy level the reported values refer to. To illustrate this, 1 kg DM of standard pig feed contains approximately 18.4 MJ of gross energy, which is equivalent to approximately 9 MJ of net energy. Thus, reporting the energy intake or dietary concentration is highly misleading unless the energy level is specified.

Figure 20.8. Parr 6300 Calorimeter, ISO-9831 [24]. (Photo: Henry Jørgensen).

Analytically, the GE content of feed, ingredients, faeces, urine, milk and body content may be measured in an apparatus known as a bomb calorimeter. Using bomb calorimetry

(Figure 20.8), feed, ingredients, milk, pig meat or pig fat can be oxidised completely by supplying oxygen at high pressure, and the heat released after complete oxidation can be measured. Alternatively, the energy content of feed, feed ingredients, faeces, urine, milk and body pools and heat produced during nutrient oxidation (which will be described later) can be calculated from the chemical composition using the following equations:

Feed, feed ingredients, and milk:
GE, kJ = 23.9 kJ/g x g crude protein + 39.8 kJ/g x g crude fat + 17.6 kJ/g x g ”carbohydrate”

Body pools:
GE, kJ = 23.9 kJ/g x g crude protein + 39.8 kJ/g x g crude fat

Faeces:
GE, kJ = 22.7 kJ/g x g crude protein + 39.8 kJ/g x g crude fat + 19.7 kJ/g x g ”carbohydrate”

Urine: 7.04 kJ/g x ”g crude protein” (n=1109, Jørgensen et al, unpublished).

Heat production:
GE, kJ = 18.4 kJ/g x g crude protein + 39.8 kJ/g x g crude fat + 17.6 kJ/g x g ”carbohydrate”

where 23.9 kJ/g, 39.8 kJ/g and 17.6 kJ/g denoted the contents of gross energy per g of protein, fat and “carbohydrate”, respectively, in feed, feed ingredients and milk [13]. Note that the energy values for carbohydrate is not the same as that shown for glucose in Table 20.1, because dietary “carbohydrate” include components like sugars, starch and non-starch polysaccharides and the non-carbohydrate component lignin. Note also, that the energy value in protein is markedly higher (23.9 kJ/g) in feed, feed ingredients and milk as compared with the heat production when protein is oxidised (18.4 kJ/g; Table 20.2). Indeed, the heat produced during protein oxidation correspond to 77% of the gross energy content of the protein, because a substantial fraction of energy from protein is lost through urea, which is excreted via urine. This will further be described in section 7.

5. Energy metabolism in pigs

From the animal perspective, the daily amount of energy supplied and the amount ingested may be quantified, and the fate of this energy reveals where energy is partitioned within the animal (Figure 20.9).

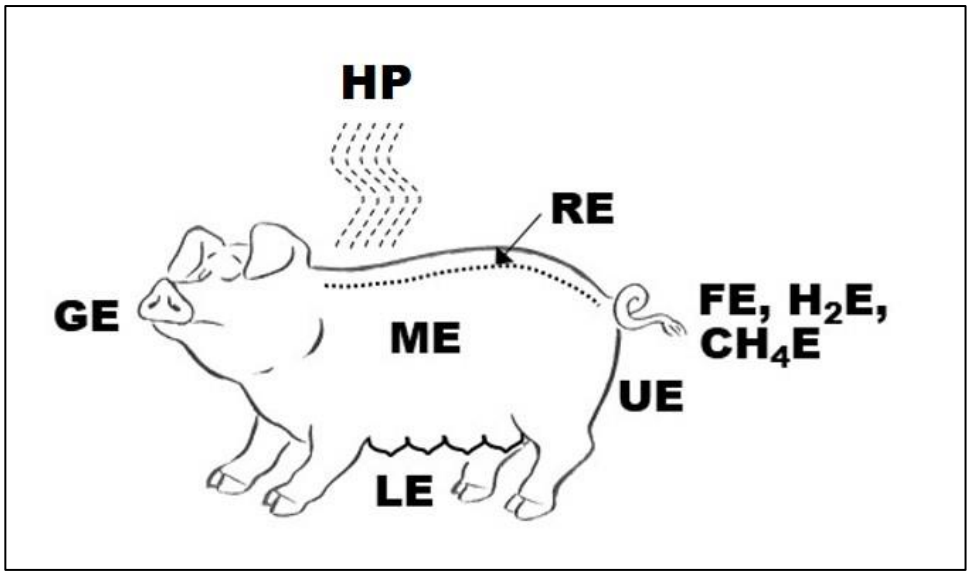


Figure 20.9. Energy metabolism in pigs and sows (GE is gross energy, ME is metabolisable energy, HP is heat production, LE is liquid energy secreted in milk, FE is faecal energy, H_2E and CH_4E are energy loss via hydrogen and methane, respectively, and UE is energy loss via urine).

The animal requires energy for different purposes like maintenance, retention, reproduction (e.g. mammary growth and milk production) and other traits (described later). These aspects denote energy intake (input from feed) and energy expenditure ("output" used for different purposes), and the difference between energy intake and energy expenditure denotes the energy balance.

Energy balance, kJ/d = Energy intake, kJ/d – Energy output, kJ/d

where the energy balance refers to the amount of energy retained in the body (i.e. energy retention), energy intake refers here to gross energy (feed supply corrected for feed refusals times gross energy density of the diet), and energy output refers to energy loss in faeces, urine, gases, heat, energy retained in growth (muscle and fat) and energy secreted via colostrum and milk. Note that energy intake may also refer to intake of for example metabolisable energy, and then the energy output will NOT comprise energy loss in faeces, urine and gases (see also section 6). When describing quantitative energy

metabolism of animals, we distinguish between the following physiological concepts which all can be measured in animal trials (Table 20.5):

Table 20.5. Supply and intake of energy and utilisation of metabolisable energy (ME; MJ/d).

Energy	Abbreviation	Approach / calculation
Supply of Gross Energy	GE supply	Feed supply x $Diet_{GE}$
Intake of Gross Energy	GE intake	(Feed supply - feed residue) x $Diet_{GE}$
Intake of Digestible Energy	DE intake	Intake of gross energy – energy in faeces
Intake of Metabolisable Energy	ME intake	Intake of digested energy – energy in urine and gases
Intake of Net Energy	NE intake	NE for maintenance + retained energy
Utilisation of Metabolisable Energy		
Heat	HP[1]	RQ- method
Milk	LE[2]	Milk yield x $Milk_{GE}$
Retained energy (= E balance)	RE[3]	CN-method or comparative slaughter method

[1] Heat production (HP) can be measured by indirect calorimetry (gas exchange) using the RQ method (RQ = respiratory quotient), or as a difference using the CN method (CN = carbon nitrogen balance) or the comparative slaughter method: HP = Intake of metabolised energy – (RE + LE). See paragraph 6.1.2.6. for a definition of RQ and section 9 for a description of the methods.

[2] LE refers to lactation energy (i.e. energy secreted through sow milk).

[3] Retained energy can be quantified using the CN method or the comparative slaughter method. In addition, RE can be determined by the RQ method as a difference: RE_{RQ} = ME – (HP_{RQ} + LE). Calculations of RE using these methods are also described in details in section 9.

5.1. Energy supply

Energy supply is the amount of energy on a daily basis administered to an animal. The energy supply is calculated as the feed supply multiplied with dietary energy concentration where the dietary energy concentration can be at different energy levels (gross, digestible, metabolisable or net energy, see below). When calculating the energy intake, it is important that all traits (feed supply, feed leftover and energy concentration) are expressed on the same basis; all traits must be expressed on either dry matter basis or as-fed basis. It is important to stress that the variation in energy concentration among different diets is rather low (most pig and sow diets contain approximately 1.00 to 1.10 feed units per kg), and therefore the feeding curve (i.e. feed units supplied per day) is the major determinant of the energy supply.

5.2. Energy intake

Energy intake is the amount of energy ingested by the animal and can, like the energy supply, be expressed at different energy levels (gross, digestible, metabolisable or net energy, see below). Note that the difference between energy supply and energy intake

is that energy intake is corrected for feed residues and then multiplied by energy density of the diet. Thus:

Feed intake, kg/d = Feed supply, kg/d – feed leftover, kg/d.

Energy intake (MJ/d) = Feed intake (kg/d) × dietary energy (MJ/kg).

It is important to emphasise that the feed intake is the most important factor for the energy intake and also of paramount importance when studying energy metabolism. If the energy intake is unknown, it makes no sense to quantify energy metabolism or energy utilisation. In commercial settings, energy supply is normally reported instead of energy intake, and if trials are carried out without reporting the energy intake, it is important to carefully reduce the feed supply if animals have feed leftovers.

5.2.1 Gross energy (GE) intake

The GE intake is the amount of energy manifested as heat when feed is completely oxidised (i.e. when combusted in a bomb calorimeter at high pressure, at high temperature and in presence of abundant O_2) per kg of feed multiplied by the daily feed intake (Figure 20.8). Energy is stored in the chemical components of food as chemical energy. The heat of combustion is the maximum amount of energy that potentially may be available for use by animals, but in reality much less energy is available for the animal. Gross energy of different nutrients varies, but typical values are: protein 23.9, carbohydrate 17.6 and fat 39.8 kJ/g (originally, the constants 5.7, 4.2 and 9.5 kcal/g were used, and the constant 4.185 kJ/kcal may be used to convert from kcal to kJ or vice versa according to Kleiber [48]. The differences between these nutrients primarily reflect the C: H ratio and the O and N contents. Glucose ($C_6H_{12}O_6$) has 1 atom of oxygen per atom of carbon, whereas a fat molecule, for example glycerol trioleate ($C_{57}H_{104}O_6$), has 6 atoms of oxygen per 57 atoms of carbon. Thus, fat requires more oxygen during complete oxidation and releases more heat per gram during combustion. In other words, fat is much more energy-dense than protein and carbohydrates. As a consequence, the gross energy density of diets is mainly determined by the dietary fat level. A common pig diet (containing 3% fat) contains approximately 18.4 MJ GE/kg DM, but if 8% fat is supplemented (i.e. the diet contains approximately 11 % dietary fat), the energy density is approximately 20 MJ GE/kg DM. Almost all pig diets used in practice are within 18 to 20 MJ GE/kg DM. Consequently, the daily intake of gross energy is to a great extent determined by the feed intake, whereas

the energy density only plays a minor role. It should, however, be emphasised, that although the GE concentration of diets only vary approximately 10% (from 18 to 20 MJ GE/kg DM), the utilisation of dietary energy may vary substantially more, depending on the macro nutrient composition, as will be clear to the reader in section 7.

5.2.2. Digestible energy (DE) intake

The DE intake is the amount of ingested gross energy that is digested and may be calculated using one of the following equations:

DE, MJ/d = GE intake, MJ/d – total energy output in faeces, MJ/d

DE, MJ/d = GE intake, MJ/d x energy digestibility (%) / 100

where DE denotes the amount of (total tract) digestible energy and GE is the gross energy intake. Note that on a daily basis, the feed intake has a major impact, as GE intake increases linearly with the feed intake. The energy density in the diet (GE concentration per kg of DM) and the energy density in faeces (GE in faeces) may be measured using a bomb calorimeter, whereas the feed intake and amount of faeces excreted daily can be quantified for pigs housed in metabolic cages. The energy digestibility can be calculated from the total collection or by using a marker technique, as will be described later. The ratio between DE and GE represents the digestibility of energy, which may also be referred to as faecal digestibility or total tract digestibility of energy. Energy digestibility may also be quantified at terminal ileum using cannulated pigs (surgically modified [37] [19]), and then the energy digestibility obtained is denoted ileal digestibility of energy, which is now used in the current Danish energy evaluation system (named physiological energy). The amount of ileal digestible energy comprises only energy which is enzymatically digested in the small intestine, whereas the total tract digestibility comprises both energy digested enzymatically and energy fermented by bacteria in the hindgut [33]. Hindgut fermentation results in end-products like gases (especially methane but also hydrogen) and energy compounds that may be net absorbed to portal blood. These compounds include lactate and short chain fatty acids like acetate, propionate and butyrate. Both the total tract digestibility and the ileal digestibility of energy is greatly affected by the chemical composition of the diet and thus by the feed ingredients used. For instance, increasing the dietary content of fibre increases considerably the energy loss in faeces, indicating that the total tract digestibility of energy is lowered (see section 7 for

more details). Indeed, the dietary content of fibre is of major importance for the energy digestibility, whereas dietary levels of fat and protein play a less important role for energy digestibility of diets (Figure 20.10). It should be stressed that different sources of fibre, fat and protein affect the energy digestibility differently and may deviate substantially from that shown in Figure 20.10. The quantitative impact of dietary intake and diet composition on energy loss in faeces, urine and heat is described in section 7.

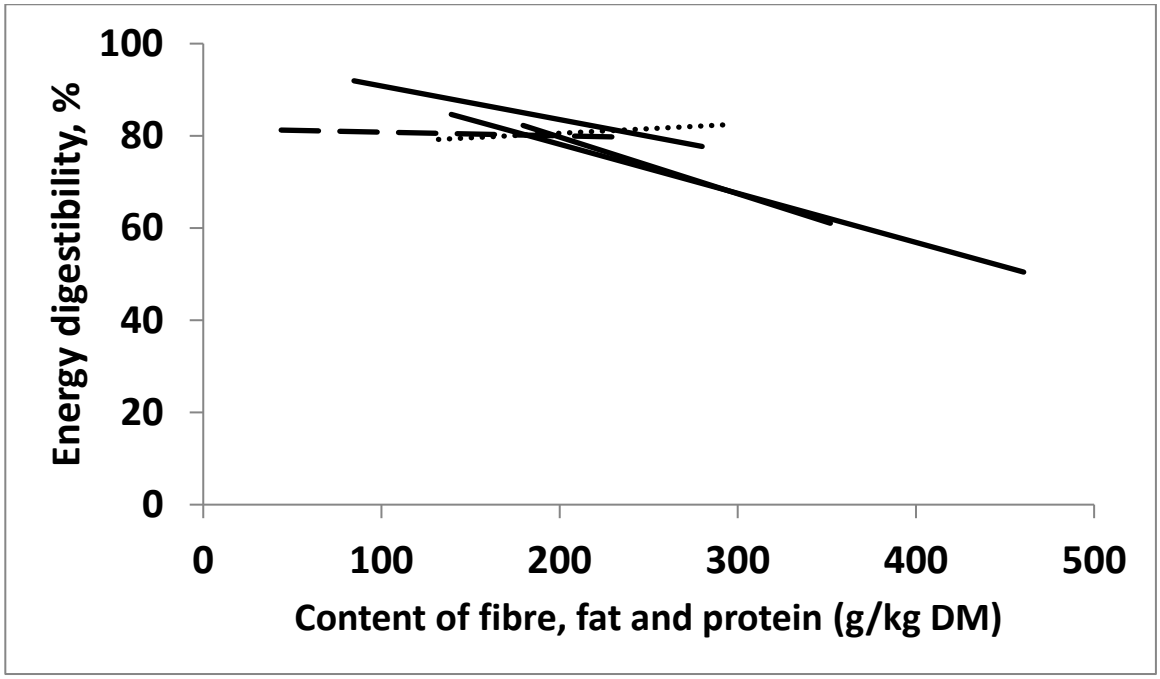


Figure 20.10. Impact of dietary fibre (three solid lines are shown which represent 3 different fibre sources [31] [32] [33], dietary fat (dashed line [29]) or dietary protein (dotted line [29]) on total tract energy digestibility. The data have been gathered from collection trial with growing pigs housed in metabolic cages.

5.2.3. Metabolisable energy (ME) intake

The ME intake is the amount of energy available to the animal for body functions (maintenance, growth, production of milk and heat increment due to processes not included in maintenance, see sections 5.3 to 5.5). Thus, the intake of metabolisable energy may directly be compared with the energy expenditure, and if the intake of metabolisable energy meets the energy expenditure of the animal, the energy balance is zero (i.e. energy is neither retained nor mobilised). The metabolisable energy may be transformed to other forms of energy in the body, regardless of type of transformation and whether the transformations are of any use to the animal. The ME may be determined from balance trials as follows:

$$ME, MJ/d = GE, MJ/d – FE, MJ/d – UE, MJ/d - CH_4E, MJ/d$$

where ME is metabolisable energy, GE is gross energy, FE is faecal energy, UE is energy loss in urine assessed from the daily urine production and energy content of urine measured in a bomb calorimeter, and CH_4E is loss of energy via methane which may be measured in respiration trials. Thus, metabolisable energy can be measured only if the amount of faeces and urine production is quantified, for instance by means of total collection. Alternatively, urine production may be quantified using a marker (e.g. para amino hippuric acid) which constantly may be infused into the blood (see section 9), and the amount of faeces may be quantified using a digestibility marker [42]. Energy loss via methane production is relatively small in pigs, and in growing pigs fed a standard diet, energy loss via methane typically account for 0.2-0.5% of GE. However, pigs and sows fed diets high in fermentable fibres have a considerably greater loss of energy via methane and it may be as high as 2.7% of GE [41]. Energy loss as methane may be quantified using respiration chambers.

5.3. Heat production

The heat production (HP) is the energy produced by the intermediary metabolism in the body and accounts normally for the majority of the energy consumed by the animal. Thus, understanding the factors that may reduce the heat production of animals is important to improve feed utilisation. Heat production arises from oxidation of carbohydrate, fat and protein. Total heat energy includes heat produced due to maintenance processes and the so-called heat increment (HI). The pig produces heat as a result of various processes of which some are of vital importance for the animal, such as respiration and blood circulation. Other processes are muscle activity as well as heat production in connection with feed intake and the subsequent digestion and metabolism of nutrients. The pigs' heat production can basically be separated into maintenance and heat increment (HI). The heat due to maintenance is a fundamental and substantial loss of energy related to maintaining a living animal, whereas heat increment can be regarded as extra heat loss due to e.g. growth, physical activity (above that required for maintenance) and thermoregulation (if ambient temperature is below the thermoneutral zone). These aspects will be described in details in section 6.

5.4. Milk energy (LE)

The LE denotes liquid energy and represents the amount of energy secreted via milk. The LE is therefore a product of the milk yield and gross energy concentration of the milk. Theoretically, the LE is easy to assess, but in practice it is indeed a challenge to quantify milk yield of sows (see Varmløse Hansen [83], Theil et al. [77] and Hansen et al. [20]).

5.5. Energy balance or retained energy (RE)

The retained energy (RE) is the amount of energy retained in the body, which is also referred to as the energy balance.

$$\text{Energy balance (or RE)} = GE - FE - UE - HP - LE$$

where GE is gross energy, FE is faecal energy, UE is urine energy, HP is heat energy, and LE is liquid energy secreted in milk in MJ/d. Energy retained in the body is the body energy accretion, while milk energy is secreted as fat, protein and lactose (a milk-specific carbohydrate). Energy retained may be split into energy retained as protein and energy retained as fat, whereas energy retained as carbohydrate is normally assumed to be zero in growing and adult animals.

5.6. Net Energy (NE)

The net energy is for a growing pig defined as the amount of energy required for maintenance (at NE level, i.e. NEm) added to the amount of energy retained in growth due to energy retained, which is the sum of energy retained in protein and fat [34]. The net energy concept was used in Denmark until 2004 and is still widely used in many countries worldwide (e.g. France, Netherlands and USA). The concept was developed for growing pigs to optimise diets for pigs and to rank feed ingredients according to how much energy their supplied to the complete ration. The system is also being used for pregnant and lactating sows, even though it has some limitations for sows. For instance, NE for maintenance has never been measured for sows. Furthermore, even though lactating sows are fed huge amounts of energy, they are typically experiencing a negative energy balance and consequently, like lactating cows, sows mobilise energy from their own energy depots mainly during early lactation. With other words, while growing pigs prioritise their maintenance energy requirement and then their requirement for growth, the lactating sows prioritise their milk production prior to their energy requirement for maintenance

(which is seldom met). To evaluate net energy properly for lactating sows, it is important to correct for how much energy is being supplied from the sow body, as was recently done by Pedersen et al. [65].

6. Energy expenditure (output)

Energy is used for different purposes, and the proportion of gross energy from the diet that is used differ depending on the physiological stage. For instance, growing pigs use approximately 25 to 30% of the dietary GE for retention, whereas lactating sows secrete approximately 50% of the dietary GE into milk, while they concomitantly mobilise 10% extra energy from the body (negative energy balance; Figure 20.11).

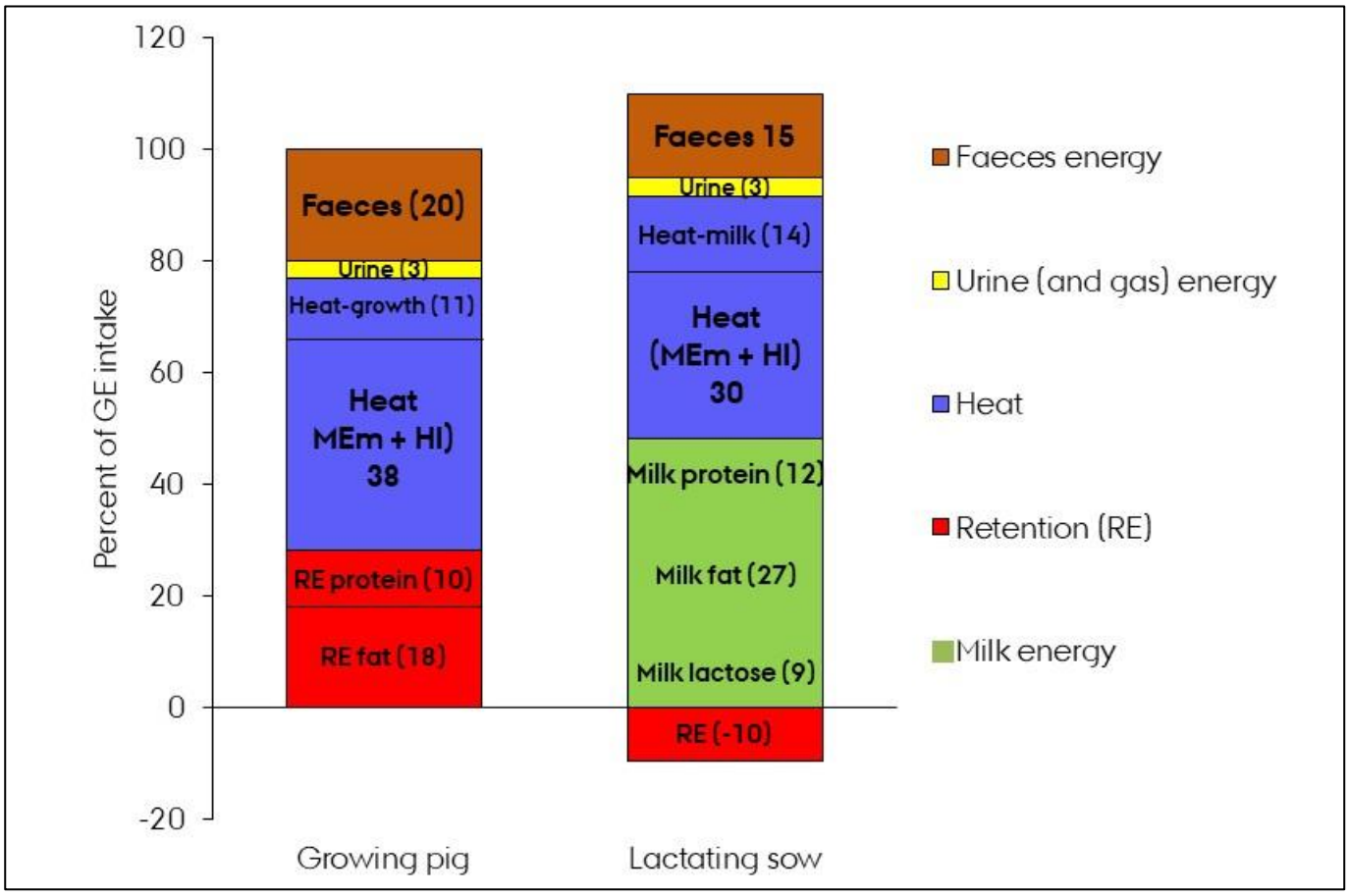


Figure 20.11: Fate of dietary gross energy fed to growing pigs and lactating sows. The energy below zero for lactating sows represents energy being mobilised from the body (mainly from body fat) to support the high demand of energy for milk production (milk fat).

6.1. Heat Production

Animals are continuously producing heat and losing it to their surroundings, either directly by radiation, conduction and convection or indirectly by the evaporation of water. Heat may be regarded as an obligatory heat loss (termed maintenance) and heat increment (additional heat loss above maintenance). The heat produced due to maintenance is the greatest contributor to the total heat production of pigs and sows, whereas the heat increment normally contributes less to the total heat production. Indeed, 52%, 90% and 67% of the total heat production of growing pigs, pregnant sows and lactating sows, respectively, represent energy required for maintenance [34] [74] [77]. The heat increment is heat loss due to inefficient utilisation of energy for anabolic processes (growth, reproduction and milk production), additional heat production due to need for thermoregulation and additional heat production due to physical activity above the (minimal) level of physical activity included in the concept of maintenance. The heat increment is high if the energy efficiency is low and vice versa. Typical values for partial energy efficiencies of using metabolisable energy for protein retention, fat retention, growth (i.e. protein and fat combined), reproduction and milk production are shown in Table 20.6. Partial energy efficiencies describe how efficient metabolisable energy is utilized for specific purposes, e.g. growth or milk production. These partial efficiencies account for the utilization of energy above maintenance, whereas the efficiencies of utilizing plasma metabolites shown previously in Table 20.4 included the energy required for maintenance (the energy requirement for maintenance is described in the next section, 6.1.1.). The total heat production varies diurnally and peaks in the post-absorptive phase after feed consumption due to heat increment (Figure 20.12). The figure illustrates the oxygen consumption, not the heat production, but oxygen consumption explains approximately 80% of the variation in heat production. The post-absorptive increase in heat production is referred to in the literature as either diet-induced thermogenesis, thermic effect of feeding or specific dynamic action. We will use the term diet-induced thermogenesis (DIT). The DIT increases postprandial due to energetic costs associated with transport of nutrients through the gastro-intestinal tract, transport of nutrients (e.g. glucose and amino acids) via the blood and into tissues, and energy loss associated with anabolic processes like synthesis of fat and protein for retention. The DIT may be split into a short-term effect of feeding and a long-term effect of feeding (Figure 20.12; Van Milgen

et al. [84]). It should be emphasised that part of the DIT is included in maintenance (see below).

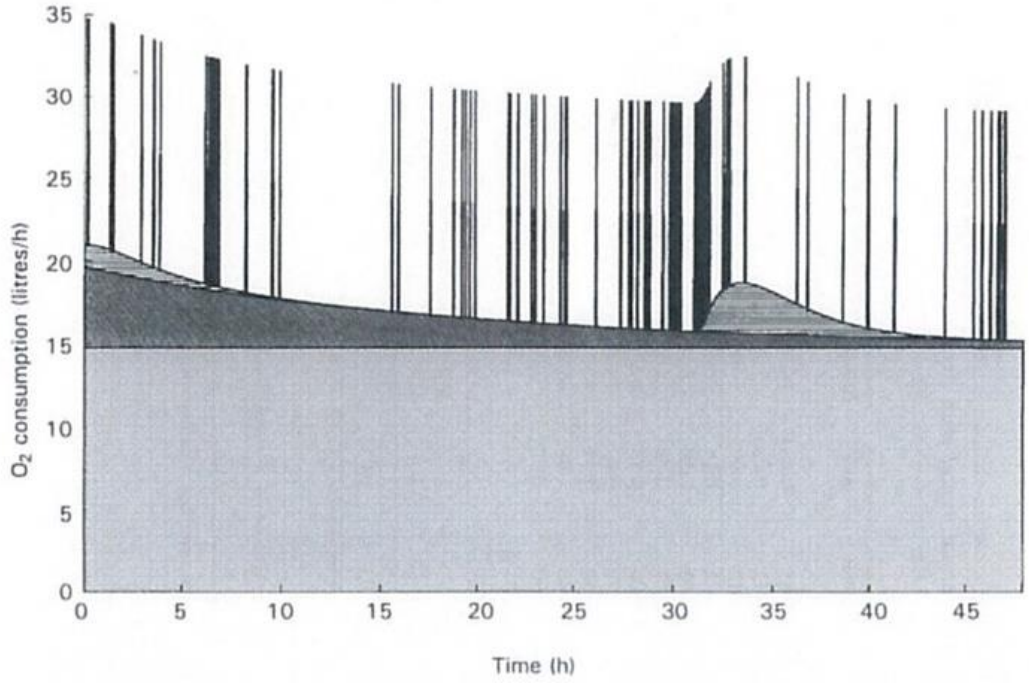


Figure 20.12. Components of O_2 consumption in a 40-kg growing pig. The animal was subject to a 31-h fast after which it received a test meal (one third of the daily *ad libitum* intake). The components included fasting-resting O_2 consumption ( ), the adaption from a fed-resting to a fasting-resting state ( ), the thermic effect of feed ( ) and O_2 consumption due to physical activity ( ). The heat production may be calculated from the O_2 consumption as HP, kJ/h = O_2 consumption (L/h) x 21 kJ/ L O_2 consumed (modified from Van Milgen et al. [84]) by assuming a respiratory coefficient of 1.0.

Table 20.6. Partial energetic efficiencies[1] (in %) of dietary metabolisable energy and associated heat production.

Partial efficiencies			Heat increment
k_p – Efficiency of protein retention	60%[2]	(Strathe et al., [69]	40%
k_f – Efficiency of fat retention	80%[3]	(Strathe et al., [69]	20%
k_g – Efficiency of growth	73%[4]		27%
k_r – Efficiency of reproduction	50%[5]		50%
k_l – Efficiency of milk production	78%[6]	(Theil et al., [75]	22%
k_m – Efficiency of body mobilisation	89%[7]		11%

[1]Partial efficiencies describe the energetic efficiency above maintenance.

[2]k_p values are reported across different studies within the interval 52-63 % (Strathe et al., [69]).

[3]k_f values are reported across different studies within the interval 60-88 % (Strathe et al., [69]).

[4]Calculated as 0.67 x k_f + 0.33 x k_p, which represent the relative distribution of energy being retained in growing pigs as fat and protein, respectively.

[5]Assumed value, Feyera & Theil, [16].

[6]Milk energy output corrected for body mobilisation and expressed per kg of metabolic live weight was regressed on ME intake per kg of metabolic live weight to obtain the partial efficiency.
[7]Assumed value, Noblet et al., [56].

6.1.1. Energy requirement for maintenance

Knowledge of the energy requirement for maintenance (ME_m) is of significance to estimate the energy requirement and for predicting dietary energy (see sections 6 and 8), because the maintenance energy is a substantial part of the daily energy requirement (Figure 20.10). The energy requirement for maintenance can be defined as the minimum energy needed by the animal for minimal physical activity, minimal energy used for thermoregulation and energy used to maintain a dynamic equilibrium for protein and fat turnover. For adult animals, a zero energy balance is equivalent to a constant live weight over time, but this is not the case for growing animals. If growing pigs have a zero energy balance, they have a positive protein retention and a negative fat retention (whereby the sum of retained energy is 0 MJ/d). Thus, growing pigs fed at maintenance will gain in weight because protein retention binds approximately 4.2-fold water whereas negative fat retention hardly affect the water retention. Figure 20.13 shows the classical model and terms used when estimating energy requirement for maintenance (adapted from Wenk et al. [86]). The figure shows an important aspect of energy utilisation (represented by the slopes), namely that ME is utilised efficiently below maintenance but less efficiently above maintenance.

In other words, the efficiency for maintenance (k_m) is higher than the partial efficiency for growth (k_g). If animals are fed below or at maintenance, all heat produced is of value for the animal due to energy required for thermoregulation (see later), but above maintenance, additional heat is no longer of value to the animal and is consider as loss of energy due to increased heat production (or heat increment). Maintenance corresponds to the amount of energy required by the animal to be kept in energy equilibrium, i.e. at a zero energy balance. This is the amount of energy that corresponds to the heat production of the animal when both nitrogen and carbon balances are zero. This definition is acceptable for mature, non-productive animals, but it is difficult to use for growing or re-productive animals in which the energy retention changes in relation to the physiological stage. The energy balance should always be above zero in growing animals as they retain fat and protein, whereas lactating sows typically experience a negative energy balance. Indeed,

milk production is both highly demanding and highly prioritised, and therefore milk is typically produced at the expense of body mobilisation. In such cases, a maintenance requirement must be regarded as a theoretical value. However, this value is included in many calculations for estimating the efficiency of energy utilisation and for estimating energy requirements for growth, reproduction and milk production.

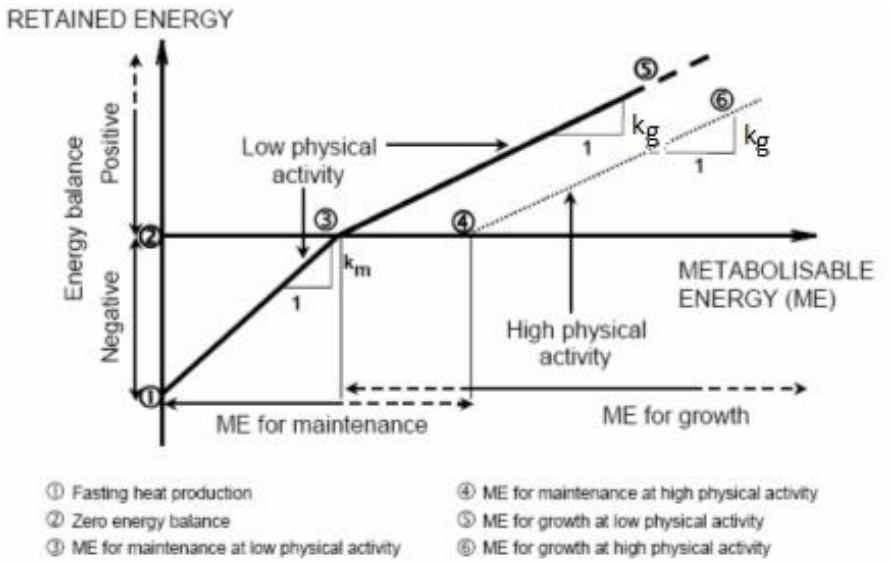


Figure 20.13. The classic model of relation between energy retention and metabolisable energy intake. The k_g and k_m represent the partial energetic efficiencies above or below zero energy balance, respectively (adapted from Wenk et al. [86], see also Pedersen et al. [63]).

The energy requirement for maintenance may be expressed in terms of either metabolisable energy (MEm) or net energy (NEm), depending on which energy system is applied. For growing pigs, the NE required for maintenance was considered in the previous Danish energy evaluation system used until 2004. A number of different experimental methods are available for determination of maintenance requirement but it is important to stress that energy requirement for maintenance can be quantified either at ME or NE level (Just et al. [34]), and is then referred to as MEm or NEm. In quantitative terms, MEm is greater (approximately 420 to 460 kJ per $kg^{0.75}$) than NEm (325 to 375 kJ per $kg^{0.75}$). The heat production during fasting is another way of expressing the heat loss, and this metabolic rate is lower than the heat being produced when animals are fed at or above maintenance. The heat production during fasting is much better defined than heat production at maintenance because a minimal level of physical activity is included in the

latter, but minimal physical activity is difficult to define. On the basis of a series of results of estimates of energy metabolism in animals ranging in size from mice to elephants, Brody [5] and Kleiber [46] found that fasting heat production (HE_f) is a function of live weight (LW) raised to the power of 0.75 (referred to as kg of metabolic live weight): HP_f, kJ/d = 295 × LW, $kg^{0.75}$. It was generally accepted to use the exponent 0.75 both for growing and mature animals in order to facilitate comparison between different species, breeds and individual animals. Later, however, other exponents were introduced; for example, the British Agricultural Research Council recommends 0.63 for pigs (ARC, [2]) while NRC [58] use 0.60 for growing pigs, and 0.68 has been reported for suckling piglets [55]. Indeed, the exponents are typically estimated lower than 0.75 if individuals are compared within the same species and will give slightly more precise estimates of HP_f than if 0.75 is used as exponent. Note that the heat production is higher when fed at maintenance as compared with heat production during fasting (at same live weight), because the diet induced thermogenesis and physical activity is higher when fed at maintenance. In order to reach maintenance energy intake, the animal has to stand up while eating, whereas fasting animals voluntarily reduce their physical activity to a minimum to spare energy.

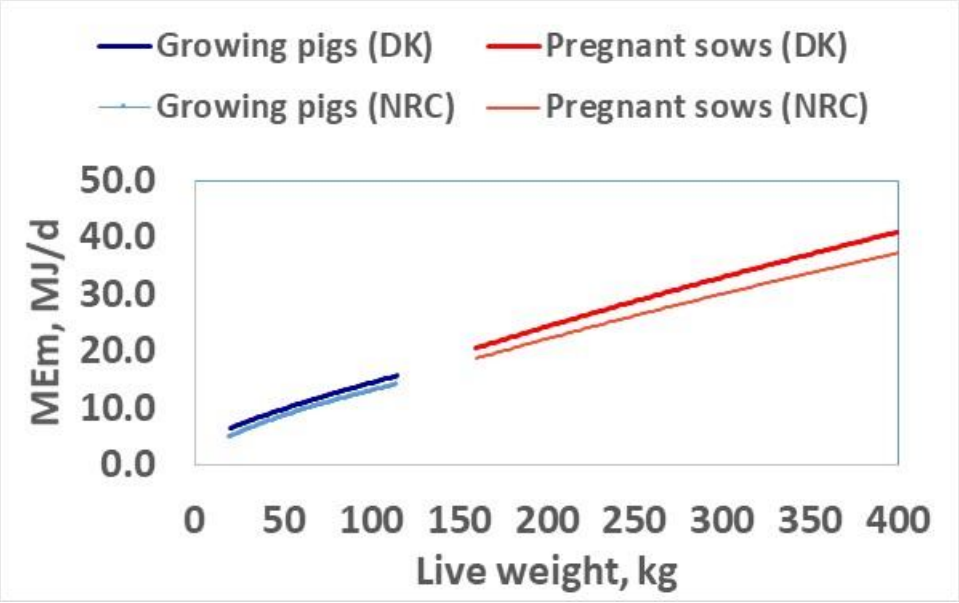


Figure 20.14. Metabolisable energy required for maintenance (MEm) for growing pigs and pregnant sows depends on the live weight of the animal. Experimental data from Danish experiments with growing pigs [80] and pregnant sows [74] are shown along with the current recommendation according to NRC [58].

In pig production, maintenance is considered a necessary part of the production cost due to the heat associated with intermediate metabolic processes, but the cost due to heat

production should be minimised as it does not give any economical return. The metabolisable energy required for maintenance (MEm) increases curvilinearly with increasing live weight as shown in Figure 20.14, whereas it is regarded being constant per kg of metabolic live weight ($kg^{0.75}$). As a rule of thumb, a common pig diet contains approximately 13 MJ of ME per kg of diet [79], and therefore a growing pig weighing approximately 85 kg require 1.0 kg of feed for maintenance each day while a pregnant sow weighing 220 kg, or a lactating sow weighing 205 kg require 2.0 kg feed each day for maintenance (Figure 20.14). As an example, the maintenance requirement for a growing pig may be calculates as 3.14 MJ/d + 85 $kg^{0.75}$ x 0.360 MJ/($kg^{0.75}$ x d), which is equivalent to 13.2 MJ/d (and 1.0 kg of feed). The metabolisable energy required for maintenance is 4.5-5.0% higher for lactating sows than for gestating sows [73] [57]. It should, however, be noted that maintenance energy requirement of lactating sows is a hypothetical measure, because lactating sows prioritize their milk production above their maintenance, and therefore most lactating sows experience a negative energy balance. Nonetheless, the concept of maintenance requirement is used when using a factorial approach and two recent Danish experiments ([64], [65]) showed that predicted and measured ME requirements agreed fairly well, indicating that metabolisable energy required for maintenance also can be applied for lactating sows.

According to NRC [56][57], the ME_m can be estimated as follows:

Growing pigs: MJ/d = 0.440 MJ/($kg^{0.75}$ x d) × LW, $kg^{0.75}$

Pregnant sows: MJ/d = 0.420 MJ/($kg^{0.75}$ x d) × LW, $kg^{o.75}$

Lactating sows: MJ/d = 0.460 MJ/($kg^{0.75}$ x d) × LW, $kg^{o.75}$

According to Danish studies, the ME_m can be estimated as follows for growing pigs and sows:

Growing pigs: MJ/d = 3.14 MJ/d + 0.360 MJ/($kg^{0.75}$ x d) × LW, $kg^{o.75}$ (Thorbek et al., [80])

Growing pigs: MJ/d = 0.476 MJ/($kg^{0.75}$ x d) × LW, $kg^{o.75}$ (Just et al., [34])

Pregnant sows: MJ/d = 0.459 MJ/($kg^{0.75}$ x d) × LW, $kg^{o.75}$ (Theil et al., [74])

Lactating sows: MJ/d = 0.482 MJ/($kg^{0.75}$ x d) × LW, $kg^{o.75}$ (Theil et al., [75])

In general, energy for maintenance accounts for approximately 25% of the ME intake of lactating sows at peak lactation and 35% for growing pigs fed ad libitum. In gestating

sows, however, maintenance accounts for almost 100% of the ME intake in mid-pregnancy and 50-70% in late pregnancy.

6.1.2. Heat increment

Heat increment (HI) refers to additional heat produced above maintenance. The heat increment depends on the amount of feed ingested and the composition of the diet. The HI is also affected by traits like fat and protein retention, pregnancy, milk production, physical activity, and thermoregulation. The HI increases with increasing energy intake (feed intake) because the transport and digestion of feed in the alimentary tract require energy and because nutrients are being net absorbed, transported and metabolised. The heat increment is minimized when pig diets are well balanced according to the nutrient requirements of the pigs. If, for instance, a pig diet contains excess protein (relative to net energy), then the pig is not able to efficiently utilise all the dietary protein for growth, and part of the dietary protein is used as a fuel (energy purpose), which increase the HI. If the dietary amino acid profile is not well balanced, this will also increase the HI.

6.1.2.1. Heat increment due to fat and protein retention

Increasing retention of fat and protein will increase HI due to inefficient anabolic processes. This heat production forms part of the heat increment and depends on the extent and type of the anabolic processes. The heat increment associated with growth can be calculated from the partial energetic efficiencies of retaining fat and protein and the amount of e.g. energy retained. Indeed, energy retained in protein occur with 60% efficiency, whereby the remaining 40% is lost as heat increment [68]. Likewise, energy retained in fat occur with 80% efficiency, whereby the remaining 20% is lost as heat increment. Growth of pigs, which roughly consist of 2/3 of the energy being retained as fat and 1/3 of energy retained as protein yield an overall efficiency of growth being 73%, which means that 27% is lost as HI (Table 20.6). The reason is that all processes (also biological) are associated with inefficient utilisation of energy with energetic efficiencies below 100%, and the lower the energetic efficiency, the more heat is being produced.

6.1.2.3. Heat increment due to pregnancy and milk production

The efficiency of utilising ME for reproduction (k_r; i.e. foetal retention, uterus and placental growth, mammary growth and colostrum) is unknown, but is expectedly

considerably lower than the efficiency for milk production. In a recent modelling study, k_r was assumed to be 50% [16] but this has not hitherto been quantified.

Milk is produced with a partial efficiency of 78% [77]. Thus, if a sow secretes 50 MJ/d of milk energy, the heat production associated with the milk production (heat increment) is 14.1 MJ/d which may be calculated as: Heat increment = (50 MJ / 0.78) – 50 MJ. The efficiency of utilising ME for milk production has previously been reported to be 72% [55], but these authors underestimated the sow milk yield because they used the weigh-suckle-weigh technique [20] and consequently underestimated the efficiency of converting ME into milk. A recent mathematical approach indicates that the efficiency in modern high-prolific, high-yielding sows may be as high as 80% [85], indicating that the efficiency of converting ME into milk increases with milk yield.

6.1.2.4. Heat increment due to physical activity

Heat production due to physical activity is an important source of variation between different animals and may be affected by housing condition and feeding. The importance of physical activity for heat increment is evident in Figure 20.15, where sow posture was recorded with a photocell [73].

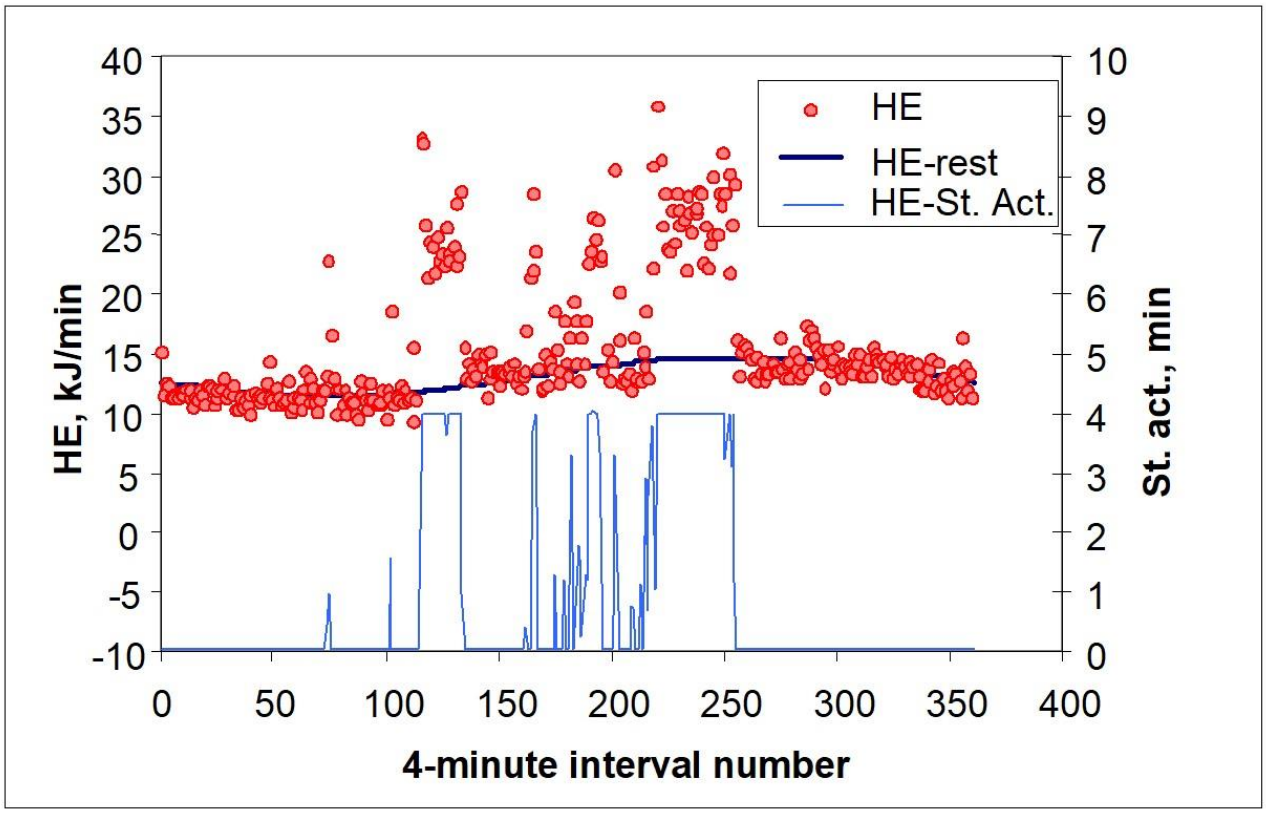


Figure 20.15. Diurnal variation in heat production and impact of physical activity on heat production in a pregnant sow. The red dots represent measured heat production in a respiration chamber during 4-minute intervals on the left Y-axis. A fitted cosine-curve indicates the predicted heat production during resting. Activity of the sow was measured with a photo sensor (blue line), and the data show how many minutes the sow was standing within each 4-minute interval on the right Y-axis.

From the figure it may be noticed that the heat production approximately doubles when the sow changes from lying to standing posture due to heat increment. The heat production was measured each 4th minute, and the experiment illustrated how fast a change in physical activity affects the total heat production of that animal. Physical activity is typically rather low in farm animals and especially for pregnant sows prior to 2013, where they were fixed in pens. In such case, the minimal physical activity agrees quite well with the concept of maintenance. However, pregnant sows are now group-housed, and consequently their heat production due to physical activity is no longer negligible. Likewise, pigs housed in large groups and sows housed outdoors may have substantial costs associated with physical activity, which in turn increases their total heat production.

6.1.2.5. Heat increment due to thermoregulation

The ambient temperature of the surrounding air may have a great influence on heat production of pigs. Pigs, like other animals, have a thermo-neutral zone (Figure 20.16) where the heat increment and thereby the total heat production is minimal. The thermoneutral zone is defined between the lower critical temperature (LCT) and the upper critical temperature (UCT) and describes the temperature range in which the animal heat production is minimal, and the adjustments due to altered behaviour occur without changing the total heat production. Above the thermoneutral zone, the heat production increases because the animals pant and hyperventilate and thus spend energy to avoid increment of body temperature. Since pigs' ability to sweat is limited, the increased need for thermoregulation at high temperature can only be achieved by increased respiration rate, and therefore pigs' ability to adapt to high temperatures is limited. With short-term increase in ambient temperature from 17°C to 40°C for 2 hours, it was found that the respiratory rate rose from approx. 30 to over 200 breaths per minute in 100-kg boars [71], indicating that high temperature is problematic for pigs. If the ambient temperature is below the thermoneutral zone, the heat production is elevated due to shivering thermogenesis in order to maintain a constant body core temperature. Theoretically, the lower and upper critical temperatures appear to be well defined, but in practice there are no well-defined boundaries, and knowledge of especially the upper critical temperature is limited [51]. In recent experiments, the thermoneutral zone has been found to range from 22°C to 25°C. The lower values reported in older experiments can be partly attributed to a difference in the pigs' insulation (subcutaneous fat). This indicates that modern pigs are more sensitive to cold compared with their ancestors because pigs are bred to be lean at slaughter [7]. The thermoneutral zone is dependent on factors other than temperature and may include air speed, humidity and floor/bedding material. Other factors include the animal's age/weight, genotype, body condition (back fat thickness) and group size. In addition, factors such as feeding intensity and utilization of feed nutrients are also important.

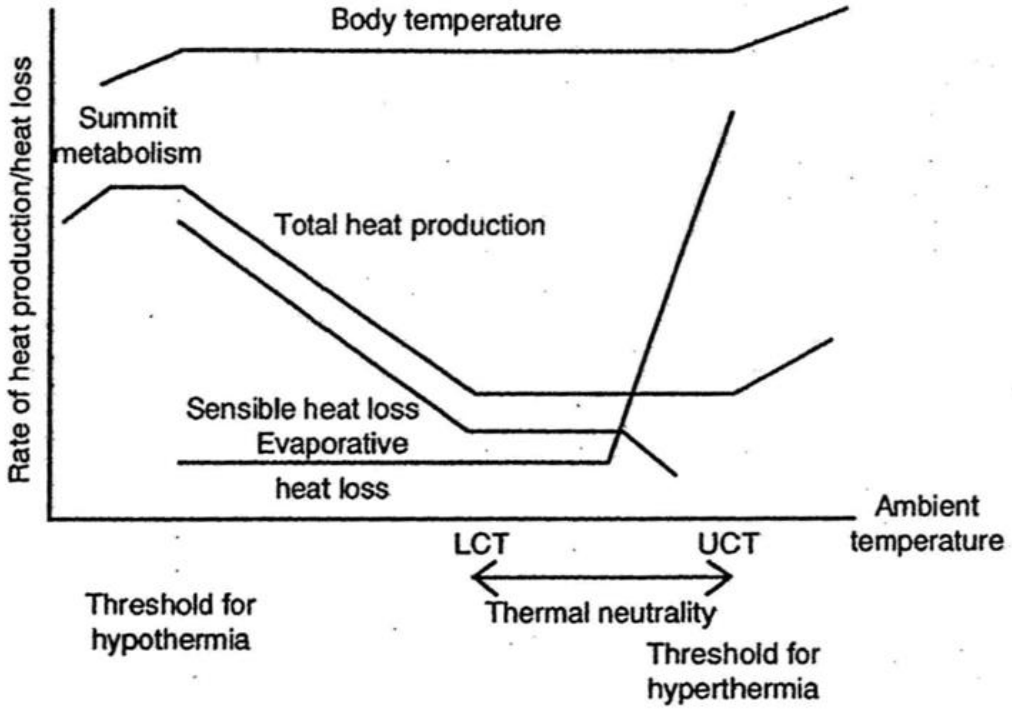
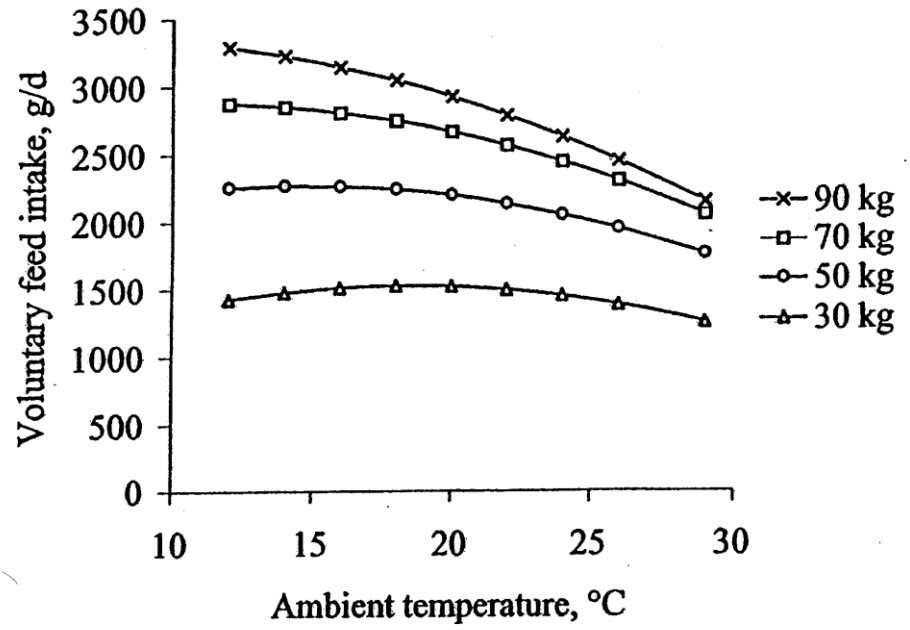


Figure 20.16. Relation between heat production or heat loss and ambient temperature [51]. The lower comfort temperature (LCT) represents the lowest ambient temperature before the animal heat production starts to increase, and UCT represents the upper comfort temperature.

Normally, heat increment due to thermoregulation is minimal for farm animals and can be ignored for pigs housed conventionally because the ambient temperature is normally within the thermoneutral zone. However, under certain circumstances, substantial amounts of energy may be spent on thermoregulation, for instance when pigs are housed outdoors during winter or for pigs produced in hot climate. Under Danish conditions, it is important to stress that the ambient temperature, even within the thermoneutral zone, may affect the voluntary feed intake of pigs and in turn the ratio between protein and fat retention, but ambient temperature may also affect animal behaviour as well as the health status of the pig. For instance, pigs housed in cold climate will huddle together, whereas in warm conditions, pigs will try to cool by wallowing, which may be in the dunging area and in turn affect the health negatively. Heat-stressed pigs reduce their feed intake in order to reduce the diet induced thermogenesis, and the lowered feed intake will reduce the growth rate. In contrast, pigs at lower temperature will to a certain degree increase their feed intake, (if they are fed ad libitum), to compensate for the increased need for thermoregulation. The influence of temperature on feed intake was demonstrated in a

French study (Figure 20.17) by Quiniou et al. [66]. The study showed that increasing the ambient temperature had a greater negative impact on feed intake of large pigs compared with that of smaller pigs.



Variation of voluntary feed intake (VFI, g/d) with temperature (T, °C) and body weight (BW, kg) calculated using the equation:

$$VFI = -1264 + 73.6BW - 0.26BW^2 + 117T - 2.40T^2 - 0.95T \times BW.$$

Figure 20.17. Impact of ambient temperature on voluntary feed intake [66].

The need for thermoregulation interacts with feed intake and feed composition, especially because dietary fibre increases fermentation. Thus, microbial fermentation of fibrous materials results in fermentation heat in addition to production of short-chain fatty acids, lactic acids and gases (methane and hydrogen). This heat increment may play a useful role in cold environments because it may replace or reduce the additional need for energy required for thermoregulation. This is illustrated in Figure 20.18 which shows the energy efficiency depending on the ambient temperature and dietary fibre content. Pigs were fed with high or low fibre diets and kept at low or high temperature (13°C and 23°C, respectively). The study showed that reducing the temperature from 23°C to 13°C increased the proportion of the metabolisable energy used for thermoregulation and

concomitantly reduced the proportion of energy retained (note that the proportions here sum up to 100% of metabolisable energy). However, the heat production increased when the ambient temperature dropped from 23°C to 13°C, and it was most pronounced for pigs fed the low fibre diet, indicating that pigs fed the high fibre diet took advantage of the heat increment originating from fibre fermentation in the hindgut.

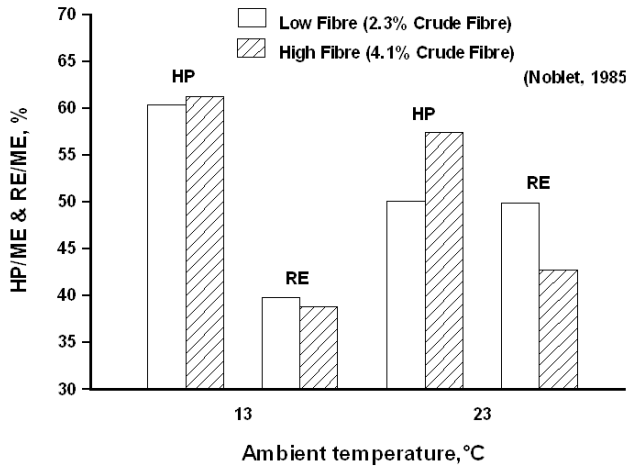


Figure 20.18. Interaction between ambient temperature and dietary fibre on heat production (HP)and retained energy (RE) in pigs fed low or high fibre at either 13 or 23 °C [53] [38].

6.1.2.6. Heat increment due to diet composition

Additional heat is produced when dietary ingredients are digested and metabolised and depends on which nutrients are ingested and what the dietary nutrients are utilised for. The study described above (Figure 20.18) with fermentation heat from digested fibres emphasize this. For growing pigs and lactating sows, substantial amounts of energy are used for fat retention (from de novo fat synthesis), and, under these circumstances, ketogenic energy sources (short-chain fatty acids from fermented fibres and triglycerides from dietary fat) are more efficiently utilised than glucogenic energy sources (primarily net absorbed glucose and lactate from digested starch) and therefore ketogenic energy sources may reduce the heat increment and in turn the total heat production. However, if energy is utilised for heat production (e.g. for maintenance purposes), then glucogenic energy is efficiently utilised. Intake of dietary protein in excess of that required also increases the heat increment and thus total heat production [65]. The impact of dietary

composition on energy utilisation (including heat production) will be described in detail in section 7.

6.1.2.6. Nutrient oxidation and intermediary metabolism

Heat production is the end-product when nutrients are being oxidised. The heat produced by an animal may be split into fractions originating from oxidation of carbohydrates, protein and fat (OXCHO, OXPROT and OXFAT, respectively). These three classes of nutrients are presented in descending order in terms of how important they are for the intermediary metabolism to fuel cellular processes. For pigs, the main substrate for oxidation is dietary carbohydrates which normally account for more than 80% of the substrate oxidation pattern (Figure 20.19, adapted from Theil et al., [75] [78]).

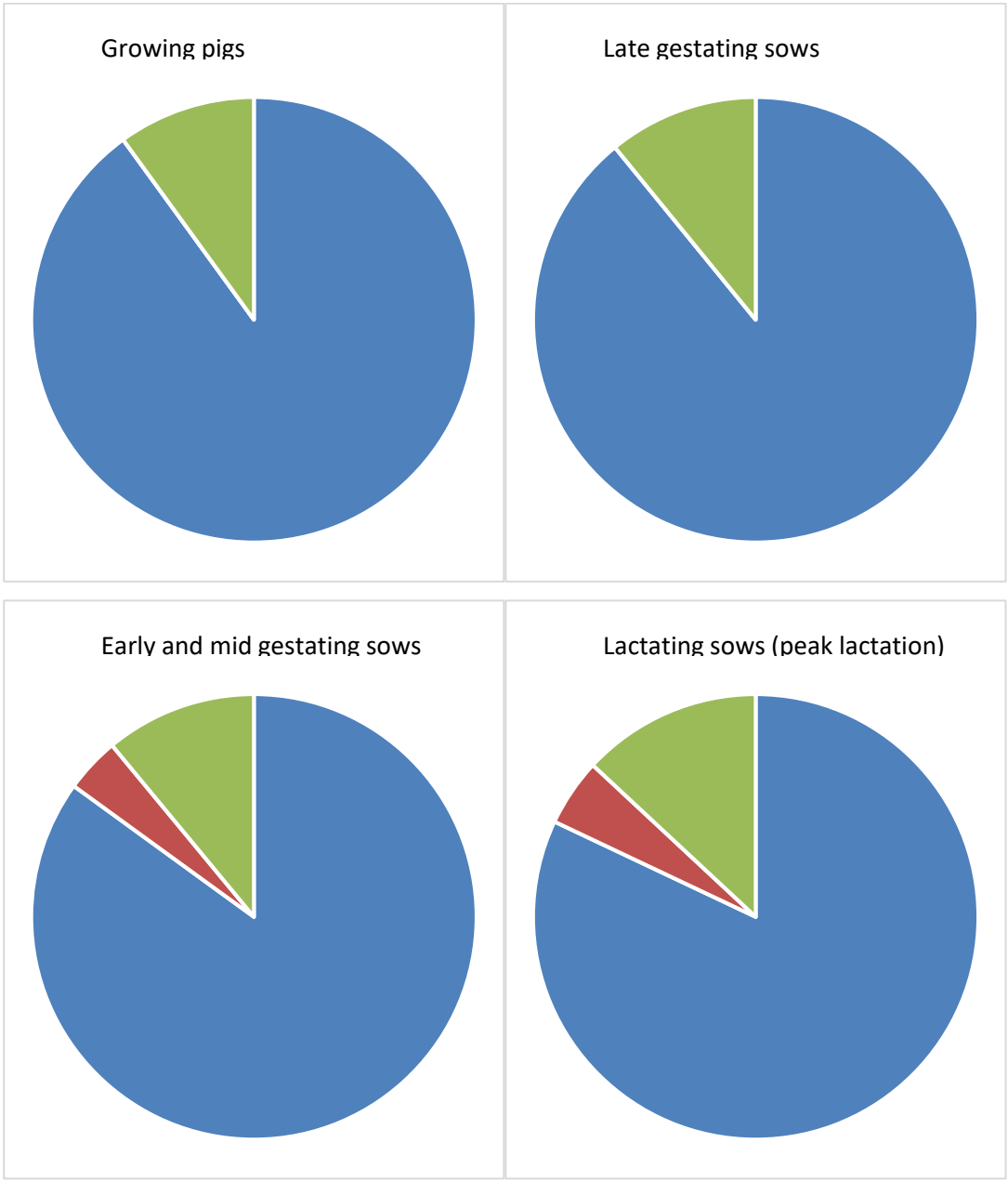


Figure 20.19. Substrate oxidation patterns in growing pigs [11], gestating sows (early/mid gestation and late gestation; [74]) and in lactating sows [75]. Oxidation of carbohydrates (OXCHO) is shown in blue, oxidation of fat (OXFAT) is shown in red, and oxidation of protein (OXPROT) is shown in green.

Omnivore animals like pigs have a strong preference for oxidising glucogenic energy, utilising amino acids for growth or milk protein production instead of oxidising them, and a strong preference for preserving ketogenic energy for either fat retention (growing pigs) or milk fat production (lactating sows). The preference for storing ketogenic energy is inherited through the evolutionary history which favoured animal survival during the winter periods with limited availability of food. The preference for storing ketogenic energy is a

way to store energy in a highly condensed form, but it costs energy to synthesise fat from carbohydrates, so to maximise efficiency in the long run, pigs utilise glucogenic energy for oxidation and ketogenic energy for storage. Glucogenic energy originates mainly from starch assimilated as glucose but minor amounts are also being taken up as lactate. Protein is also a common substrate for oxidation, and OXPROT contributes normally with 10-15% of the total heat production of pigs. Protein oxidation happens all the time as evidenced by the yellow colour of urine and arises from oxidation of amino acids originating from the protein turnover; surplus of dietary protein and mobilised body protein from skeletal muscles. Oxidation of fat is the smallest contributor to the total heat production of pigs, and when growing pigs are fed ad libitum (corresponding to 2.7-3-fold above maintenance), the oxidation of fat is zero. In this physiological phase, substantial amounts of de novo fat is synthesised from glucose and retained as fat, and it would be energetically unfavourable if de novo synthesis of fat (synthesis of long chain fatty acids from C-2 units, which is an energy requiring process) occur concomitantly with oxidation of fat (breakdown of fatty acids into C-2 units is also requiring energy). In contrast to fat metabolism, protein is constantly being synthesised and degraded, which is energetic inefficient. It is not completely clear why this happens, but enzymes are constantly being produced and degraded to regulate cell metabolism. If energy is abundantly available, i.e. when fed above maintenance, fat is the preferred substrate for conserving energy, and fat is synthesised for energy accumulation in body tissues, which may be used later in life where the energy intake is below maintenance. During the evolution, fat retention was a clear advantage to combat low energy intake during the winter time, but for farm animals this is not an issue, except for outdoor-housed pigs/sows. The only situation where fat oxidation becomes an important substrate for oxidation is when pigs are in a negative energy balance, and it is of special importance during lactation. Indeed, lactating sows are typically exposed to a substantial negative energy balance, most pronouncedly during early lactation [64]. When the energy intake is inadequate to meet the energy requirements for maintenance and milk production, fat is mobilised, and part of the substrate oxidation comes from oxidized fat [77]. However, fat oxidation normally accounts for less than 10% of the total heat production, and typically fat oxidation is zero [75]; [12].

The substrate oxidation pattern may be revealed by measuring the O_2 consumption and the CO_2 production either for the whole animal using respiration chambers or for an

organ using multicatheterised (surgically modified) animals [49]; [17]. The respiratory quotient, RQ, may then be derived as follows:

$$RQ = CO_2 \text{ production} / O_2 \text{ consumption}$$

where CO_2 production and O_2 consumption may be in L/d (used to study whole animal metabolism) or mmol/h (used to study organ metabolism). Note that the RQ is a ratio without any unit, although in certain cases it may be worth using the unit L CO_2/L O_2 or mmol CO_2/mmol O_2. The RQ value depends on which substrates are being oxidised (Table 20.7).

Table 20.7. Oxidation of nutrients and impact on the respiratory quotient (RQ).

Substrate oxidation	Proportion of HP (%)	RQ
Carbohydrates (OXCHO)	80-90%	1.00
Protein (OXPROT)	10-15%	0.82
Fat (OXFAT)	0-5%	0.70

Oxidation of carbohydrates results in an RQ value of 1.0, while oxidation of protein on average give a mean RQ value of 0.82; the RQ value differs depending on which amino acids are being oxidised. If animals are synthesising fat de novo, the RQ value exceeds 1.0 and the RQ of mammary gland of sows may be as high as 1.8 at peak lactation due to substantial de novo fat synthesis [49]; [17]. The underlying reason is that CO_2 is produced when fatty acid carbon chains are elongated without any O_2 consumption. Conversely, when fat is mobilised and used for oxidation, the RQ is as low as 0.7, because O_2 is consumed in the oxidative phosphorylation pathway while less CO_2 is produced, as compared to glucose oxidation (Figure 20.3). In summary, knowledge on the gas exchange and especially the RQ value both tells whether the animal is fed above or below maintenance as reflected by high or low RQ values, respectively, and indicate which nutrients are fuelling the intermediary metabolism (carbohydrates, protein or fat).

To sum up, heat production account for the greatest loss of energy (Figure 20.11) for both growing pigs and reproductive sows. Maintenance is the greatest contributor to heat production, but heat increment is also a substantial amount. The heat increment derives from diet induced thermogenesis, physical activity, thermoregulation, growth and milk production.

6.2. Growth

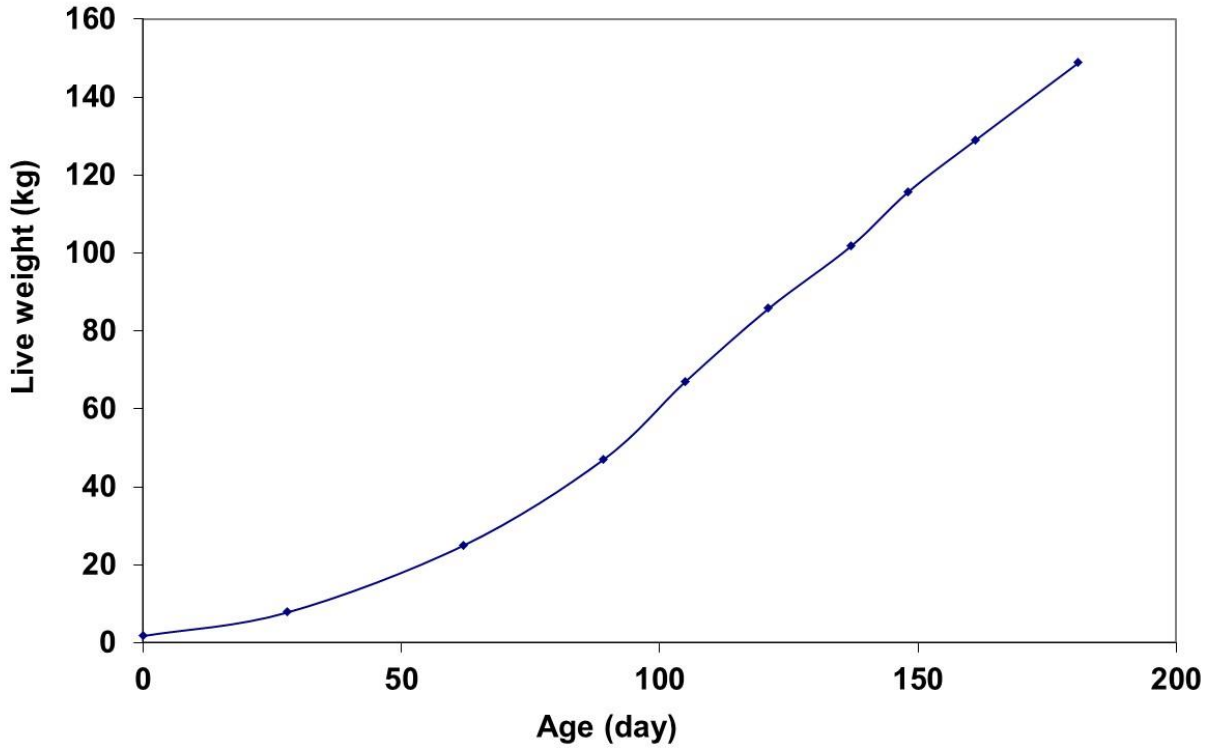


Figure 20.20. Development in pig live weight with age.

Pigs have a potential for growth [13] and a typical growth curve of pigs is illustrated in Figure 20.20. The growth processes do not only include synthesis and retention of body fat and protein. A major proportion of the synthesised components is degraded again, for example about two-thirds or more of the protein pool is broken down. This means that only one-third or less of synthesised protein will be retained. Therefore, in young growing pigs, the growth rate is determined by the difference between synthesis and degradation of musculature, fatty tissue, bones etc. The distribution of some substrates in growing pigs are summarised in Figure 20.21.

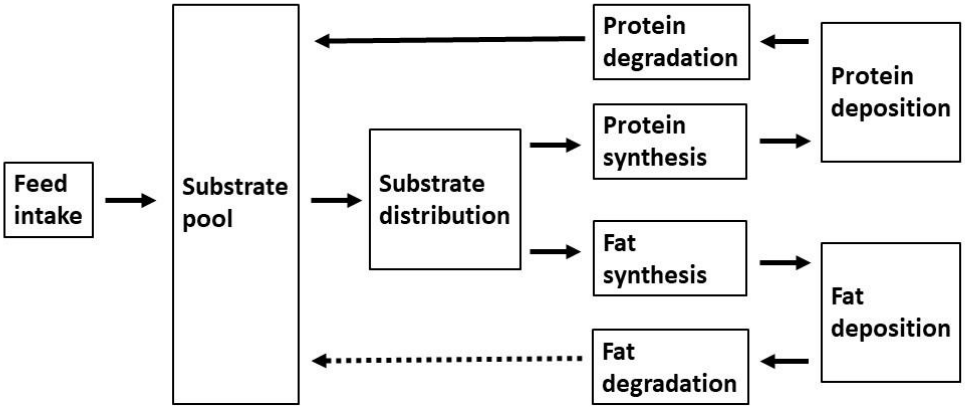


Figure 20.21. Distribution/fate of ingested nutrients in growing pigs.

In a new-born pig, protein synthesis constitutes about 15% of the muscle mass per day. But since the protein degradation at the same time amounts to about 9%, the actual increase of the muscle mass is about 6% per day. In other words, the daily protein retention is 6/15, or 40% of the protein synthesis. However, in a pig weighing about 150 kg, the protein retention has decreased to 15% of the protein synthesis. Consequently, as the animals mature, synthesis and degradation will diminish, and at maturity the retention will approach zero [61]; [8].

Calculation of the energy and nutrient requirement for growth is based on the amounts of nutrients and energy retained on a daily basis. These values can be estimated either by means of balance experiments or from slaughter experiments, where animals are killed and analysed for macrochemical composition at different ages (and different live weights), or through measurements in metabolism cages and respiration chambers. When the values for nutrient and energy utilisation for growth are known, the requirements can be estimated factorial.

Since most of the energy evaluation systems for pigs used today are based on metabolisable energy, the following description will primarily deal with metabolisable

energy requirements. Metabolisable energy is the amount of energy available for metabolism in the body, but just like your own salary, ME can only be used once. It is important to stress that all the ME can be accounted for if all animal traits like heat production, energy output in milk and energy retention is measured. As shown in Figure 20.22, distinction is made between ME for maintenance (ME_m) and ME for growth (ME_g). The ME_m is used for maintenance processes which is prioritized higher than energy retention in growing pigs and gestating sows. The ME for growth (ME_g) may further be divided into ME utilized for protein retention (ME_p) and ME utilized for fat retention (ME_f). The energy retained in protein is termed RPE, and the energy retained in fat is termed RFE. The total energy retained is the sum: RE = RPE + RFE.

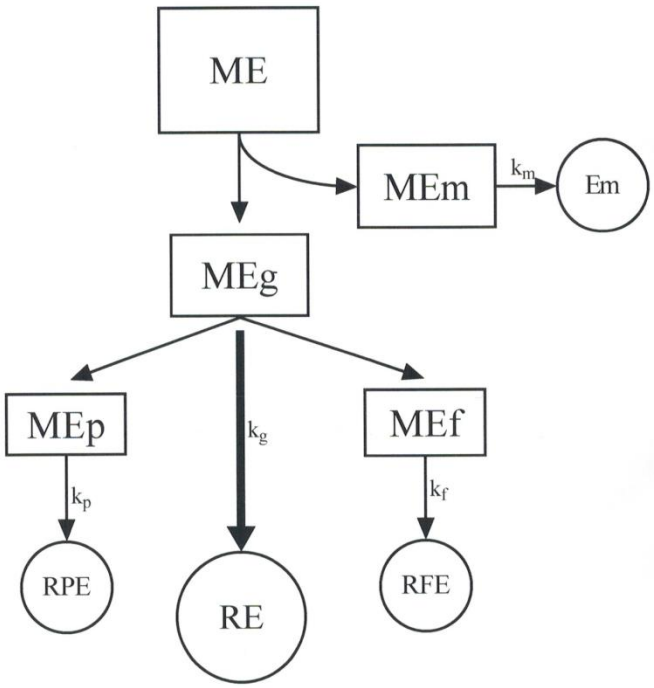


Figure 20.22. The partition of metabolisable energy into ME for maintenance (MEm), growth (MEg) and energy retained in protein (RPE), fat (RFE) and total energy retention (RE). Note that heat increment due to RPE and RFE is not shown, whereas energy retained as fat and protein are both shown separately (RPE and RFE) and together (RE). Energetic efficiencies refer to utilization of ME for maintenance energy (k_m); for energy retained as protein (RPE; k_p), for energy retained as fat (RFE; k_f); or energy retained without distinguishing between protein or fat (RE; k_g).

In order to evaluate the utilisation of energy for growth and other productions we have to know the energy requirement for maintenance since $ME_g = ME_{Total} - ME_m$. As previously discussed, the results of fasting trials with growing pigs are inaccurate.

Therefore, the maintenance requirement is often estimated by trials using different feeding levels. Such a method does not only give a value for maintenance but also a value for the utilisation of energy. The total coefficient of utilisation for growth (k_g) can be determined by a one-dimensional regression, while the partial efficiencies of ME utilisation for retention of protein (k_p) and fat (k_f) can be calculated by means of multiple regressions:

$$ME, MJ/d = b1 \times LW, kg^{0.75} + b2 \times RPE + b3 \times RFE$$

where b1 × LW, $kg^{0.75}$ is the maintenance requirement for MJ ME/$kg^{0.75}$/d, 1/b2 = k_p, 1/b3 = k_f, and RPE and RFE are energy retained as protein and fat in MJ/d, respectively. It is generally agreed that in growing pigs, the efficiency of ME for fat energy retention is about 80% (k_f = 0.80), whereas the energetic efficiency of protein energy retention is approximately 60% (k_p = 0.60; Table 20.6). However, it is important to stress that there is substantial variation in k_f and especially in k_p, depending on genetic and nutritional factors.

The procedure for estimation of the energy requirement for maintenance and growth for growing pigs from 20 kg LW to 100 kg LW can be exemplified by the following. Assuming that the coefficient of utilisation of ME for energy retention in protein, k_p, is 0.60, whereas the coefficient for fat, k_f, is 0.80, we can calculate that 1/0.60 = 1.67 kJ ME is required for each kJ of retained protein, and 1/0.80 = 1.25 kJ of ME is required for each kJ stored fat. Since one gram of retained protein and fat contains 23.9 and 39.8 kJ/g (Table 20.2), the ME required per gram of protein and fat amounts to 40 kJ and 50 kJ ME, respectively. The energy requirements for retention of fat and protein and heat due to maintenance (MEm) and heat increment (HI) due to protein and fat retention are shown in Table 20.8. The total ME requirement can finally be calculated factorially as follows:

Retained energy = Retained energy as protein + retained energy as fat

Total heat production = ME required for maintenance + HI (due to retention of fat and protein)

Total ME-requirement, MJ/d = Retained protein + Total heat production.

And the % of energy being retained relative to ME-requirement can be calculated, which express how efficiently total dietary ME is being retained. This % should NOT be compared with the partial efficiency of ME for growth (k_g), because the latter include only the utilisation of ME above maintenance. Note that the efficiency (RE/ME-req) increases

from 37 to 48% during the growing/finishing period, which reflects that pigs retain steadily more fat as they approach slaughter weight. However, it should be stressed that while energy is being retained more efficiently with increasing live weight, pigs are becoming less feed efficient, which will be described in section 10. The explanation is that growth and feed efficiency is mainly affected by protein retention, whereas the energy being retained in pigs is only a small proportion of the total energy consumed (Figure 20.11). In contrast, retention of energy as fat has a major impact on the energy retention but only a minor impact on the growth rate.

Table 20.8. Calculation of energy requirement in growing/finishing pigs using a factorial approach.

Body	Retained energy (RE)				Heat		ME	RE/ME-Req
weight	Protein (RPE)		Fat (RFE)		MEm	HI	Requirement	
kg	g/d	MJ/d	g/d	MJ/d	MJ/d	MJ/d	MJ/d	(%)
20	85	2.03	80	3.18	6.54	2.15	13.91	37
40	130	3.11	140	5.57	8.87	3.47	21.01	41
60	165	3.94	220	8.76	10.90	4.82	28.42	45
80	185	4.42	300	11.94	12.77	5.93	35.06	47
100	190	4.54	370	14.73	14.52	6.71	40.50	48

MEm, Metabolisable energy for maintenance, was calculated according to Thorbek et al. [80] using the equation $3.14 + 0.36 \times kg^{0.75}$ (MJ/d). Heat increment (HI) due to growth may be calculated factorial as retained the sum of ((protein energy/k_p) - protein energy) + ((retained fat energy/k_f) - retained fat energy), where k_p and k_f are 0.6 and 0.8 (Table 20.6).

6.3. Energy requirements for reproduction

Gestating animals must be fed a sufficient amount of feed with an adequate composition to ensure birth of strong and healthy offspring. It is necessary to have a thorough knowledge of the requirements for dietary nutrients and energy because the requirements of the foetus will take priority over the maternal requirements. As a consequence, the sow will mobilise energy from her own body and support foetal growth if energy intake becomes insufficient. The requirements can be estimated on the basis of the stored quantities of certain nutrients by measuring the total contents in uterus (including growth of foetuses, placenta, fluids and membranes) at specific times and deduct the results from the uterine contents of non-pregnant animals. Similarly, energy required for mammary growth may be revealed by slaughter experiments [45], whereas energy secreted in colostrum may be quantified by multiplying colostrum yield with the gross

energy content of colostrum [78]. After farrowing, substantial amounts of energy is required for milk production, and, at peak lactation, more energy is secreted daily via the milk than is used by the sow for maintenance. For all the traits described above, extra energy is lost due to the heat increment caused by reproduction and milk production, which like other biological processes, operate at efficiencies lower than 100%. Estimates reviewed by Noblet et al. [56] show that on average, the efficiency of ME utilisation for energy retention in uterus is 50%, and in mammary gland the efficiency for energy retention is around 75-80%. In addition to heat increment due to foetal growth etc., additional energy is also required around farrowing for physical activity due to nest building and uterine contractions during farrowing [16], when piglets are expelled through the birth canal. The energy requirement changes rapidly day by day in late gestation and throughout lactation due to rapid changes in energy requirements for foetal and mammary growth, and colostrum and milk production.

During lactation, the energy requirement for milk production increases day by day until peak lactation around d 17 to 19 [20]. The milk yield and hence the energy required for milk production increases with litter size. However, in modern high prolific sows, the litter size is typically 13 to 14 piglets, and, consequently, it is not the litter size but the lactation capability of the sow which limits the milk yield and determines the energy requirement for milk production. A high-producing sow secretes around 15 kg and 65 MJ of milk, and concomitantly 18 MJ are lost as heat due to heat increment (assuming k_l = 0.78; Table 20.6).

6.4. Factorial calculations of energy requirement

The energy requirement on a daily basis may be calculated factorial, i.e. all partial requirements for specific processes like maintenance, growth and heat increment may be added to estimate the whole animal requirement. To make such a factorial approach, it is important to build a schematic model which includes all traits/compartments with quantitative importance. Such models are illustrated for growing pigs in Table 20.8 and for late gestating and lactating sows in Figure 20.23 [16].

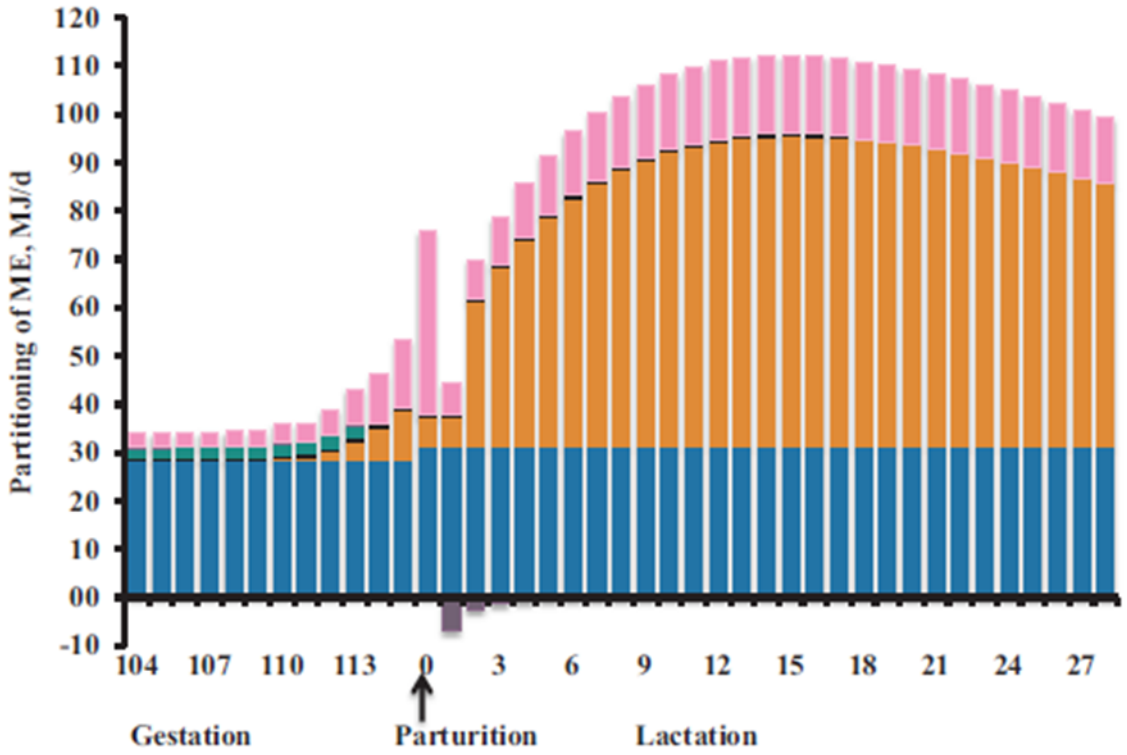


Figure 20.23. Partitioning of calculated metabolisable energy for maintenance (blue bars), colostrum/milk production (orange bars), mammary growth (black bars), foetal growth (green bars), uterine components (purple bars) and additional heat loss (pink bars) in sows in late gestation (normal gestation length is 115 days), at farrowing (d 0) and during a 4 week lactation period.

When the traits/compartments are defined, the partial requirement for each trait/compartment may be calculated separately and added to estimate the animal requirement at specific days (or specific physiological stages). Note that contributions may be negative, which illustrates body mobilisation, along with regression of specific organs tissues to the blood. Body mobilisation is not relevant for growing pigs, as they are fed well above maintenance (around 2.7 × ME_m), but body mobilisation is important especially for lactating sows. For instance, mobilisation of energy may arise from the uterus which regresses after parturition. Immediately after parturition, the fresh weight of the uterus is around 6 kg, but at weaning (4 weeks later) the fresh weight has been reduced to roughly 1 kg. Furthermore, in early lactation, the energy intake is not sufficient to meet the sow energy requirement, and consequently the sows mobilise body fat and body protein to support the need for energy and nutrients for milk production [65]. As shown in Figure 20.23, most of the energy for late gestating sows is required for maintenance during gestation, whereas minor amounts are required for growth of foetuses, mammary glands, uterus and uterine membranes, and placentas. During the last week of gestation,

colostrum production becomes important, and at parturition extra energy is required for nest building and labour associated with giving birth to the piglets (uterine contractions). Unfortunately, no studies have quantified how much energy is converted into heat during nest building or during farrowing. After parturition, the energy output in milk steadily increases and becomes the most important factor for the total energy requirement. At peak lactation, the energy required for milk production (energy secreted and heat energy due to milk production) is around three times higher than the energy required for maintenance (Figure 20.23).

7. Energy utilisation and efficiencies

Utilisation of energy describes how efficiently energy is utilised for different purposes, and this is important to understand in order to improve feed efficiency. Energy utilisation represents the proportion of energy intake utilised for a specific purpose (e.g. energy utilised for growth, heat production and milk production). Energy utilisation may be reported relative to intake of gross energy, digestible energy or metabolisable energy. As an example, energy digestibility refers to how many per cent of ingested energy is being digested (i.e. DE × 100/GE). Similarly, metabolisability refers to the per cent of the gross energy that is available for metabolism (i.e. ME × 100/K_gE). Energy utilisation may also represent how efficiently ME is utilised for growth, protein retention, fat retention or for milk production. To keep the concept rather simple, and to improve the understanding the fate of dietary energy, the energy utilisation in the following sections refers to the proportion of dietary gross energy that is lost in faeces, urine and heat intake or secreted as milk or retained as growth. Under most circumstances, the majority of the gross energy ingested by growing pigs is lost as heat, followed by the energy retained as growth, energy lost in faeces, and the smallest proportion is the energy lost in urine. The same is true for sows, expect at peak lactation where energy secreted into milk exceeds the total heat production.

A number of factors like the chemical composition of the diet, the physical form of the diet and environmental temperature, significantly influence the utilisation of energy in pigs. The influence of chemical composition of the diet has been investigated systematically for growing pigs using the comparative slaughter technique. Balanced diets, i.e. diets with optimal concentrations of crude protein, essential amino acids and other nutrients like

minerals and vitamins per feed unit (net energy basis), were fed to growing pigs to meet their requirement for essential nutrients and to obtain equal growth rates from 20 kg to 90 kg live weight. Results from these experiments are in the following used to illustrate how energy utilisation is affected by increasing energy intake [34], increasing levels of crude fibre [31]; [33], increasing dietary crude protein [28] or increasing dietary crude fat [30].

7.1. Impact of feed intake on utilisation of GE

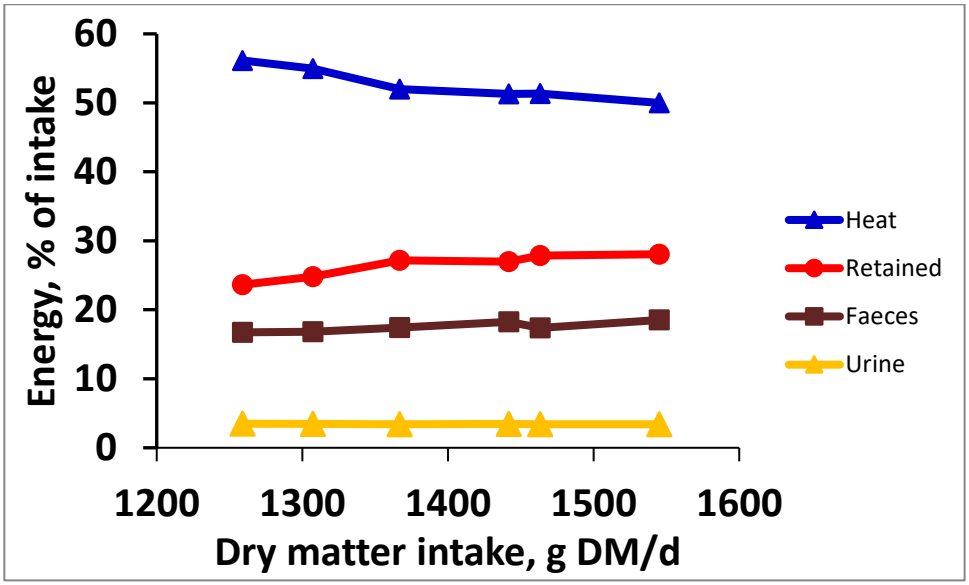


Figure 20.24. Utilisation of energy in growing pigs fed increasing levels of feed (DM intake ranged from 1259 to 1445 g/d as average feed intake from 20 to 90 kg live weight). The gross energy intake in group 1 through 6 was 23.8, 24.7, 25.8, 27.3, 27.7 and 29.2 MJ GE/d, respectively [34].

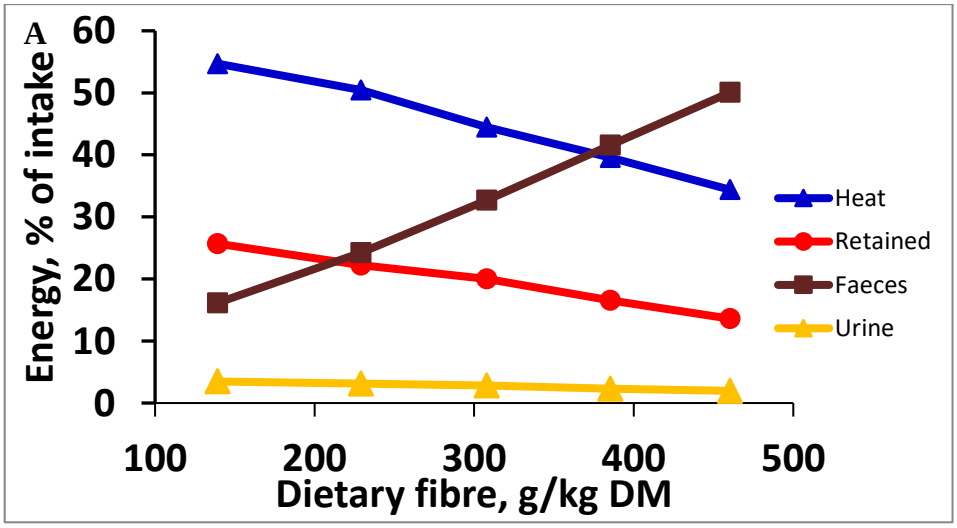
When pigs are fed increasing amount of feed within the range of 1259 g DM/d (group 1) to 1545 g DM/d (group 6), the DM intake, and hence GE intake, has a rather small impact on the energy utilisation (Figure 20.24). The proportion of energy lost in faeces and urine was rather constant relative to intake, while the energy lost as heat dropped slightly (from 56% to 50%), and the energy retained increased slightly (from 24% to 28%). To avoid mistakes, it is important here to state that this retention is not comparable to that presented in Table 20.8 (37-48%), because in Figures 20.24-20.27, retention is expressed relative to GE, whereas in Table 20.8, retention is expressed relative to ME. Note that all these pigs were fed considerably above their maintenance requirement as indicated by energy retention being clearly positive for all groups. If the study had included a group fed at maintenance (equivalent to approx. 600 g DM/d), the energy utilisation would likely be the following approximate values: 80% lost as heat, 17% lost as faeces and 3% lost in

urine, while 0% would be retained (remember that maintenance is defined as zero retention). Note also before reading the following sections that by increasing the DM intake, the daily intake of protein, fat, fibre and digestible carbohydrates increases all by the same fold change as the dietary energy if the diet composition is not changed as in this study. In the following, we will describe what happens if the feed composition is changed instead of changing the amount of feed. Remember that the diet composition always represents 100%, so if one component increases, one or more of the other dietary components will inevitably decrease.

7.2. Impact of dietary fibre on utilisation of GE

Dietary fibre represents the largest fraction of the diet which is not digested by endogenous enzymes (see Chapter 8 for details), and they are fermented in the hindgut to a certain extent depending on the fibre source. In general, inclusion of high levels of dietary fibres depresses the energy digestibility of the diet, whereby less energy becomes available for production or reproduction. However, the energy digestibility depends on the fibre sources and on the inclusion level as previously shown in Figure 20.10.

A highly consistent response of dietary fibre is increased loss of energy through faeces (Figure 20.25) due to decreased energy digestibility, and the energy digestibility drops in general by 1.2% for each percent unit increase in dietary fibre.



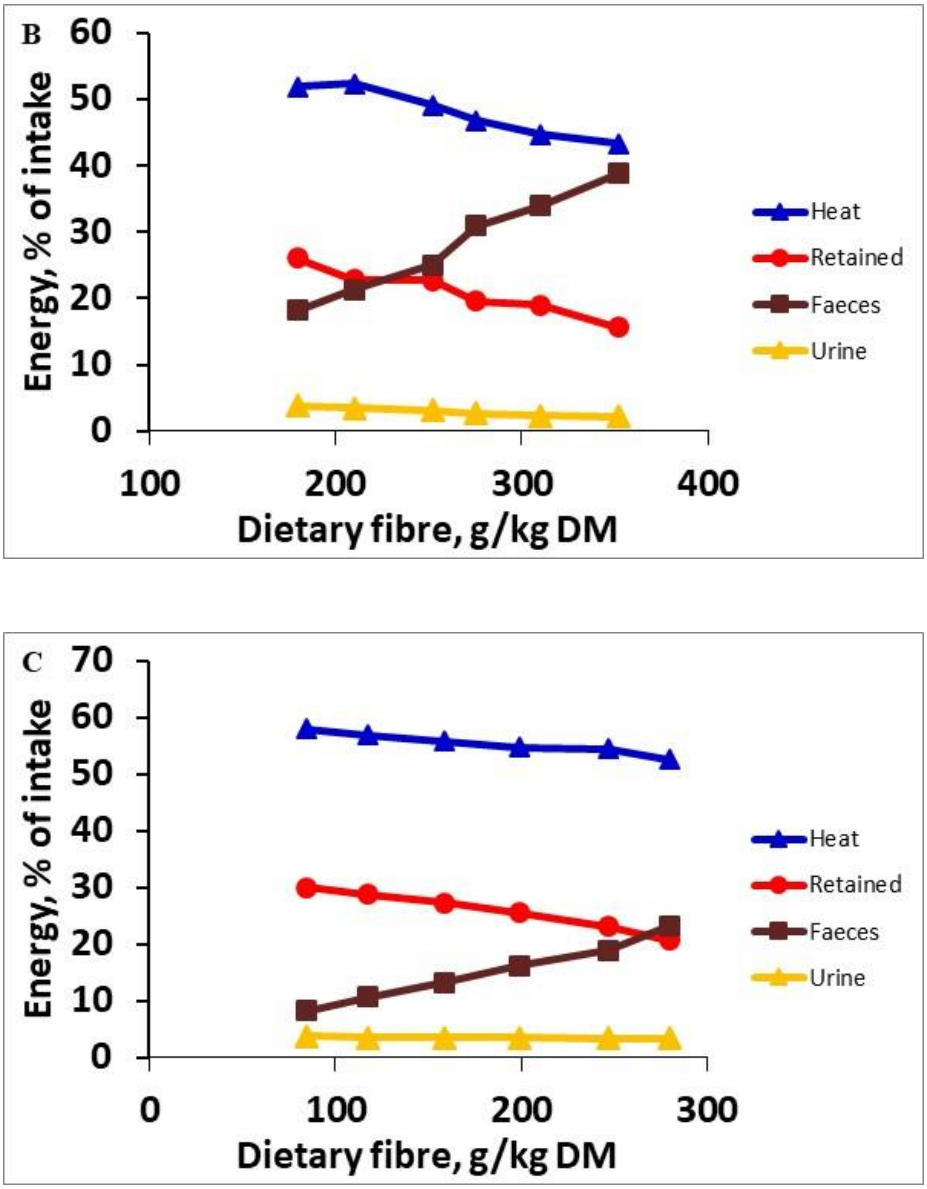


Figure 20.25. Utilisation of gross energy in growing pigs fed increasing levels of dietary fibre. In study A [31], pigs were fed 139 to 460 g DF/kg DM with increasing supply from oat and decreasing fibre from barley and wheat. The gross energy intake in group 1 through 5 was 24.8, 27.1, 30.3, 35.3 and 40.9 MJ GE/d, respectively. In study B [32], pigs were fed from180 to 352 g DF/kg DM with increasing supply of dietary fibre from barley straw. The gross energy intake in group 1 through 6 was 25.0, 26.6, 27.4, 30.6, 31.6 and 32.4 MJ GE/d, respectively. In study C [33], pigs were fed from 85 to 280 g DF/kg DM with increasing supply of dietary fibre from potato starch and cellulose. The gross energy intake in group 1 through 6 was 23.6, 24.5, 25.7, 25.6, 27.0 and 28.2 MJ GE/d, respectively.

Although the depressing impact of dietary fibre to some degree depends on the source of the feedstuff, the fibre content of a diet is by far the most important predictor of energy digestibility and the overall energy value of ingredients and diets for pigs (see section 8). Another reason why dietary fibres reduce the energy utilisation is that dietary

fibre increases the length and weight of the digestive tract [38]. Even though the digestive tract represents only about 5% of the whole body, the digestive tract is highly metabolically active and is responsible for 25-29% of the total heat production [88]; [25]. Thus, when animals are introduced to a high-fibre diet, they need to expand the lumen capacity of the gastrointestinal tract, and energy costs associated with intestinal growth may help to explain why the energy utilisation drops with more than 1% for each additional percent of dietary fibre. The latter is due to decreased digestibility of nutrients other than fibre, e.g. protein, fat and carbohydrates, because fibre may prevent the digestive enzymes from reaching these undigested components.

The carbohydrate composition, i.e. the proportion of digestible to total carbohydrates (see Bach Knudsen and Lærke [3] for details), has a significant impact on the site for carbohydrate degradation (small v. large intestine) on the type of products net absorbed from the gastrointestinal tract (monosaccharides, v. SCFA), on the absorption kinetics of energy in the post prandial phase [66], and on the overall utilisation of energy originating from the diet. Firstly, ingested fibres are not degraded enzymatically and will be substrate for fermentation processes, which will lead to a significant loss of energy as H_2, CH_4 and microbial growth whereby approximately 25% of the energy in the substrate is lost. While the loss as H_2 is relatively low, the loss as CH_4 is quite significant, and in sows it may represent 2-4 % of the gross energy intake, while it represents approximately 1% in growing pigs [41].

Beyond digestion, the fibre content in the diet has no impact on energy loss in urine. The impact of fibre on heat production (or energy retention) is rather small although it likely depends on whether the animal uses the energy for oxidation or produces de novo fat (for retention) or for milk fat production. It is interesting to note that the heat production decreases with increasing dietary fibre. Most likely, this reflect a higher energetic efficiency when animals have a high de novo fat synthesis. If glucose is used as precursor for fat synthesis, 2 carbons out of 6 are lost in the conversion from glucose to acetyl Co-A, indicating a substantial loss of energy. In contrast, if energy is net absorbed as acetate, this precursor can easily be converted to acetyl Co-a and used for de novo fat synthesis without undergoing the substantial metabolism glucose has to undergo, before acetyl Co-A can be used as substrate for de novo fat synthesis. Overall, dietary fibre increases the

fermentation heat and reduces the energy digestibility and thereby cause a substantial loss of energy, but beyond the gastro-intestinal tract the short chain fatty acids seems to be utilized more efficient in animals with a high de novo fat synthesis. These aspects are of much higher relevance for sows than for growing pigs as sows are more efficient in fibre fermentation and because their de novo fat synthesis is wanted when restoring body condition in gestation and when producing fat rich milk in lactation.

7.3. Impact of dietary crude protein on utilisation of GE

Dietary protein should preferentially be used for protein retention (growing pigs), mammary and foetal growth (pregnant sows) or milk protein synthesis (lactating sows) to reach a high protein utilisation, which in turn ensures a high energy utilisation. Utilisation of dietary crude protein depends on the content of standard ileal digestible lysine (the first limiting amino acid in pig and sow diets) per unit of net energy and on how well-balanced the amino acids are relative to ideal protein [58], [59], [60] [20]. In short, if the standard ileal digestible CP or if the amino acid profile is not well balanced in accordance with the animal requirement, then more protein (amino acids) are oxidised. Therefore, to obtain a high feed utilisation (e.g. high gain to feed conversion in growing pigs), the ratio between dietary lysine (or dietary protein) and net energy should be optimised. The reason is that dietary protein or dietary amino acids supplied in excess of the animal's requirement will be catabolised and utilised as energy. This also happens if protein or amino acids are fed in excess of dietary net energy, because energy supply is prioritized higher than protein supply.

The impact of dietary protein concentration on energy utilisation has been demonstrated in a study with growing pigs using the comparative slaughter trial [28]. Pigs were fed one of six diets with increasing levels of crude protein (ranging from 12% to 30 % of dry matter in the feed) as shown in Figure 20.26.

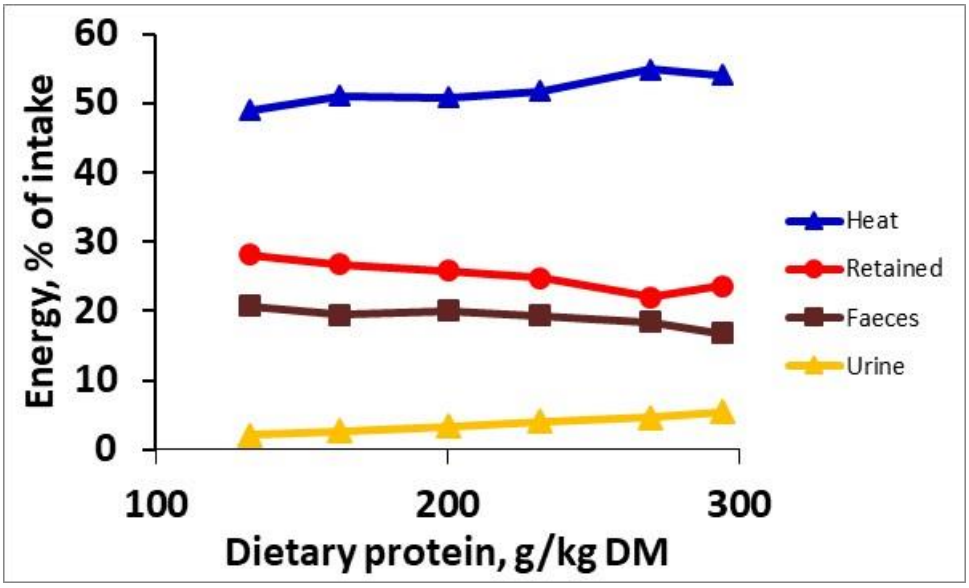


Figure 20.26. Utilisation of gross energy in growing pigs fed increasing levels of dietary protein (crude protein; CP). The dietary protein ranged from 132 to 294 g CP/kg DM, and the gross energy intake in group 1 through 6 was 32.1, 29.8, 29.3, 29.2, 29.2 and 30.2 MJ GE/d, respectively [29].

The amino acid concentrations were in accordance with the recommendations for growing pigs [29] throughout the experiment (i.e. the protein to net energy-ratio decreased during the growing phase, but pigs were fed increasing levels of excessive crude protein). The recommendations for growing pigs have changed since 1982, due to improved knowledge on amino acid requirements for growth, but the proportions relative to gross energy intake has not changed much. The study showed that increasing dietary protein slightly decreased the energy lost in faeces, indicating that the energy digestibility of the protein source was higher than the energy digestibility of the remaining dietary fraction. Moreover, increasing the dietary crude protein concentration increased the heat production from 49% to 54% because protein oxidation is costly due to urea synthesis, and concomitantly the proportion of energy lost in urine also increased from 2% to 5%. As a consequence, the energy utilised for retention dropped from 28% to 24%. These changes illustrate that diet composition is highly important for utilisation of energy in the diet, also beyond the level of digestible energy. In a recent study, it was shown that utilisation of dietary energy fed to lactating sows dropped, if sows were fed excess dietary protein [65], which illustrates that the trends are comparable between pigs and sows, whereas the fate of energy differ greatly between growing pigs and lactating sows.

7.4. Impact of dietary fat (lipids) on utilisation of GE

Fats and oils are important dietary ingredients in animal production owing to their high energy value and the gross energy content which is roughly twice as high compared with the gross energy concentration of dietary carbohydrates and twice as high for protein, if it is oxidised (see Table 20.1). Three aspects are important for energy utilisation from dietary fat. First of all, the inclusion level of supplemented dietary fat affects greatly gross energy intake. It is important to consider that pig diets typically contain 3-6% crude fat, which means that the dietary energy concentration normally vary only slightly. Secondly, the concentration of fatty acids relative to the crude fat content is important to know because crude fat may contain fat components with little or no energy value (e.g. cholesterol, tocopherol and wax depending on the fat source), whereas triglycerides has a very high energy value. Thirdly, the fat digestibility is important for the energy value of the feed as demonstrated in Table 20.9.

Table 20.9. Chemical composition and energy digestibility for different fat sources [38].

Fat source	**GE, MJ/kg DM**	**Fatty acids, %**			**Digestibility, %**	
		Saturated	**Un-saturated**	**Polyun-saturated**	**Fat**	**Energy**
Animal fat	39.48	38.5	43.7	7.2	90	89
Fish oil	39.08	25.7	30.9	26.8	85	89
Rapeseed oil	40.35	5.8	57.1	30.9	93	95
Soya oil	39.50	13.9	23.5	57.9	91	91
Palm oil	40.76	45.4	36.6	10.6	85	83
Palm oil mix	39.04	45.5	31.7	9.3	72	62
Oil by-product	38.88	20.2	24.3	8.4	67	62
Fish oil	39.24	23.6	35.2	25.0	94	95
Rapeseed oil	39.57	6.8	57.2	30.1	93	96
Coconut oil	37.43	76.3	6.5	2.2	94	90

Fat digestibility is affected by fat source, processing of the fat (remember that most fat is by-products) and content of for example lecithin. Lecithin may help to improve the emulsifying properties when micelles are formed in the digestive tract prior to fat absorption (see Lauridsen and Krogh Jensen for [50]). Overall, different fat sources are frequently used in pig feeds, and while the gross energy concentration of different fat

sources is rather constant, the concentration of digestible, metabolisable and net energy levels may vary considerably.

When dietary fat is digested and absorbed, most of the fat is incorporated into body lipids or secreted as milk fat (see Figures 20.3 and 20.11). Only a minor amount of fat may be oxidised to yield energy in the form of ATP to fuel the body.

If fat is used as an energy source, the efficiency of utilising ME for oxidation is 66-67% (see glycerol, palmitate and stearate; Table 20.3). In contrast, the efficiency is higher (80%; Table 20.6) if ME is used for fat retention in growing pigs or for milk fat production in lactating sows. Growing pigs are fed around 2.7 times their maintenance requirement, and therefore they do not oxidise fat. Instead, they retain substantial amounts of fat, which to a great extent is de novo synthesised from glucose. Consequently, including more fat in the diet under these conditions reduces the need for de novo fat synthesis. Since utilisation of dietary fat for fat retention is highly efficient, less heat is produced if the dietary fat concentration increases as demonstrated in a model experiment with growing pigs fed diets ranging from 4% to 24% fat in the dry matter fraction in the feed (Figure 20.27, [30]). This experiment was carried out to evaluate the net energy content from dietary fat and to achieve this, much more fat was included in the high fat diets than used in commercial pig feeding. It should be emphasised that growing pigs are normally fed very low levels of dietary fat (30-40 g/kg DM), because consumers want to buy lean meat.

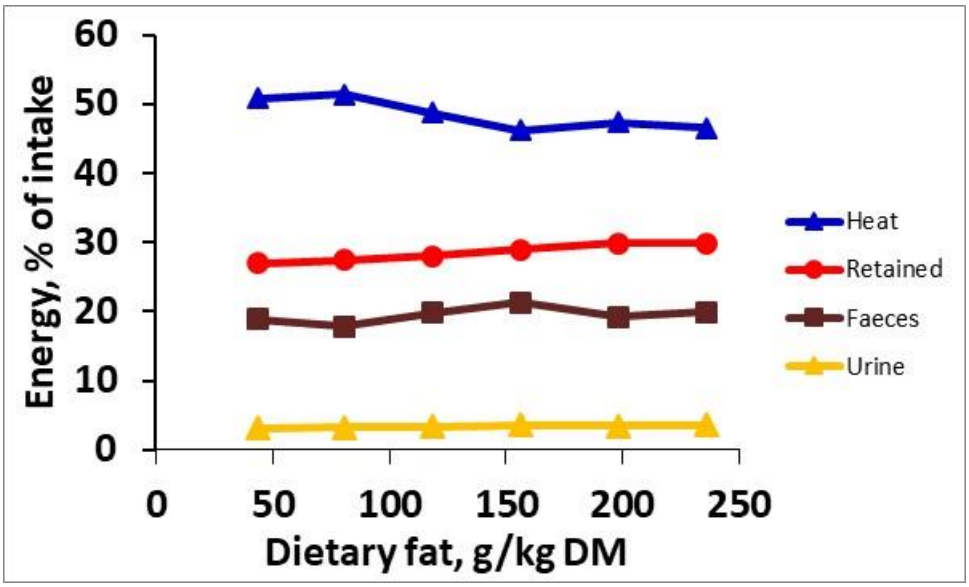


Figure 20.27. Utilisation of gross energy in growing pigs fed increasing levels of dietary fat, ranging from 44 to 236 g fat/kg DM and the gross energy intake in group 1 through 6 was 28.1, 27.3, 28.5, 28.6, 28.1 and 28.2 MJ GE/d, respectively [30], [39], [40].

7.5. Other factors with impact on energy utilization

7.5.1. Age of the animal and feed intake

The intestine, most pronouncedly the large intestine, develops as the pigs grow older, which makes heavy pigs like sows able to digest/ferment more fibrous diets (Table 20.10). An increasing level of feeding may diminish the efficiency of digestion as it increases rate of passage. The degree of digestion in the large intestine is sensitive to the period of time where undigested material is subjected to fermentation. Thus, if the feed intake increases, the passage rate increases and this leaves less time for enzymatic digestion and bacterial fermentation. Age of the pig also affect the energy utilization, especially because fibres are more efficiently fermented by large animals (sows) as compared with smaller animals (growing pigs); a factor that, however, is confounded with the feed intake. For instance, when growing pigs and adult sows were fed at similar feeding level, no difference in digestibility was found [42]. Adult dry/pregnant sows are normally fed close to maintenance to control body condition and ensure that the live weight of the sows is not increasing too much, whereas sows during the last trimester typically are fed approximately 1.7 times maintenance to meet their requirements for reproduction. When late pregnant sows approach farrowing, their feed supply is typically reduced, which leads to increased digestibility [62]. The opposite happens at peak

lactation where sows are fed as much as 4 times their maintenance requirement, and the sows respond by decreasing the energy digestibility [24] because the digesta passage rate increases considerably.

7.5.2. Physical form of the diet

There are many reasons for processing feedstuffs and grains. Among the most important is altering the physical form or particle size such as grinding to promote mixing with other ingredients. In addition, reducing the particle size increases the surface area, which helps endogenous and microbial enzymes to reach their substrates, and this in turn improves the digestibility of nutrients. From the data in Table 20.10 [36] it is evident that grinding the diet is more important for young pigs than for adult sows, most likely because of the lower digestive and fermentative capacity in younger pigs.

Table 20.10. Influence of grinding (finely v. coarsely) and increasing dietary fibre (crude fibre) on the digestibility of energy at different classes of pigs [36], [15].

Grinding	Fine (1 mm screen)			Course (4 mm screen)		
Crude fibre, % DM	5.4	10.1	16.7	5.4	10.1	16.7
Live weight						
20 kg	82	71	57	79	69	55
90 kg	83	75	62	83	74	60
225 kg	81	76	64	82	76	67

From studies with ileal cannulated pigs fed diets based on coarsely ground cereals it can be estimated that if digestibility of starch in the small intestine drops with 5 percentage points (from 97% to 92%), it will result in a drop in the net energy concentration of approximately 1% (see section 8 for details). The digestibility of protein and fat will also be lower when feeding a coarsely ground cereal diet compared to a pelleted diet as a consequence of encapsulation of nutrients and a higher endogenous secretion. The combined decrease in the digestibility of nutrients and the higher energy cost due to endogenous secretions have in some studies resulted in 4-5% decreased growth performance.

7.5.3. Enzyme addition to diet

Addition of functional ingredients are being more and more common in modern pig production for various reasons. Fibre degrading enzymes may be added to swine diets

and it was recently shown that a mono-component xylanase added to a lactation diet increased the digestibility of dry matter, organic matter, protein and non-starch polysaccharides by 0.8, 0.8, 1.7 and 2.7 percentage points, respectively, whereby the energy digestibility increased by 1.0 percentage point [89]. It is also becoming increasingly common to use exogenous fibre degrading enzymes for growing/finishing pigs and even for nursery pigs.

8. Prediction of dietary energy

Knowledge on energy contents of diets is crucial because swine nutrition is optimal when nutrients are balanced with the dietary energy content. Farmers mix their own diets and feedstuff companies mix feed each day, and for them, it is highly important that the energy in the pig diets is predicted as close as possible to the real dietary content. To reach that, it is crucial to have an energy evaluation system, which preferably is both precisely (i.e. evaluate feed ingredients correctly relative to each other) and accurately (i.e. predict the dietary content as close as possible to the realised amount of energy. Countries like Denmark, France, Netherland, Germany, and USA/Canada has different energy evaluation systems, however, it is not the purpose of this chapter to describe similarities and differences across different systems applied in different countries. This section will describe how dietary contents of GE, DE, ME, NE and potential physiological energy can be predicted from feedstuff analyses. Also, equations are presented to convert between these energy levels in order to compare international literature from different countries based on different energy evaluation systems.

Originally, the energy evaluation was based on the classical proximate Weende analyses [21], [22]. It was developed in the German research facility Weende, and according to the Weende analyses, the dietary DM consist of crude fat, crude protein, crude fibre, ash, and N-free extract (NFE). Crude fibre represent the part of dietary fibre which is least fermentable, whereas the NFE fraction represent the remaining carbohydrate fraction including enzymatically digestible fraction like starch and the more fermentable fibre fractions like hemicellulose. The NFE fraction represents the majority of the feed and is calculated as a difference from other feedstuff analyses: NFE = DM - crude fat - crude protein - crude fibre – ash.

To illustrate (see Figure 20.28) advantages and disadvantages when using different energy evaluation systems, the DE/GE-ratio is shown to illustrate how much improvement is obtained when using the DE system (as compared with a GE system), the ME/DE-ratio is shown to illustrate how much improvement is obtained when using the ME system (on top of the DE system) and NE/ME-ratio is shown to illustrate how much improvement is obtained when using the NE system (on top of the DE and ME systems). The NE system is applied in many countries worldwide, and it formed the basis in Denmark for calculating the energy value as feed units prior to 2004. Since 2004, Denmark has used the concept of potential physiological energy. The potential physiological energy system will briefly be mentioned, whereas a full description will be given in a later chapter.

8.1 Digestible energy

This system was the first energy evaluation system applied in practice and it was adopted to take into account the substantial loss of energy via faeces, in order to account for feed ingredients with low digestibility. From Figure 20.28 (left column) it may be seen that the energy digestibility, i.e. the DE/GE ratio, increases with increasing inclusion of fat, protein and NFE contents, whereas the energy digestibility decreases with increasing contents of crude fibre and ash in the diets. Analysing the dietary contents of crude fat, crude protein, crude fibre, ash, and NFE has been the classical way of predicting the dietary contents of DE, which was the predominant energy system in the past. The advantage of this system is that it is simple, as DE can easily be measured by collection of faeces or DE can be estimated based on in vitro analyses.

8.1.1. Metabolisable energy

The ME system was adopted to take into account the minor loss of energy via urine and gases. Evaluating energy at the ME level is regarded being superior to the DE level, mainly because dietary protein is evaluated more correct and this system may be regarded a “fine tuning” of the DE system. From Figure 20.28 (middle column) it may be seen that the ME/DE-ratio increases with increasing inclusion of dietary NFE, whereas the ME/DE ratio decreases with increasing inclusion of protein and ash. In contrast, the dietary content of fat and crude fibre has no effect on the dietary DE/ME-ratio. Note that the majority of DE is metabolisable (typically 96 to 97% in diets for growing pigs), and that the improvement in energy evaluation going from DE to ME level is fairly small, as indicated by

rather small changes in DE/ME-ratios across dietary inclusion levels of crude fat, crude protein, crude fibre, ash, and NFE. The advantages is mainly that the ME system evaluate the energy value of protein more correctly as energy lost in urine is taken into account (relevant for protein content of the diets). Another advantage of the ME system is that ME is the “currency” of energy required by the animals (see section 6.4), and when performing animal studies, utilization of all ME can be measured in a fair number of animals.

8.1.2. Net energy

The NE system was developed for growing pigs to account for how efficiently pigs retain energy for growth and it takes into account how much heat is produced due to maintenance (NE required for maintenance, NEm, which should not be confused with MEm). From Figure 20.28 (right column) it may be seen that proportion of ME that is utilised as NE increases with dietary fat, whereas it decreases for dietary protein, crude fibre, ash and dietary NFE. The advantage with the NE system is that pigs fed different diets with the same amount of net energy should ideally retain the same amount of energy (although it may be either as fat or protein or a combination thereof). It is important to stress that even though two groups of pigs are fed the same amount of NE, they do not necessarily obtain the same growth rates, because the NE system does not distinguish between energy retained as fat and energy retained as protein (recall that retained protein increases growth rate with 5.2-fold due to water retention [26], [44]. Net energy may also be used for evaluating sow diets, where energy in milk is regarded the output merely than energy retained in fat and protein. However, lactating sows normally mobilise energy from their own body, and this has not been taken into account until recently, where feed efficiency of lactating sows based on NE corrected for body mobilisation (NE_c) was suggested by Pedersen et al. [65].

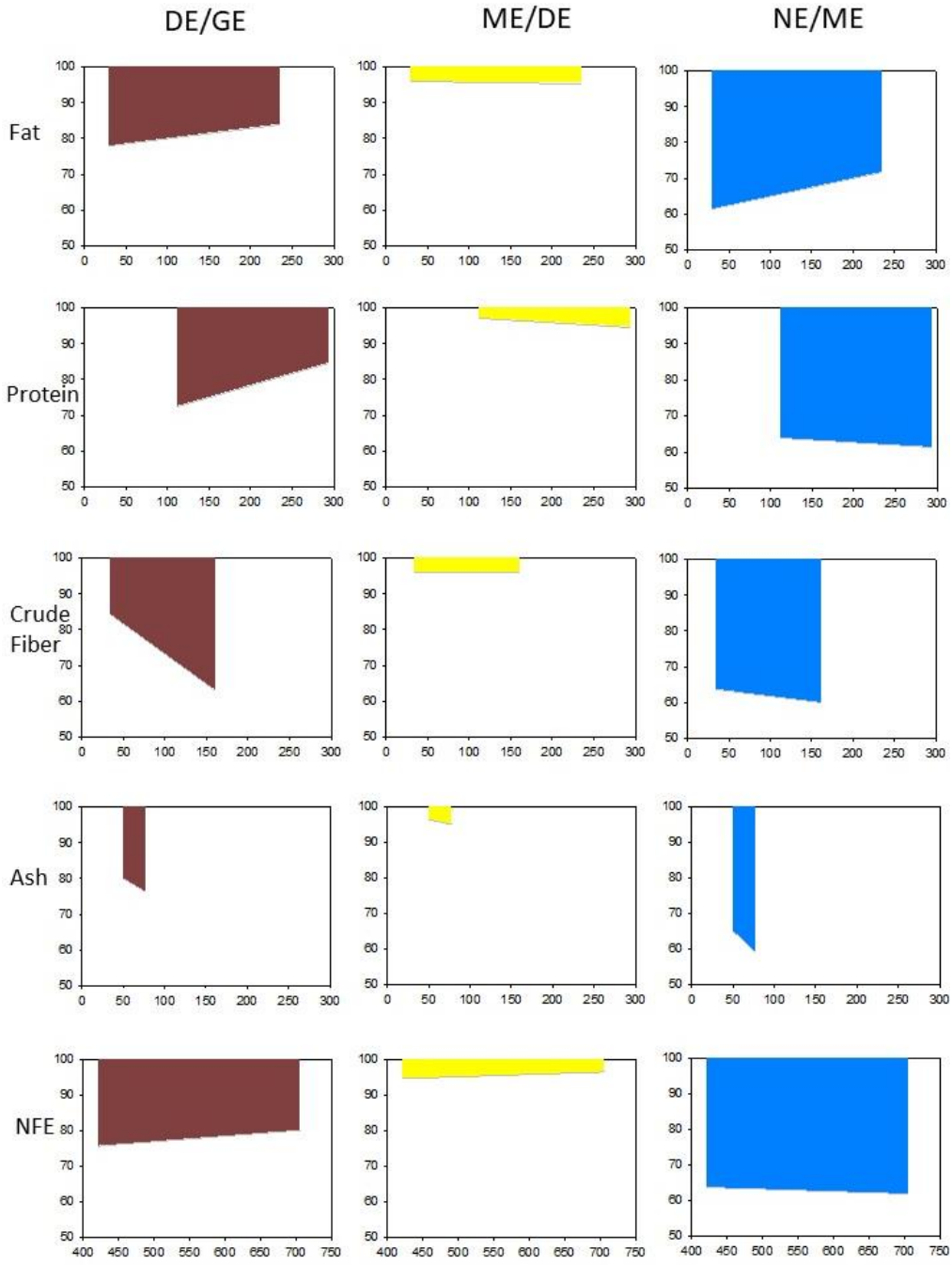


Figure 20.28. In the first column (DE/GE), the brown area represents the amount of energy lost in faeces and the white area below represents the amount of gross energy being digested with varying contents of dietary crude fat, crude protein, crude fibre, ash, and NFE. In the second column (ME/DE), the yellow area represents the amount of energy lost in urine (and gases like CH_4 and H_2) and the white area below represents the amount of digested energy being metabolised with varying contents of dietary crude fat, crude protein, crude fibre, ash, and NFE. In the third column (NE/ME), the blue area represents the amount of energy lost as heat (disappear as CO_2 into the atmosphere) and the white area below represents the amount of metabolised energy being net utilised (according to the NE system used in Denmark until 2004) with varying contents of dietary crude fat, crude protein, crude fibre, ash, and NFE. Note that part of the NE (represented by the white area below the blue area in figure 20.28) is also lost as heat, namely the amount of heat required for maintenance on a net energy basis (NEm). Note that all Y-axes start at 50%.

8.1.3. Potential physiological energy and the Danish feed unit

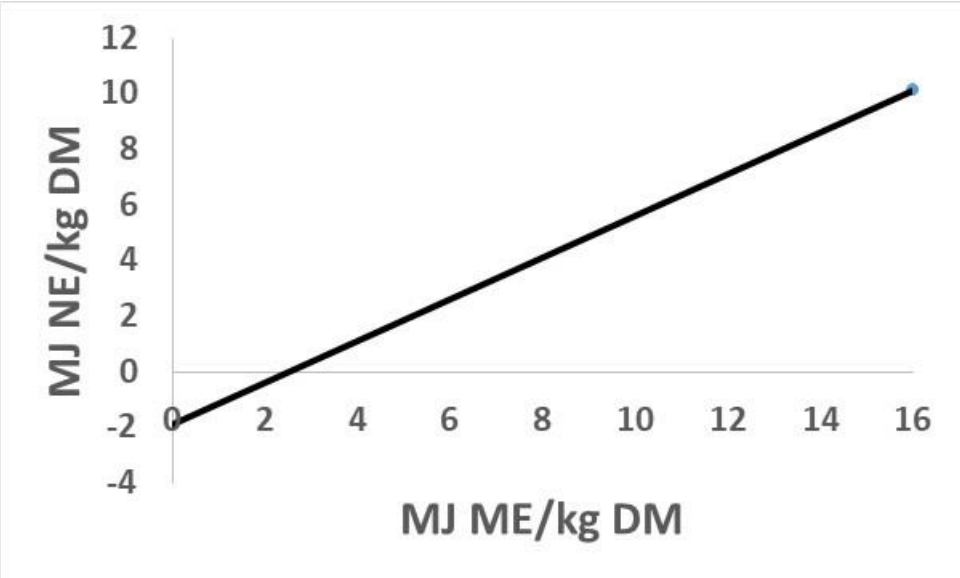


Figure 20.29. Relationship between ME and NE in balanced pig diets (R^2=0.90; data not shown [25], [27], [28].

Feeding in Denmark is based on the Danish Feed Unit, which is a calculated value. Historically, the feed unit was identified as the growth potential of pigs fed 1 kg of barley, corresponding to 7.72 MJ NE. From 1983 to 2004, the feed unit (FUp) was calculated based on a linear relationship between NE and ME (Figure 20.29), which was obtained from a great number of experiments where ME and NE was measured on pigs fed balanced diets. Based on this relationship, the dietary content was calculated by defining that 1 FUp was equivalent to 7.72 MJ NE.

Since 2004, feed units in Danish pig diets have been calculated based on the content of potential physiological energy. According to this concept, organic matter digestibility at the end of the small intestine and for the total tract are measured by two in vitro analyses (In Danish, EFOSi and EFOS). Dietary analyses of dry matter, ash, protein, and fat are used to estimate the amount of digested crude protein, crude fat, carbohydrates other than fibre, and fibre per kg of feed based on the two in vitro analyses. The potential energy value for the pig diets is subsequently calculated on an ATP basis by assuming that protein contains 9.9 kJ per g digested protein, 31.7 kJ per g digested fat, 11.7 kJ per g digested carbohydrates other than fibre, 7.0 kJ per g fermented fibre in pigs and 9.0 kJ per

g fermented fibre in sows. Moreover, the system accounts for a negative contribution for fibre (In Danish UTSi) due to increased cost of transporting undigested material through the gastrointestinal tract. Thus, the system distinguishes between feed units for pigs (FUpig) and for sows (FUsows), because sows are more efficient in extracting energy from dietary fibres than growing pigs [82], whereas no differences between pigs and sows beyond the gut level is taken into account, where ketogenic energy sources (fat and short chain fatty acids) ideally should be given a higher value for animals where de novo synthesis is wanted. In the potential physiological energy system it is assumed that all digested (or fermented) energy is completely oxidised by the pig, which certainly is not the case because pigs and sows has a very strong preference for oxidising glucogenic energy substrates (primarily starch). Thus, the potential physiological energy system has some disadvantages. The most important ones are: 1) the potential physiological energy system cannot be validated, because it is a theoretical system, 2) the potential physiological energy system does not take into account how much dietary protein is utilised by pigs for growth and by sows for milk protein, and 3) The system does not acknowledge that fat is prioritised for retention (pigs) or milk fat (lactating sows) and dietary fat is under normal feeding conditions not oxidise at all. Therefore, the assumption that all digested energy is oxidised is not valid, which is evident from the fact that growing pigs retain approximately 25 to 30% of ingested gross energy and lactating sows secrete approximately 50% of the ingested gross energy into milk. The advantage of the potential physiological energy system is that the energy value may be estimated in diets with a fair number of analyses and used to control pig feed produced by the feed industry. It is not the purpose of this chapter to describe the potential physiological energy system in details, as this will be done in another chapter.

The dietary recommendations may be presented in 3 different ways when formulating diets in Denmark, and therefore it is relevant to illustrate how much energy (approximately) is contained in 1 Feed unit, in 1 kg of feed and in 1 kg of DM (Table 20.11). These values are fairly close to each other and causes some misunderstanding especially when dietary recommendations or analysed contents in diets are converted between these units.

Table 20.11. Energy contents in typical diets used for pigs and sows

	1 Feed Unit	1 kg feed	1 kg DM
Gross energy, MJ	15.4	16.2	18.4
Digested energy, MJ	12.8	13.4	15.3
Metabolisable energy, MJ	12.4	13.0	14.8
Net energy, MJ	7.7	8.1	9.2
Feed units	1.00	1.05	1.19

To avoid confusion, it is shown how the Danish recommendation of standardised ileal digestible lysine (SID) for lactating sows (currently 7.7 g SID/feed unit) may be converted to a recommendation per kg of feed or per kg of DM (Table 20.12). The same principle applies when formulating diets per feed unit and converting these into per kg of feed.

Table 20.12. Dietary lysine concentration for lactating sows

	per Feed Unit	per kg feed	per kg DM
Lysine concentration (g SID)	7.7	8.1[1]	9.2[2]

[1]calculated as 7.7 g/Feed unit x 1.05 Feed Unit/kg feed

[2]calculated as 7.7 g/Feed unit x 1.19 Feed Unit/kg DM

8.2. Prediction of dietary content of energy (MJ GE, DE, ME and NE per kg DM)

Dietary energy concentration at either GE, DE, ME or NE level can be predicted from the macro nutrient composition of the diet (Table 20.13). In the following, a great number of equations are presented, which allow conversion of energy from one energy system to another. The data represent knowledge collected from a great number of animal experiments within energy utilization / energy evaluation in pigs carried out at “Landøkonomisk Forsøgslaboratorium”, “Statens Husdyrbrugsforsøg”, “Danmarks JordbrugsForskning” and since 2007 Aarhus University. For the interested reader, it is recommended to pay attention to whether a certain dietary component is important or not for gross- , digestible-, metabolizable and net energy concentrations (this section) and energy utilization (section 8.3). Note for instance that dietary crude fibre hardly account for any variation of the gross energy concentration ($P = 0.16$), whereas it has a great impact on DE, ME and NE concentration in the diet ($P < 0.001$). It is indeed the hope from the authors that the equations presented below (Tables 20.13, 20.14, and 20.15) may be used in the future by people working in the feed industry and in academia to convert the energy concentrations, energy utilization, or energy predictions reported in one system to corresponding values using another system.

Table 20.13. Prediction of gross- , digestible-, metabolizable, and net energy concentration using dietary analyses

Gross energy, MJ/kg DM (n=244)	r	P-value
GE = 18.81		
GE = 17.87 + 0.0179 x dietary fat	0.96	***
GE = 18.00 + 0.0038 x dietary protein	0.39	***
GE = 18.67 + 0.0020 x dietary crude fibre	0.10	0.16
GE = 19.04 – 0.0038 x dietary ash	–0.06	0.36
GE = 23.64 – 0.0080 x dietary NFE	-0.78	***
GE = 0.0354 x dietary fat + 0.0218 x dietary protein + 0.0210 x dietary crude fibre + 0.0180 x dietary NFE	(R^2=0.93)	***, ***, ***, ***

Digestible energy, MJ/kg DM (n=244)	r	P-value
DE = 14.78		
DE = 13.74 + 0.0199 x dietary fat	0.58	***
DE = 11.11 + 0.0172 x dietary protein	0.51	***
DE = 16.92 – 0.0035 x dietary NFE	–0.28	***
DE = 16.52 – 0.0288 x dietary ash	–0.06	0.37
DE = 16.78 – 0.0296 x dietary crude fibre	–0.66	***
DE = 0.0329 x dietary fat + 0.0238 x dietary protein + 0.0146 x dietary NFE – 0.0128 x dietary crude fibre	(R^2=0.76)	***, ***, ***, ***

Metabolisable energy, MJ/kg DM (n=244)	r	P-value
ME = 14.16		
ME = 13.18 + 0.0187 x dietary fat	0.57	***
ME = 11.14 + 0.0142 x dietary protein	0.47	***
ME = 15.60 – 0.0024 x dietary NFE	–0.25	***
ME = 16.09 – 0.0285 x dietary crude fibre	–0.67	***
ME = 16.32 – 0.0357 x dietary ash	–0.08	0.21
ME = 0.0322 x dietary fat + 0.0210 x dietary protein + 0.0146 x dietary NFE – 0.0124 x dietary crude fibre	(R^2=0.75)	***, ***, ***, ***

Net energy, MJ/kg DM (n=86)	r	P-value
NE = 8.77		
NE = 7.77 + 0.0202 x dietary fat	0.46	***
NE = 0.21 + 0.0121 x dietary protein	0.28	***
NE = 10.79 – 0.0033 x dietary NFE	–0.16	0.15
NE = 10.18 – 0.0208 x dietary crude fibre	–0.61	***

NE = 11.78 – 0.0496 x dietary ash	–0.29	***
NE = 0.0283 x dietary fat + 0.0127 x dietary protein + 0.0088 x dietary NFE – 0.0106 x dietary crude fibre	(R^2=0.80)	***, ***, ***, ***
NE = 0.9336 x GE – 9.277	0.57	***
NE = 0.7172 x DE – 1.752	0.92	***
NE = 0.7532 x ME – 1.815	0.93	***

8.3. Prediction of energy utilization (DE/GE-, ME/DE-, ME/GE-, NE/ME-, and NE/GE-ratios)

Utilisation of energy (e.g. digestibility and metabolisability) can be predicted from macro nutrient composition of the diet (Table 20.14). Note that energy digestibility is negatively influenced by increasing dietary content of crude fibre because additional energy is lost through faeces, whereas energy metabolisability is negatively influenced by increasing dietary content of protein because additional energy is lost through urine. As a corollary, the ME/GE ratio (i.e. the combination of digestibility and metabolisability) is both negatively influenced by dietary crude fibre and dietary protein.

Table 20.14. Prediction of digestibility and metabolisability (utilization) of energy using dietary analyses

Energy digestibility (100 x DE/GE; %) (n=244)	r	P-value
DE/GE = 78.56		
DE/GE = 62.60 + 0.0747 x dietary protein	0.36	***
DE/GE = 77.03 + 0.0294 x dietary fat	0.15	*
DE/GE = 69.15 + 0.0155 x dietary NFE	0.13	*
DE/GE = 86.88 – 0.1377 x dietary ash	–0.14	*
DE/GE = 89.78 – 0.1661 x dietary crude fibre	–0.76	***
DE/GE = 0.1271 x dietary protein + 0.1058 x dietary fat + 0.0838 x dietary NFE – 0.0721 x dietary crude fibre	(R^2=0.72)	***, ***, ***, ***

Energy ME/DE x 100 (%) (n=244)	r	P-value
ME/DE = 95.84		
ME/DE = 91.87 + 0.0065 x dietary NFE	0.41	*
ME/DE = 95.87 – 0.0004 x dietary crude fibre	–0.07	0.30
ME/DE = 95.96 – 0.0024 x dietary fat	–0.05	0.44
ME/DE = 99.09 – 0.0152 x dietary protein	–0.53	***
ME/DE = 98.84 – 0.0497 x dietary ash	–0.28	***
ME/DE = 0.1028 x dietary crude fibre + 0.1017 x dietary fat + 0.1014 x dietary NFE + 0.0999 x dietary protein	(R^2=0.53)	***, ***, ***, ***

Energy metabolizability (100 x ME/GE; %) (n=244)	r	P-value
ME/GE = 75.28		
ME/GE = 62.54 + 0.0596 x dietary protein	0.41	***
ME/GE = 73.89 + 0.0266 x dietary fat	0.14	*
ME/GE = 63.16 + 0.0200 x dietary NFE	0.18	**
ME/GE = 86.05 – 0.1596 x dietary crude fibre	–0.76	***
ME/GE = 85.71 – 0.1730 x dietary ash	–0.18	**
ME/GE = 0.1123 x dietary protein + 0.1047 x dietary fat + 0.0834 x dietary NFE – 0.0696 x dietary crude fibre	(R^2=0.70)	***, ***, ***, ***

Net Energy (100 x NE/ME; %) (n=86)	r	P-value
NE/ME = 62.54		
NE/ME = 59.82 + 0.0504 x dietary fat	0.55	***
NE/ME = 66.38 – 0.0064 x dietary NFE	–0.10	0.42
NE/ME = 65.66 – 0.0148 x dietary protein	0.12	0.34
NE/ME = 76.21 – 0.2221 x dietary ash	–0.40	***
NE/ME = 64.75 – 0.0303 x dietary crude fibre	–0.31	**
NE/ME = 0.1210 x dietary fat + 0.0726 x dietary NFE + 0.0441 x dietary protein + 0.0410 x dietary crude fibre	(R^2=0.47)	***, ***, ***, ***

Utilization of GE as NE (100 x NE/GE, %) (n=86)	r	P-value
NE/GE = 46.8		
NE/GE = 54.57 – 0.1152 x dietary crude fibre	-0.74	***
NE/GE = 43.93 + 0.0572 x dietary fat	0.39	***
NE/GE = 61.50 – 0.2424 x dietary ash	–0.31	**
NE/GE = 34.85 + 0.0564 x dietary protein	0.28	**
NE/GE = 41.86 + 0.0080 x dietary NFE	0.08	0.45
NE/GE = 0.1052 x dietary fat + 0.0668 x dietary protein + 0.0523 x dietary NFE – 0.0586 x dietary crude fibre	(R2=0.72)	***, ***, ***, ***

8.4. Conversion between energy systems - DE, ME, NE and feed units (FUp, FUpig and FUsow) per kg DM

Often it is challenging to compare studies from the literature, because energy values often are presented based on different energy evaluation systems. To be able to recalculate energy values from one system to another based on reported values, the

following equations may be used (Table 20.15). It is highly important to emphasis that to use the equations in Table 20.15, it is absolutely essential first to express (or recalculate) the values of energy into MJ (at either DE, ME or NE levels) per kg of DM, but do not use values presented per kg of feed. In the following, FUp refer to FU for pigs (FEs in Danish) according to the net energy system described by Just [25], [27], [28], FUpig refer to FU for pigs (FEsv in Danish) according to the potential physiological energy system described by Tybirk et al. [82], and FUsow refer to FU for sows (FEso in Danish) according to the potential physiological energy system described by Tybirk et al. [82].

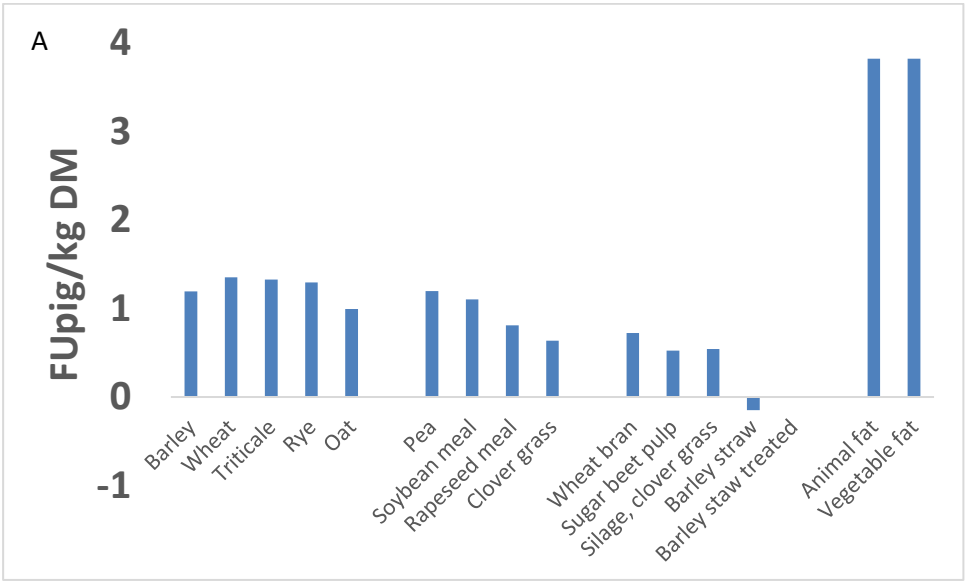
Table 20.15. Conversion of dietary energy across energy systems (DE, ME, and NE represent the dietary content in MJ/kg DM).

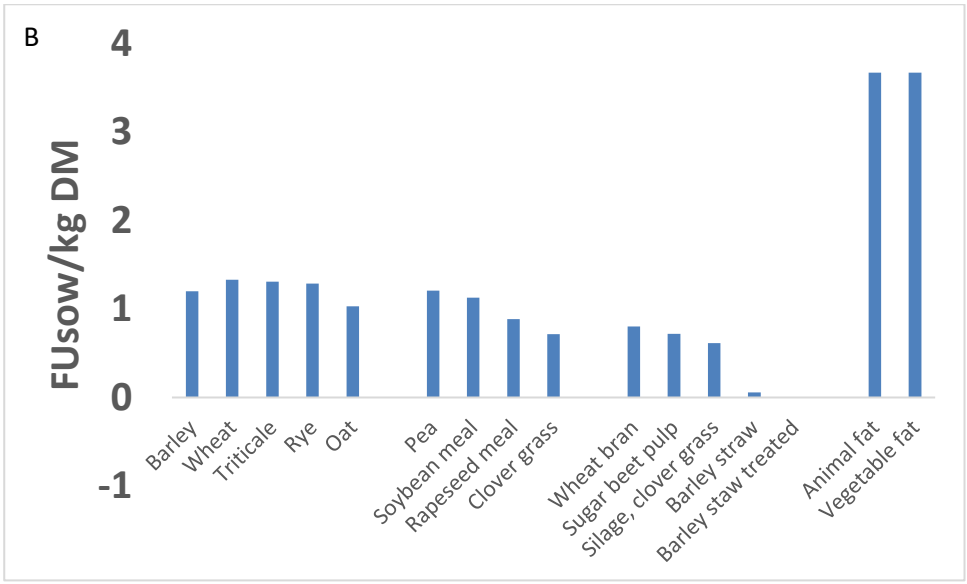
DE = -6.147 + 1.113 x GE	r=0.54	n=244
DE = 0.016 + 1.042 x ME	r=0.99	n=244
DE = 4.311 + 1.181 x NE	r=0.92	n=86
DE = 2.652 + 10.714 x FUp	r=0.99	n=86
DE = 5.520 + 9.130 x FUpig	r=0.95	n=86
DE = 4.478 + 8.979 x FUsow (dry and pregnant)	r=0.90	n=103
DE = -2.642 + 14.210 x FUsow (lactating)	r=0.87	n=17
ME = -5.500 + 1.046 x GE	r=0.53	n=248
ME = 0.078 + 0.953 x DE	r=0.99	n=248
ME = 4.054 + 1.140 x NE	r=0.93	n=86
ME = 2.507 + 10.293 x FUp	r=0.99	n=86
ME = 5.207 + 8.826 x FUpig	r=0.90	n=86
ME = 4.142 + 8.722 x FUsow (dry and pregnant)	r=0.96	n=103
ME = 4.121 + 9.096 x FUsow (lactating)	r=0.96	n=8
NE = -9.277 + 0.964 x GE	r=0.57	n=86
NE = -1.752 + 0.717 x DE	r=0.92	n=86
NE = -1.815 + 0.753 x ME	r=0.93	n=86
NE = 0.073 + 7.753 x FUp	r=0.93	n=86
NE = 1.690 + 7.063 x FUpig	r=0.94	n=86
FUp = -0.610 + 0.092 x GE	r=0.46	n=86
FUp = -0.242 + 0.0929 x DE	r=0.99	n=86
FUp = -0.244 + 0.0972 x ME	r=0.99	n=86
FUp = 0.150 + 0.111 x NE	r=0.93	n=86

FUpig =	-1.347 + 0.125 x GE	r=0.55 n=86
FUpig =	-0.446 + 0.0987 x DE	r=0.95 n=86
FUpig =	-0.457 + 0.104 x ME	r=0.96 n=86
FUpig =	-0.101 + 0.126 x NE	r=0.93 n=86
Pregnant and dry sows		
FUsow =	0.383 + 0.0343 x GE	r=0.13 n=103
FUsow =	-0.213 + 0.0904 x DE	r=0.90 n=103
FUsow =	-0.262 + 0.0983 x ME	r=0.93 n=103
Lactating sows		
FUsow =	-0.245 + 0.0797 x GE	r=0.71 n=17
FUsow =	0.433 + 0.0519 x DE	r=0.87 n=17
FUsow =	-0.312 + 0.1004 x ME	r=0.96 n=8

8.5. Energy content in feed ingredients based on Danish Feed units

The energy concentration varies greatly among commonly used feed ingredients. The energy concentration is greatest in fat sources, intermediate in energy sources like barley, wheat, triticale, rye and oat, and in protein sources with low fibre like soybean meal and peas. The lowest energy concentration is found in feed ingredients with high fibre content like sugar beet pulp, wheat bran, and silage (used in organic production), and barley straw represent the lowest energy concentration (Figure 20.30). The potential physiological energy system for pigs (Figure 20.30A) and sows (Figure 20.30B) evaluate the energy contribution from fat higher than the previous FUp system, whereas the energy contribution from protein and fibre rich sources are evaluated lower than the previous FUp system (Figure 20.30C).


A
FUpig/kg DM
4
3
2
1
0
-1
Barley
Wheat
Triticale
Rye
Oat
Pea
Soybean meal
Rapeseed meal
Clover grass
Wheat bran
Sugar beet pulp
Silage, clover grass
Barley straw
Barley staw treated
Animal fat
Vegetable fat


B
FUsow/kg DM
4
3
2
1
0
-1
Barley
Wheat
Triticale
Rye
Oat
Pea
Soybean meal
Rapeseed meal
Clover grass
Wheat bran
Sugar beet pulp
Silage, clover grass
Barley straw
Barley staw treated
Animal fat
Vegetable fat

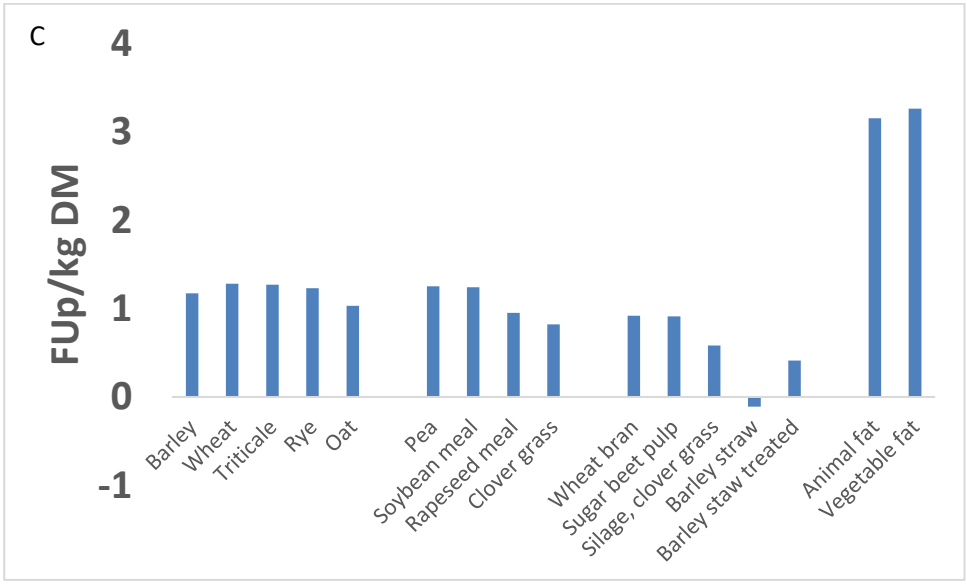

C
FUp/kg DM
4
3
2
1
0
-1
Barley
Wheat
Triticale
Rye
Oat
Pea
Soybean meal
Rapeseed meal
Clover grass
Wheat bran
Sugar beet pulp
Silage, clover grass
Barley straw
Barley staw treated
Animal fat
Vegetable fat

Figure 20.30. Content of FUpig (panel A), FUsow (panel B), and FUp (panel C) per kg dry matter (DM) in selected feed ingredients.

9. Methods and calculations of energy metabolism

9.1. Digestibility of energy (DE)

Figure 20.31. Collection of faeces is performed from the shelf below the animal, whereas urine from suckling piglets and the lactating sow is collected in the red and blue bucket, respectively (Photo: Peter Kappel Theil).

Digestibility of energy may be quantified using total collection, i.e. where pigs are housed in metabolic cages and it may even be done separately from a sow and her piglet (Figure 20.31). For nutritional studies including digestibility trials, it is important to register gross energy intake (from feed supply, feed residues and dietary energy concentration). Total collection of faeces and analysis of the energy concentration in faeces allow determination of energy digestibility based on input and output of energy. Alternatively, digestibility may be measured by means of addition of a dietary marker (chromic oxide, titanium oxide, insoluble ash, lignin [43], whereby the digestibility may be quantified from marker concentration in the faeces based on a grab sample (Figure 20.32) and concentration of the marker in the diet. Note, that the dietary concentrations of the marker and macro nutrient composition should be analysed in multiple feed samples [1], [35], [37].

Figure 20.32. Collection of fresh faeces may be used for measuring digestibility of energy and nutrients based on the marker technique (Photo: Trine Friis Pedersen).

In general, digestibility is calculated as: 100 x (input-output) / input

GE intake, MJ/d = Dry matter intake, kg DM/d x GE concentration in feed, MJ/kg DM
GE output, MJ/d = Faeces dry matter, kg DM/d x GE concentration in faeces, MJ/kg DM

Energy digestibility measured by total collection:
Energy digestibility, % = 100 x (GE intake, MJ/d – GE output, MJ/d) / GE intake, MJ/d

Energy digestibility measured by marker technique:
Energy digestibility, % = 100 - [100 x (conc. of marker in diet/ conc. of marker in faeces) x Conc. of energy in faeces / Conc. of energy in diet)]

Energy digestibility of a dietary ingredient can be measured by the difference method or by the regression method. By the difference method, digestibility of the basal diet is measured as described above (using either total collection or the marker technique), and then part of the basal diet is replaced with an ingredient of interest (e.g. 5%) in the test diet, and the remaining 95% being the basal diet. Using this procedure, the output of energy in faeces originates both from the basal diet and from the dietary ingredient of interest.

In that experimental design, the GE output in faeces originating from dietary ingredient (GE output from ingredient) may be calculated as:

GE output from dietary ingredient = total GE output - GE intake from 95% basal diet x ((100-Energy digestibility of basal diet)/100)

Energy digestibility of dietary ingredient, %
= 100 x (GE intake from ingredient - GE output from ingredient)/ GE intake from ingredient

Another approach to determine the digestibility of an ingredient is to make a dose response trial with e.g. 4 inclusion levels (0, 5, 10, and 15%) of the ingredient of interest and then measure the digestibility by total collection or marker technique as described above. Using this approach, the digestibility of the dietary ingredient of interest can be derived directly from the slope of the regression line. These studies are typically performed in metabolic cages [35] but they may be performed even under commercial settings using the marker technique (Figure 20.33).

9.2. Metabolisable energy (ME)

To quantify the metabolisable energy, it is necessary to measure energy digestibility (as described above) and in addition, to quantify energy loss via urine. Production of methane and hydrogen may also be measured and their energy contribution should be subtracted, but in practice these gases are often ignored, as they can only be measured in respiration chambers. To obtain energy output in urine, urine production needs to be quantified and the energy concentration of urine measured. Urine production (in L/d) may be quantified by total collection either in a metabolic cage or by inserting a urinary balloon catheter in the urinary bladder and emptying urine into a bucket (Figures 20.30 and 20.33). Urine production may also be quantified by infusing a marker (para-amino-hippuric acid; PAH) into the blood at a constant rate and analysing concentration of PAH in the urine, whereby the urine production may be estimated as:

Urine production (L/h) = infusion rate of PAH (mmol/h) / urinary concentration of PAH (mmol/L)

Figure 20.33. Urine collection may be done even in a commercial herd by inserting urinary balloon catheter and emptying the bucket every other hour (Photo left: Trine Bojsen Johansen; Photo right: Trine Friis Pedersen).

And then, energy in faeces (FE), urine (UE) and metabolisable energy (ME) may be calculated as:

FE, kJ/d = GE, kJ/d x (100-Energy digestibility, %)/100

UE, kJ/d = Urine production, g/d x energy in urine, kJ/g

ME, kJ/d = GE, kJ/d – FE, kJ/d - UE, kJ/d

If energy in urine is not measured, it may be predicted for growing pigs according to Just [25] and H. Jørgensen (unpublished) as:

UE, kJ/d = 97 + 37.5 x urinary N loss, g/d

The dietary concentration of ME in MJ/kg DM can be experimentally determined as:

ME, MJ/kg DM = ME, MJ/d / Feed intake, kg DM/d

These studies are typically performed in metabolic cages but they may be performed even under commercial settings using total collection of urine through balloon catheters.

9.3. Retained energy (RE)

9.3.1. CN-method

In this approach, energy retention may be calculated on the basis of the assumption that all retained carbon and nitrogen (hence CN-method) are deposited in the form of protein and/or lipid. Using this technique, carbohydrate retention (glycogen storage) is assumed to be zero. Knowing the content of carbon in protein and lipid, energy deposition is derived by multiplying the amounts of retained protein and fat by their respective combustion values, i.e. 23.86 kJ/g protein and 39.76 kJ/g lipid [9]. This technique require

that animals are kept in a respiration chamber in order to measure the carbon loss through CO_2 and CH_4. In the following it is described how nitrogen and carbon balances may be quantified, and how these can be used to derive energy retained as protein and fat, whereas the sum is equal to total retained energy.

9.3.1.1 Retained energy as protein

The nitrogen (N) balance, equal to retained N, can be measured as:

N-balance, g/d = N in feed – (N in faeces + N in urine + N in milk)

retained protein (RP) and retained energy in protein (RPE) may then be calculated from the N balance (g/d) as:

RP, g/d = N-balance, g/d x 6.25
RPE, kJ/d = N-balance, g/d x 6.25 x 23.86 kJ/g

9.3.1.2. Retained energy as fat

The carbon balance, equal to the carbon retention, is measured as the difference in C intake and C output as:

C-balance, g/d = C in feed – (C in faeces + C in urine + C in CO_2 + C in CH_4 + C milk)

Energy retained in fat (RFE) may be calculated by means of the carbon balance, corrected for retained carbon in protein as:

RFE, kJ/d = (C-balance-(N-balance x 6.25 x 0.52)), g/d x 39.76, kJ/g / 0.767

The constant 0.52 and 0.767 refer to the relative proportion of carbon in protein and lipid, respectively.

9.3.1.3. Retained energy according to the CN method

The total energy retention is the sum of energy retained as protein and energy retained as fat:

RE (CN), kJ/d = RPE, kJ/d + RFE, kJ/d

9.3.2. RQ-method

In this method, energy retention is calculated as the difference between the ME intake and the heat production assessed by the RQ-method (calculation of HP (RQ) is presented in section 9.5) as:

RE (RQ), kJ/d = ME, kJ/d – HP (RQ), kJ/d

9.3.3. Comparative slaughter technique

Using this approach, a group of animals are slaughtered before (zero animals) and another group of animals after a dietary intervention (e.g. at 20 and at 90 kg live weight), and the pigs are then minced and analyzed for their content of fat and protein by dividing the body into 6 different portions (blood, hair, internal organs, skin and subcutaneous fat, bones and meat) and analysed for protein (N x 6.25) and fat contents [27].

Initial pools of protein and fat for pigs slaughtered at 90 kg can be predicted from the body composition of zero pigs as:
Initial protein pool = percent of body protein/100 x initial live weight
Initial fat pool = percent of body fat/100 x initial live weight

Energy deposition can then be measured from retained protein and fat as:

RE, MJ/d = [(Final protein pool – Initial protein pool), kg x 23.86 MJ/kg +
(Final fat pool – Initial fat pool), kg x 39.76 MJ/kg] / no. of days

This technique can be applied anywhere.

9.3.4. Deuterium dilution technique

Changes in body composition, i.e. changes in body pools of fat and protein can be estimated using the deuterium dilution technique, which essentially measure the water pool ("D_2O–space") of the sow or piglet [72]. Based on prediction equations developed by Rozeboom et al. [67] the sow body composition can be estimated and if this is done e.g. in early lactation and at weaning, then the sow mobilization of protein and fat in gram/day may be estimated. To do this as accurate as possible, sow live weight (LW) and back fat (BF) also needs to be recorded. For Landrace × Yorkshire gilts, the body pools of protein and fat may be calculated as follows:

Body protein [kg] = 1.3 + 0.103 × LW + 0.092 × D2O space − 0.108 × BF
Body fat [kg] = 7.7 + 0.649 × LW − 0.610 × D2O space + 0.299 × BF

Retention or mobilization of fat and protein may then be calculated as

Retention or mobilisation of protein or fat = Pool at end – pool at start / number of days

9.4. Energy secreted in milk (Lactation energy; LE)

Milk yield may be quantified either by estimating the milk intake of individual piglets as described by Theil et al. [72] or from litter size and litter gain by using the Bayesian

approach as described by Hansen et al. [20]. The reader may also benefit from reading Theil et al. to get a deeper knowledge within sow lactation [77].

Milk energy concentration can be either measured (preferred) or calculated as:
Milk energy, MJ/kg milk = 23.9 x milk protein, % + 39.8 x milk fat, % + 16.5 x milk lactose, %

Milk energy output = Milk energy, MJ/kg milk x milk yield, kg milk/day

9.5. Heat production

The heat production of animals may be measured by four different techniques, namely 1) direct calorimetry, 2) indirect calorimetry according to the RQ method, 3) indirect calorimetry according to the CN method, and the comparative slaughter technique (Figure 20.34).

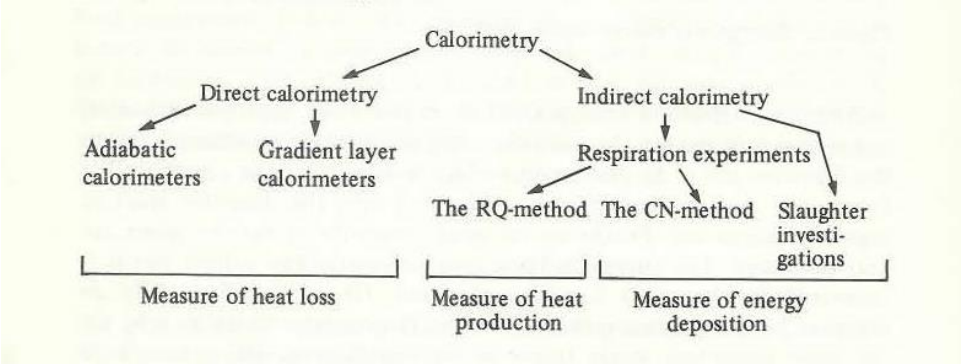


Figure 20.34. Overview of methods to study different aspects of energy components in pig nutrition [27].

9.5.1. Direct calorimetry

The heat loss from the animal due to radiation, convection and conduction may be measured directly by physical methods in specialized chambers. Evaporation losses of heat are measured on the basis of amount of air drawn through the calorimeter and its moisture content on entry and exit [52].

9.5.2. Indirect calorimetry, RQ-method

The animal's heat production is estimated on the basis of its respiratory exchanges, i.e. O_2 consumption, CO_2 production, CH_4 production and nitrogen excretion in the urine. Indirect calorimetry assessed according to the RQ-method quantify the heat production using the following equation [6].

HP (RQ), kJ/d = litres O_2/d x 16.18 + litres CO_2/d x 5.02 - litres CH_4/d x 2.17 - g UN/d x 5.99

An example of the gas exchange and the respiratory quotient recorded every 4th minute from two chambers is shown in Figure 20.35.

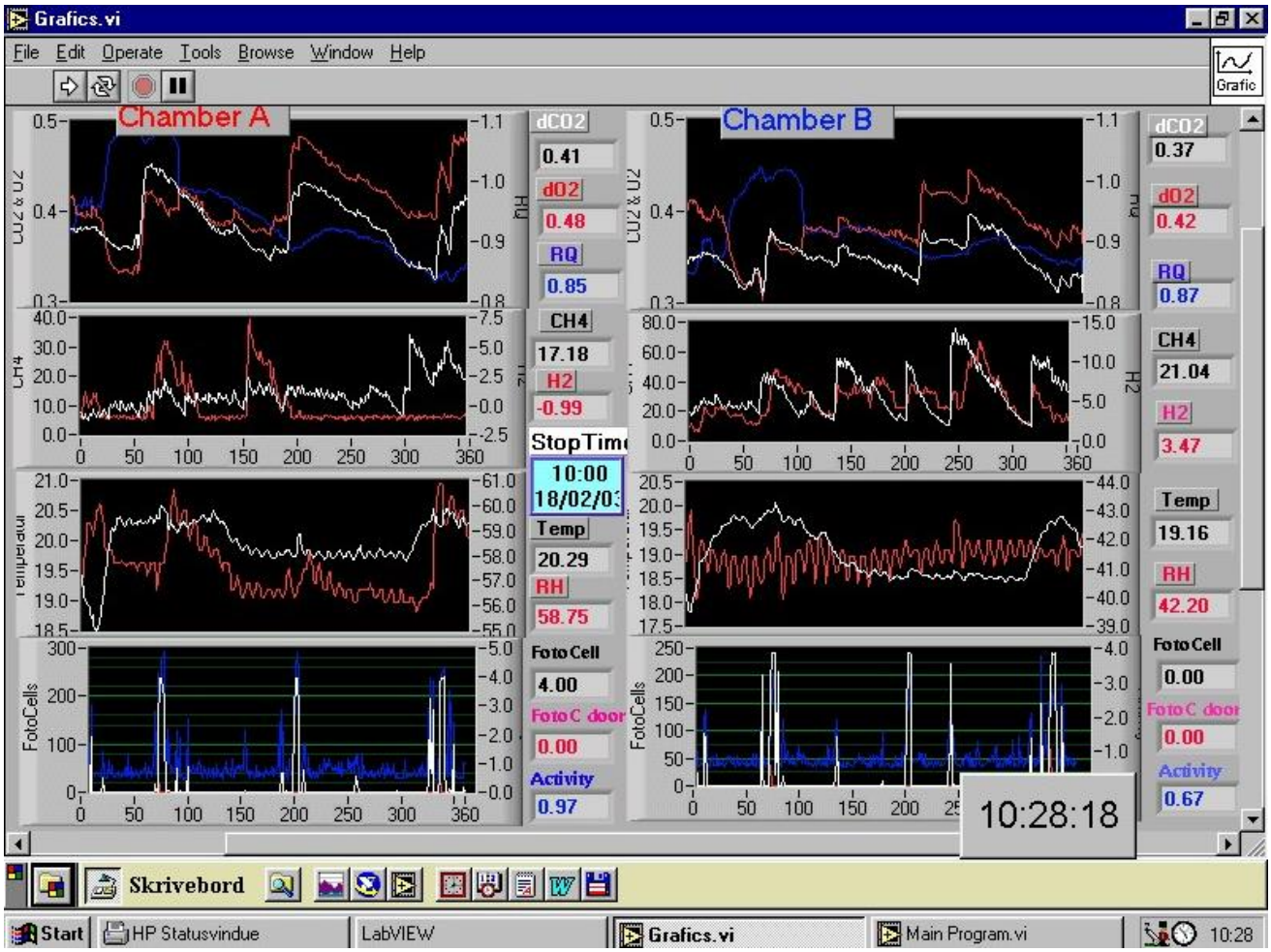


Figure 20.35. Screenshot of the computer program that register gas exchange from animals in respiration chambers (Photo: Henry Jørgensen).

9.5.3. Indirect calorimetry, CN-method

In the CN-method, heat production can be estimated as the difference between the ME intake and the retained energy according to the CN-method [9]:

HP (CN), kJ/d = ME, kJ/d – RE (CN), kJ/d

9.5.4. Comparative slaughter technique

In the comparative slaughter technique, the retained energy is quantified (see section 9.3.3) and then the heat production can be estimated as a difference between ME intake and retained energy [25], [27]:

HP, kJ/d = ME, kJ/d – RE, kJ/d

9.5.5. Other techniques

The heat production can also be estimated by means of mean daily heart rate or estimated by isotope techniques. Common isotope techniques comprise either the doubly labelled water technique [76] or the bicarbonate method. None of these techniques will be described here.

9.5.6. Physical activity

Physical activity may be recorded by means of a photocell, if pigs and sows are confined in a metabolic chamber (Figure 20.36). This give only an either/or signal, that is, either the animal is lying or standing, whereas sitting is recorded as standing. Alternative, infrared sensors can be used to detect a graded signal. Outdoor, physical activity may be recorded by e.g. GPS trackers.

Figure 20.36. Physical activity may be recorded by a photo cell (visible left to the monitor). Infrared sensors were also recording the physical activity of the animals in the respiration chambers to record graded signals. Note that the door is only open to show the experimental setup, whereas the door had to be tightly closed during respiration trials (Photo: Henry Jørgensen).

9.5.7. Carbon and energy metabolism in selected organs

Uptake of energy metabolites from the gastro intestinal tract and liver metabolism of nutrients may be quantified with the multicatheterised sow model shown schematically in Figure 20.37. Moreover, the gas exchange may also be recorded, which allow estimation of the heat production of these organs. To do this, it is necessary to continuously infuse a

blood flow marker during an 8-h sampling period while blood samples are collected once per hour. Gas exchange may be quantified by measuring the concentrations of O_2 and CO_2 in whole blood immediately after blood collection, whereas plasma is harvested and stored in a freezer for later analysis of plasma metabolites like glucose, lactate, non-esterified fatty acids, triglycerides and urea.

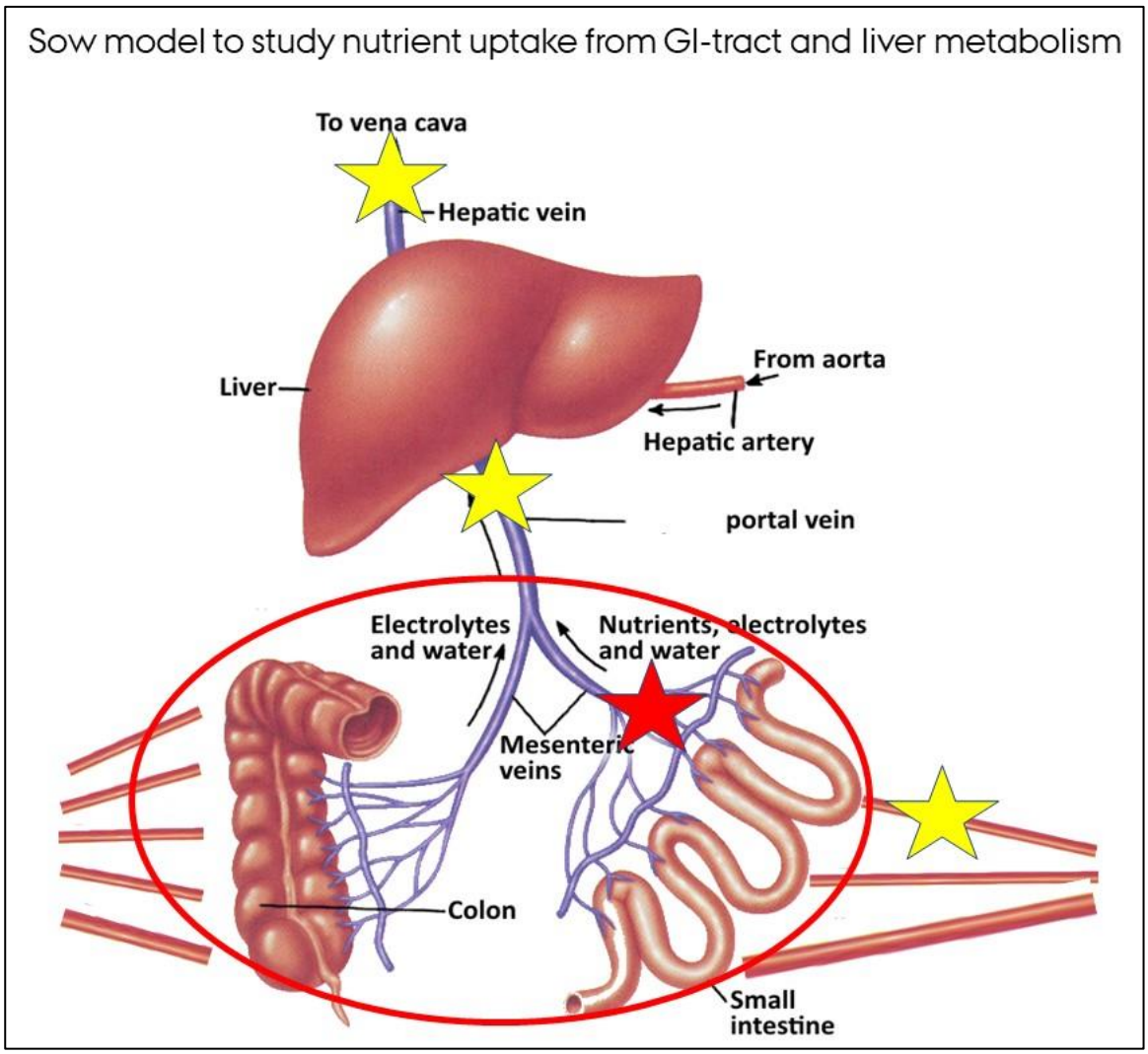


Figure 20.37. Multicatheterised sow model to quantify nutrient uptake from the gastrointestinal tract (GI-tract) and liver metabolism of macro nutrient metabolites and gas exchange. Stars illustrate where permanent catheters were inserted, the red start represent an infusion catheter for infusion, whereas the yellow starts represent catheters for blood sampling. Inserted photos show collection and handling of blood samples and experimental sows right after feed was supplied. Photos: Søren Tobberup Hansen (left), Peter Kappel Theil (middle and right).

Similar studies may be carried out with another sow model, where permanent catheters are inserted into an artery and into the mammary vein for sampling and a third catheter for infusing the blood flow marker (Figure 20.38). Again, energy utilization may be quantified by quantifying the blood flow and the arterio-venous concentration differences of plasma metabolites and whole blood concentrations of blood gas. Another way of quantifying the energy metabolism and energy balance (retention or mobilisation) is by characterising the carbon input and output and carbon balance of e.g. the mammary gland (Figure 20.39), because the energy concentration is almost constant per mol of carbon (previously shown in Figure 20.5). To estimate this balance, it is necessary also to estimate milk yield and milk composition [49].

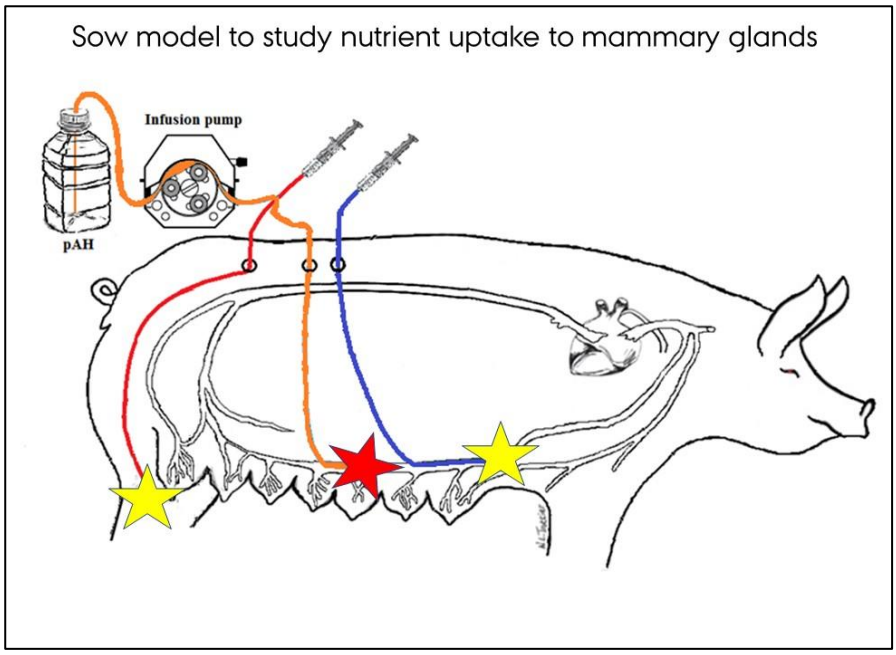


Figure 20.38. Multicatheterised sow model to quantify nutrient uptake and gas exchange to the mammary glands. Stars illustrate where permanent catheters were inserted, the red start represent an infusion catheter for infusion, whereas the yellow starts represent catheters for blood sampling.

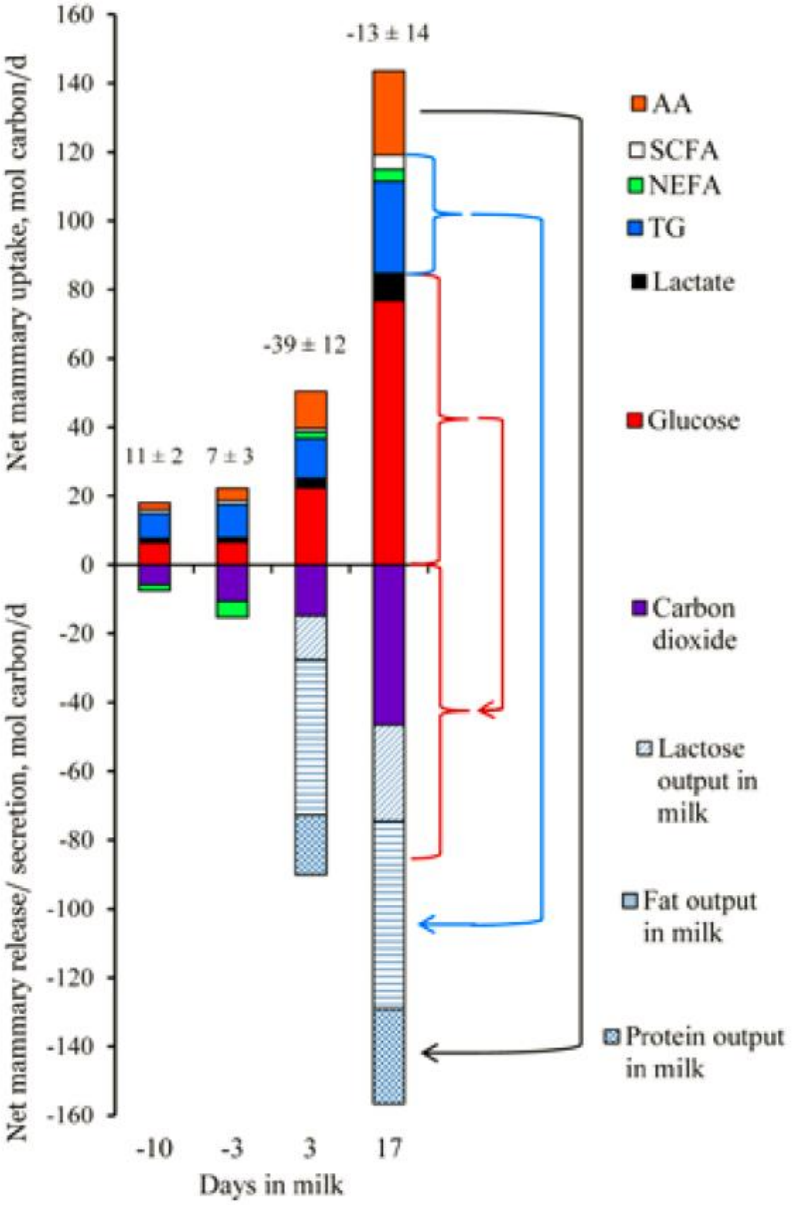


Figure 20.39. Net mammary input of carbon (positive values; mol C/d) from plasma metabolites and net mammary output of carbon (negative values; mol C/d) to plasma (negative net flux) or to milk (fat, lactose, and protein) during late gestation and lactation (−10, −3, 3, and 17 d in milk). Mammary carbon balance (input − output) ± SEM on different days in milk are indicated above the bars. The arrows indicate how plasma precursors in plasma are utilized for milk synthesis at peak lactation [49].

9.5.8. Whole animal heat production using a factorial approach

Heat production due to maintenance can be estimated according to NRC [57], [57] as:

Growing pigs: MJ/d = 0.44 × LW, $kg^{o.75}$

Pregnant sows: MJ/d = 0.420 × LW, $kg^{o.75}$

Lactating sows: MJ/d = 0.460 × LW, $kg^{o.75}$

Heat production (heat increment) due to milk production may be calculated by assuming an efficiency of using ME for milk production, k_l, of 0.78 [75].
Heat increment due to milk production = (milk energy output/0.78) – milk energy output.

Heat production (heat increment) due to growth (i.e. fat and protein retention) may be calculated by assuming an efficiency of using ME for growth, k_g, of 0.72 [69].

The total heat production may then be estimated by summing the individual contributions [16].

9.6. Oxidation of nutrients (substrate oxidation)

The total heat production may be studied in further details by investigating which nutrients (substrates) are being oxidised, and oxidised protein, carbohydrate and fat sum up to the total heat production. Thus, based on the gas exchange and N excretion in urine (UN), oxidation of protein (OXP), carbohydrate (OXCHO) and fat (OXF) and the non-protein respiratory quotient (RQnp) may be calculated according to Chwalibog et al. [10]:

$$OXP, kJ = UN, g \times 6.25 \times 18.42 kJ/g$$

$$OXCHO, kJ = (-2.968 \times O_2,L + 4.174 \times CO_2,L – 2.446 \times UN, g) \times 39.76 kJ/g$$

$$OXF, kJ = (1.719 \times O_2,L – 1.719 \times CO_2,L – 1.963 \times UN, g) \times 39.76 kJ/g$$

$$RQnp = (CO_2, L – (UN, g \times 0.774) / (O_2, L – (UN, g \times 0.957)$$

9.7. Overview of methods and recent advances

Digestibility trials has been and is still widely used to study the digestibility of raw materials. Today, focus is given not only to the animal but also to minimise the environmental impact, and increasing the digestibility is an efficient way of minimising that. Quantification of urine is not carried out to a great extent, partly due to practical challenges and likely also because only a minor amount of energy is lost through urine. However, when focusing on protein and nitrogen metabolism, between 15 and 30% of the nitrogen is secreted through urine, and this aspect deserves more attention, although not from an energetic perspective. Heat production of pigs has been studied to some extent, but considering that the majority of the energy is lost through heat, this area deserves much more attention. This technique require specialised equipment and skilled personnel to run

such trials. Since 2000, many respiration facilities has been torn down, but recently new research groups are building new facilities and hopefully this research area will receive some attention in the future, because heat production is important to minimise in order to maximise feed efficiency of pigs and sows. Physical activity has a great impact on the heat production, but this has not received much attention, partly because pigs and sows are confined. However, for organic pigs housed outdoor, and for gestating sows housed in groups, physical activity certainly plays a role. The comparative slaughter technique was used extensively many years ago, but not much recently. Today, the deuterium dilution technique or dexa scanning become increasingly popular, because repeated measurements on individual pigs can be performed. Energy secretion through colostrum and milk has been studied intensely in Denmark during the last decade, and is today fairly simple to do even in practical herds after prediction models were developed to estimate the yield of sow colostrum [78] and sow milk [20]. Isotope techniques are rather expensive and mainly used for laboratory animals like mouse and rats. During the last 10 years, advanced studies involving multicatheter techniques has been developed, which allow quantification of gas exchange and net uptake and release of energy metabolites across central organs like the gastrointestinal tract, liver and mammary glands [18], [23], [49].

10. Feeding strategies and practical implications

In practical pig feeding, the dietary content used are per kg of feed, not per kg of dry matter. Typical pig diets contain 130 to 175 g fibre per kg, lowest in lowest in diets for weaners and growing pigs and highest in sow gestation diets. Typical fat content range within 25 to 55 g fat per kg, with the lowest concentration in grower-finishing diets and highest concentration in lactation diets, but it may be even higher in feed supplement to suckling piglets where as much as 85 g per kg may be used. Dietary protein is within 100 to 200 g protein per kg for all classes of pigs, lowest in gestation diets, intermediate in lactation diets and highest protein concentration in weaner diets. The ash content vary only slightly from 35 to 55 g per kg across all pig diets. With respect to energy, typical pig diets range within 16-17 MJ GE per kg, 12-14 MJ DE per kg, 11.5-13.5 MJ ME per kg, 7.0-9.3 MJ NE per kg, 90-120 FUpig per kg, and 90-120 FUsow per kg of feed.

Feed intake is the most important aspect for performance and feed efficiency of pigs (sometimes referred to as the first law of nutrition), and the reason is that more feed is

equivalent to more energy. Indeed, the most important parameter to consider is likely the feed intake relative to maintenance (or fold above maintenance). Feeding curves are highly important, because all nutrient recommendations (e.g. gram standardised ileal digestible amino acids) are expressed per energy unit, and in Denmark it is expressed per feed unit (FUpig or FUsow). The animal requirements for nutrients are defined per day, and they have to be met by the energy intake (FUpig/day or FUsow/day) and the nutrient recommendations. As an example, the daily supply of lysine (in gram standardised ileal digestible lysine per day is determined as amount of feed (in FUpig/day) multiplied by dietary concentration of standardised ileal digestible lysine/FUpig. Thus, the recommended feeding curve along with the nutrient recommendations together ensure that pigs are fed properly. In the following, up to date Danish feed curves are presented for growing pigs and gilts (in FUpig/day) and for pregnant and lactating sows (in FUsow/day).

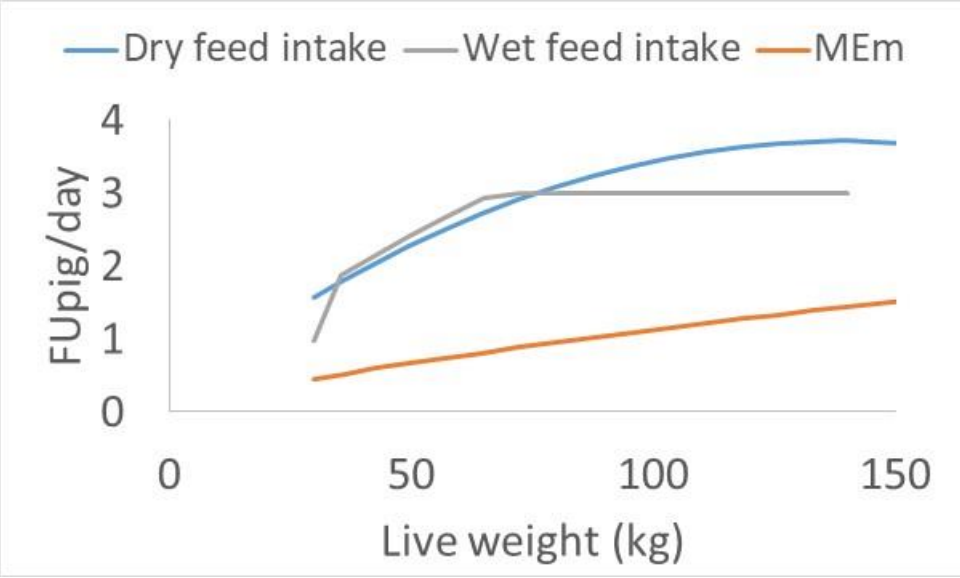


Figure 20.40. Feed curve for growing pigs fed either dry feed or wet feed (based on practical experience, E. Vils and P. Tybirk (unpublished)). The amount of feed used for maintenance (MEm) during the growing finishing period is presented to illustrate that pigs at 30 kg are fed approximately 3.4-fold above maintenance and at slaughter (113 kg) they are fed 2.9-fold above maintenance.

In herds with wet feeding systems, pigs are fed ad lib until approximately 65 kg, where after they are fed restrictedly (Figure 20.40), in order to prevent excessive fat retention and insufficient meat percentage at slaughter. In contrast, herds that use dry feed supply feed ad libitum up until slaughter. It would be better to use restricted feeding

above 65 kg, but the feeding systems do typically not allow this, which compromises the lean meat percentage at slaughter.

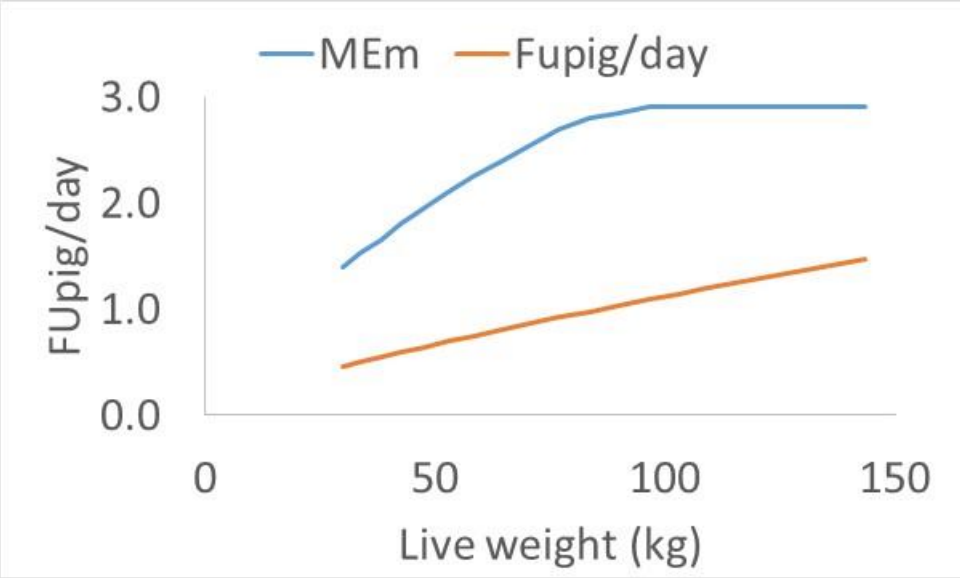


Figure 20.41. Feed curve for growing gilts. The amount of feed (in FUpig/day) used for maintenance (MEm) during the growing finishing period is presented to illustrate that growing gilts at 30 kg are fed approximately 3.1-fold above maintenance and at 113 kg they are fed 2.4-fold above maintenance (Reference: https://svineproduktion.dk/Viden/I-stalden/Foder/Udfodring/Polte accessed 15 JAN 2020) .

Growing gilts are fed restrictedly, and the amount corresponds to 85 to 90% of their ad lib intake capacity from 30 to 65 kg, where after the feed supply is kept constant (Figure 20.41). Thus, growing gilts are fed constantly around 3-fold above maintenance from 30 kg up until 65 kg, where after it is reduced gradually to 2.0-fold above maintenance at 140 kg of live weight. This strategy is adopted to control the growth rate and ensure that sows do not retain too much protein but concomitantly they need to retain sufficient amounts of fat.

Figure 20.42. Feed curve for pregnant sows according to body condition. The energy requirement for maintenance is 1.8 and 2.4 FUsow/day for sows weighing 200 and 300 kg, respectively, (Reference: https://svineproduktion.dk/viden/i-stalden/management/manualer/repro accessed 20 JAN 2020).

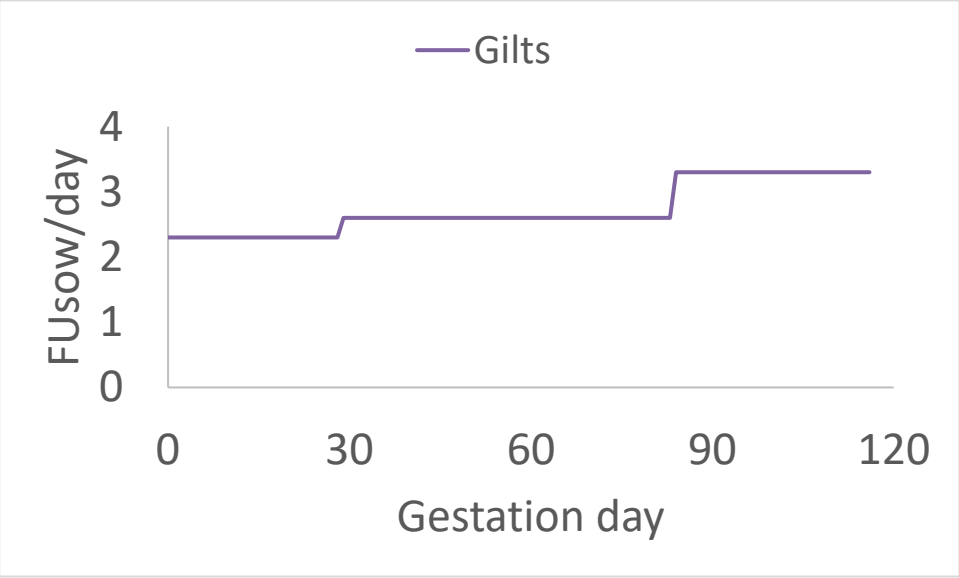


Figure 20.43. Feed curve for pregnant gilts. The energy requirement for maintenance is 1.8 FUsow/day for a gilt weighing 200, (Reference accessed 20 JAN 2029: https://svineproduktion.dk/viden/i-stalden/management/manualer/repro).

Reproductive sows are not fed according to their live weight, which is in contrast to growing pigs. Instead, pregnant sows are fed according to parity and body condition (Lean, recommended, obese), which can be assessed by recording their back-fat depth [81]. The body condition is mainly restored during the first month of gestation, but if sows are too lean after weaning, they may receive extra feed to restore body condition up until

day 83 of gestation (Figure 20.42). First parity pregnant sows have not yet lost body reserves from a preceding lactation period and therefore they are fed less feed in early gestation as compared mid gestation (Figure 20.43), where gilts still need to grow. In late gestation, gilts (3.3 FUsow/day) and sows (3.5 FUsow/day) are fed approximately 1.8 and 1.4-fold above maintenance, in order to ensure adequate supply for reproductive purposes [15].

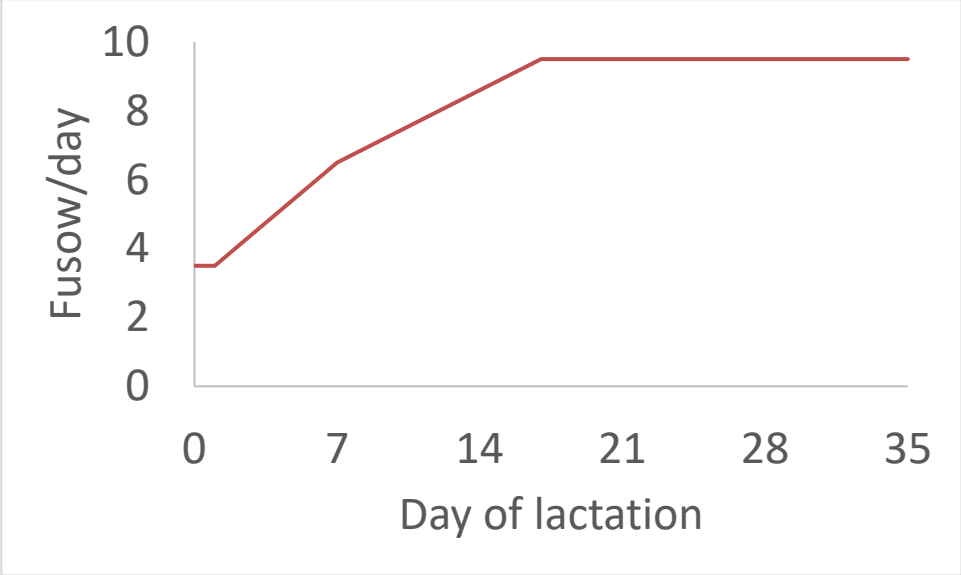


Figure 20.44. Feed curve for lactating sows. The energy requirement for maintenance is 2.0 and 2.7 FUsow/day for sows weighing 200 and 300 kg, respectively.

The feed supply to lactating sows are increased during the first 14 to 17 days until peak lactation is reached (Figure 20.44; (Varmløse Hansen et al. [83]). After that the feed supply is kept constant until weaning. The feed curve is below the energy requirement in early lactation [64], but if sows are fed to heavily after farrowing, they may drop substantially in feed intake. Thus, the recommended feed curve for lactating sows aim to maximize feed intake throughout the lactation period.

10.1. Feed efficiency

A high feed efficiency is important to improve the production economy and to minimise excretion of nutrients to the environment. Feed efficiency may be evaluated as feed conversion ratio (FCR; feed units per kg of gain), or the reciprocal value (G:F; Gain to feed ratio). The advantage of G:F ratio is that a high value is equivalent to a high feed efficiency, whereas for FCR, a low value is equivalent to a high feed efficiency.

Genetically, pigs are selected for a high feed efficiency and each year this trait is improved (Figure 20.45). However, the improvement is also due to improvements in feeding strategies (feed curves) and better knowledge on nutrients recommendations (e.g. gram standardised ileal digestible amino acids per feed unit). Another factor is also important for the feed efficiency, namely the live weight at slaughter. At present, pigs are slaughtered approximately at 113 kg live weight today, whereas typical slaughter weight was approximately 90 kg 50 years ago. This aspect makes is important when comparisons across years, countries and different herds are performed.

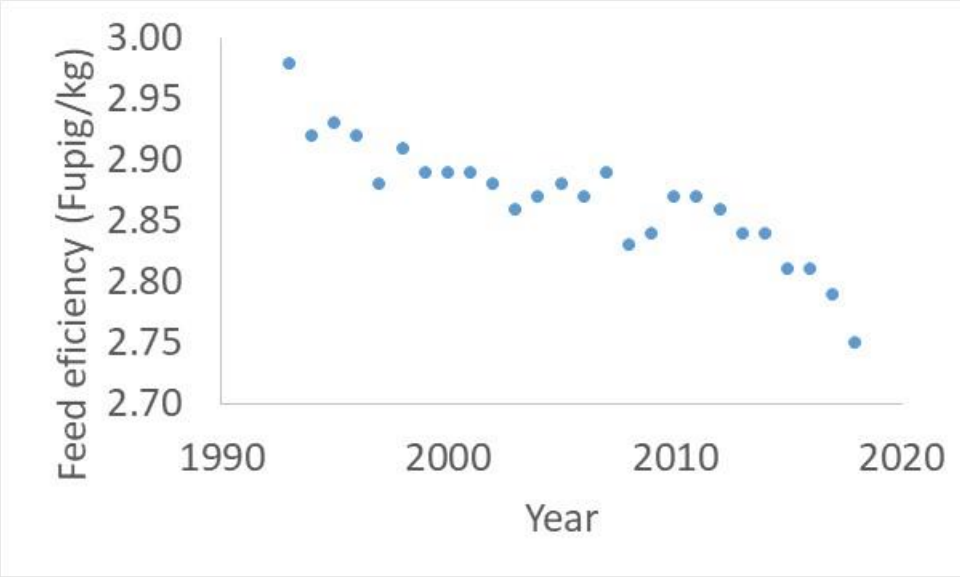


Figure 20.45. Feed efficiency of growing pigs in Denmark from 1993 to 2018.

The feed efficiency decreases as pigs grow (Figures 20.46 and 20.47), indicating that pigs during the growing/finishing period become less efficient in converting feed into growth. Interestingly, while the pigs become less feed efficient as they grow, the pigs become more efficient in retained energy (Table 20.8 showed how the efficiency of retaining energy from ME increased from 37 to 48% during the growing phase). This may seem contradicting, but the explanation is that a high energetic efficiency is favoured by a high fat retention (less heat is lost when fat is retained) and by a high live weight (less heat is produced per kg pig, because heat production is constant per $kg^{0.75}$). In contrast, a high feed efficiency is favoured by a high protein retention and a low live weight (less feed is oxidised for maintenance purposes). As pigs grow, more and more feed are needed day by day to cover the requirement for maintenance energy (MEm) but from 60 kg of live

weight, their fat retention increases substantially [13]. It should be emphasised that protein retention is the major determinant of growth rate of pigs due to 4.2-fold more water being retained [26], [44], [54] and that water contains no energy, whereas growing pigs that retain substantial amounts of fat has converted a lot of starch into de novo fat. Due to these aspects, a high energy retention is not equivalent with a growth rate.

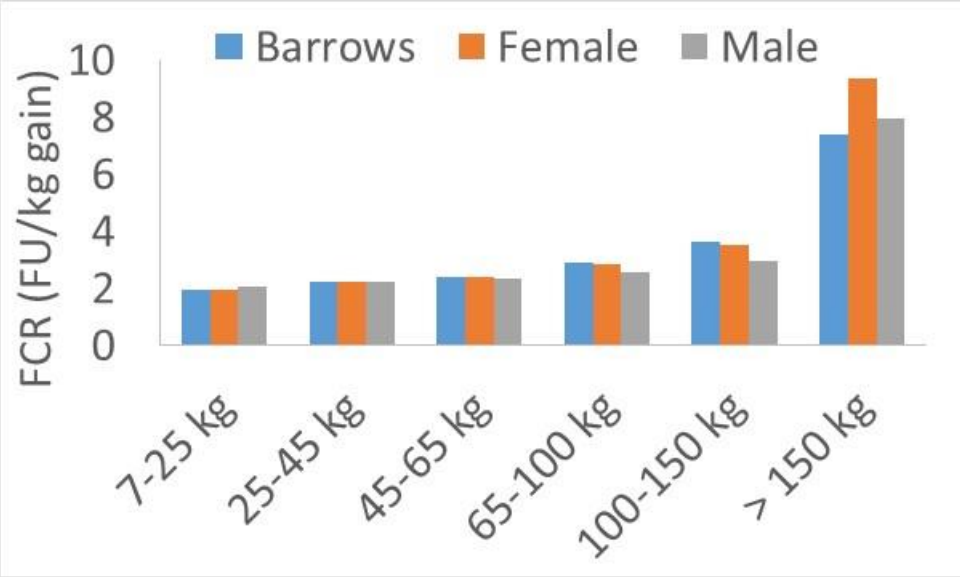


Figure 20.46. Feed efficiency, represented as feed conversion ratio (FCR; FUpig/kg gain) of slaughter pigs (Currently, Danish pigs are slaughtered around 113 kg) (Reference: Jose A. Fernandez and Allan Danfær (unpublished)).

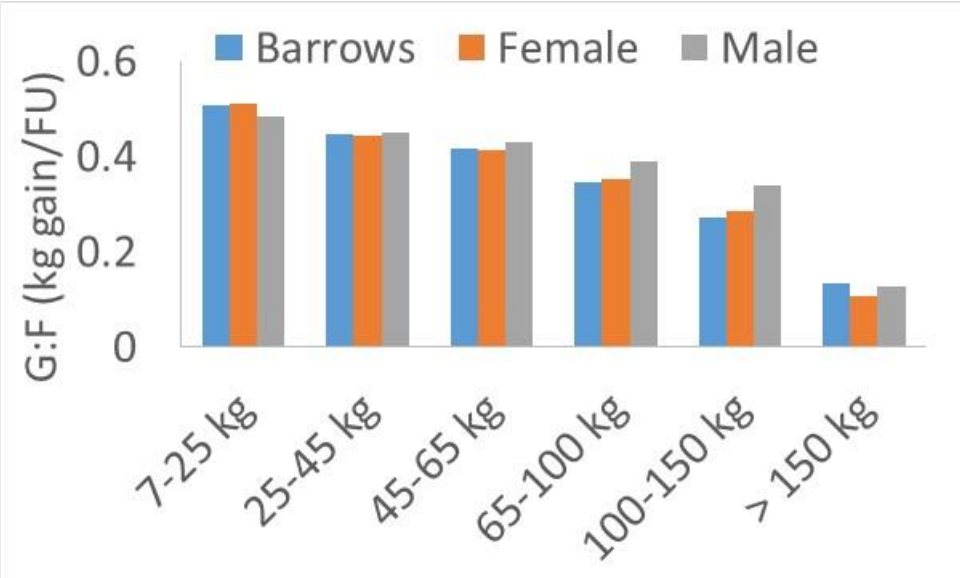


Figure 20.47. Feed efficiency, represented as Gain to feed ratio (G:F; kg gain/ FUpig) of slaughter pigs (Currently, Danish pigs are slaughtered around 113 kg)) (Reference: JA Fernandez and A Danfær (unpublished)).

11. Concluding remarks

Energy is the most important aspect when considering nutrition of pigs. Energy intake determines whether the energy balance is positive or negative, and pigs prioritise utilisation of dietary nutrients depending on their energy balance. The chapter has presented the classical way of measuring dietary energy and the concept of energy being constant in a closed system. According to that concept, energy can neither disappear nor appear, meaning that we should always be able to account for all the energy ingested and metabolised by the animal. Based on empirical data on energy lost in faeces, urine and heat, different energy evaluation systems have been developed and are being used worldwide each day. In Denmark, feed units for pigs (FUpig) and sows (FUsows) are used as the standard for expressing feeding level on a daily basis and nutrient recommendations (e.g. gram SID lysine per feed unit). Proper pig nutrition is ensured daily for millions of growing pigs and 1 million Danish sows by the recommended feeding curve, in feed units per day, and following the Danish recommendations of essential nutrients in the diets, expressed per feed unit.

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