A simulation model to predict the post-digestion nutrient use in monogastric animals

. Kaposvár University, . Institute of Agrifood Research And Technology, . Inra, . University of Newcastle Upon Tyne, . Association Française de Zootechnie, . Topigs Norsvin, . Cobb

FEED-A-GENE

Adapting the feed, the animal and the feeding techniques to improve the efficiency and sustainability of monogastric livestock production systems

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Deliverable D3.3

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1. Summary

<u>Objectives:</u> the objective of the work was to provide the simulation model to predict post-digestive nutrient use in monogastric animals, particularly pigs and poultry. InraPorc was used as the starting point and was extended with an optimization module to calibrate the input parameters according to on-farm data. Different modules have been integrated in the model:

- P-module: simulating the P and Ca metabolism
- FI-module: estimating the feed intake according to environmental conditions (dietary factors, ambient temperature and social environment)
- FA-module: predicting the fatty acid composition of the body and valuable body parts.

The pig model has been adapted to chicken. The nutrient partitioning model for pigs and chicken simulates the post-digestive utilization of energy and amino acids, as well as the Ca and P metabolism and predicts the growth performance and chemical body composition of the individual animals and birds in time.

<u>Rationale:</u>

There are number of models predicting energy and protein utilization in pigs and poultry. Despite differences, monogastric species share many similarities in their digestive and metabolic processes. For this reason, there are benefits from developing a common platform that is able to model these processes from a generic perspective, before developing species or system-specific models. A precise and well-defined model for growing animals can be used as a starting point for developing the generic model. For that reason, InraPorc seemed to be sufficient to represent the energy and protein utilization. Considering that the stoichiometry of the underlying metabolic pathways is independent of the species, the common basis and the generic approach seems to be feasible. To be able to initiate the work with InraPorc, the model was reprogrammed in the MATLAB environment that is suitable for extending and improving the model, as well as for further programming both in WP3 and WP4. The results of the simulations of the MATLAB version are identical to that of the InraPorc software. An optimization module on MATLAB was also programmed to be able to calibrate model parameters (animal profile) according to existing databases or farm data. If one has frequent data of feed intake and body weight, an optimization procedure can be run for each individual to identify the phenotypic parameters (PDmean, Precocity, FI50&FI100 and FI1&FI2, in pigs and poultry, respectively) and perform simulation by InraPorc_MATLAB afterwards.

The InraPorc software simulates the utilization of dietary energy and protein in pigs. The amount of ingested feed per day is estimated based on body weight and phenotypic traits. However, it does not take into account that dietary and environmental factors might limit the actual feed intake. InraPorc does not include equations to predict phosphorus (P) metabolism, nor does it predict the fatty acid composition of the body. These issues are included in the model development of the Feed-a-Gene project. Also, the model has been adapted to poultry. For that purpose, new species-specific parameters and equations have been developed.

The feed intake module takes into account the constrains of the amount of feed ingested by the animals. The capacity of gastro-intestinal tract, the environmental temperature, stocking density and the P-supply are considered as the key factors that may limit feed intake. A P-module was introduced to the energy and protein metabolism model predicting the bone and body P retention at different Ca and P supplies. It is a comprehensive description of the underlying mechanism of P utilization in growing and fattening pigs. The input parameters are the nutrient content of the feed, particularly dry matter, dietary Ca and P, as well as Ca and P digestibility. The equations are integrated into InraPorc_MATLAB program that is considered as a starting point for modelling the feed use mechanisms. The P-module presents the distribution of absorbed P and Ca in the body. Absorbed P and Ca are used for maintenance purposes, soft tissue (muscle and backfat), and bone tissue development. Surplus P and Ca are excreted via urine. Retention of P in the body is the sum of P retention in soft and bone tissues. Thus, the model is able to predict P-retention, urinary P excretion and digestible P requirement of swine at different body weights and upon different P supplies. The fatty acid composition is predicted based on ingested dietary fatty acids. The model accounts for the *de novo* fatty acid synthesis and for the main fatty acid metabolic transactions and simulates the fatty acid composition of the deposited fat tissues in different parts of the pig body.

The pig model represents the nutrient partitioning with a generic approach, thus the core of the model was able to be used for simulating the underlying mechanism of growth in poultry. Modules simulating the energy and amino acid metabolism, as well as the bone mineralization have been modified by using poultry specific parameters taken directly or calculated from the literature. In case of feather production, new equations have been integrated in the model. The poultry model also contains a more detailed feed intake module. However, fatty acid composition of the body is not predicted for poultry.

Teams involved:

- KU, IRTA, INRA, UNEW, AFZ, Topigs-Norsvin, Cobb
- contact person on request of the source code: Veronika Halas, halas.veronika@ke.hu

Species and production systems considered:

The model is developed for growing and fattening pigs and for broilers irrespective of the geographical region and is expected to apply across genotypes in various environmental conditions.

2. Introduction

One of the greatest challenges in precision livestock farming is to be able to supply, as precisely as possible, the animal's dietary nutrients according to the requirements. These change as the animal grows. Mathematical models can be a useful tool for that purpose because they allow to represent the animal's response to a given feed or feeding strategy as well as to evaluate the feed in terms of net energy yielding potential in different species and physiological status of farm animals. The main aim of the modelling work (WP3) is to develop a generic model to be used as a common platform to predict nutrient utilisation in pigs and poultry, while accounting for differences that exist among livestock species and production conditions. By transforming the concepts and knowledge into mathematical equations and integrating these in computer programs using simulation-modelling techniques, they are useful tools for the management of commercial units.

The aim of deliverable D3.3 of the workpackage was to provide "A simulation model to predict the post-digestive nutrient use in monogastric animals". This metabolic model will be made available as stand-alone software (part of DSS developed in T3.5) and can also be integrated in on-farm decision support systems (DSS T4.1).

There are number of models predicting energy and protein utilization in pigs and poultry. It was decided that an existing, precise and well-defined model for growing animal ought to be used as a starting point for developing the generic model in the project. For this reason, InraPorc was sufficient for representing the energy and protein utilization. Considering that the stoichiometry of the underlying metabolic pathways is independent of the species (pigs vs poultry) a common basis and generic approach was judged feasible. To be able to initiate the work with InraPorc, the model was translated into the Matlab program environment that is suitable for extending and improving the model, as well as further for programming in WP3 and WP4.

The InraPorc software simulates the utilization of dietary energy and protein in pigs. The amount of ingested feed per day is estimated based on body weight and phenotypic traits. However, it does not take into account that dietary and environmental factors might limit the actual feed intake. InraPorc does not include equations to predict phosphorus (P) metabolism or predict the fatty acid composition of body fat and fat cuts. These issues are included in the model development carried out during the Fee-a-Gene project. Also, the model has been adapted to poultry. For that purpose, new species-specific parameters and equations were developed.

3. Results

The metabolic model simulates the partitioning of digestible nutrients (i.e., amino acids, fatty acids, starch & sugars, VFAs, Ca and P) through intermediary metabolism and predicts the net protein and lipid gain, and performance according to the animals genetic potential (Figure 1). The time scale of the model is 1 day.

Figure 1. Flowchart of the metabolic model
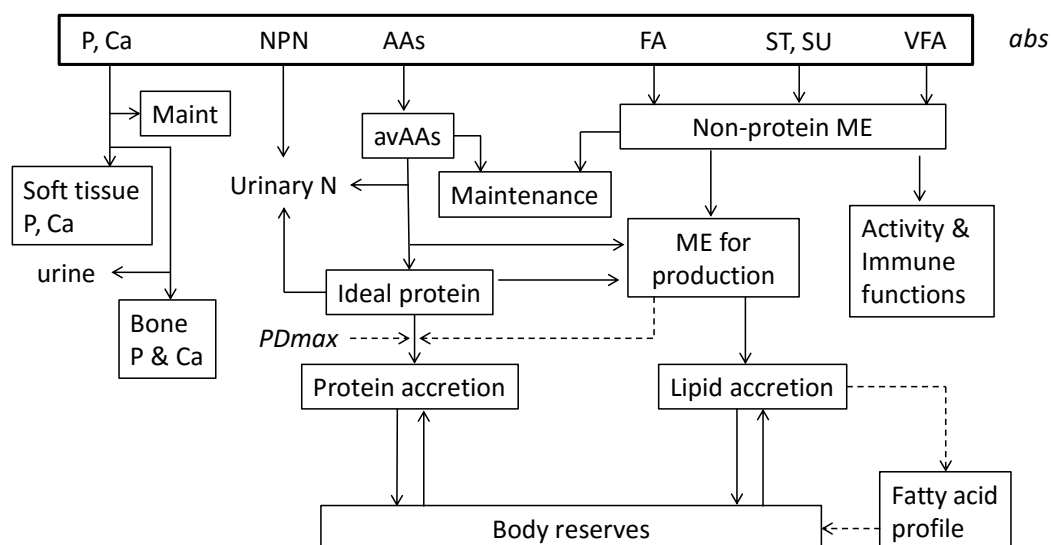
NPN: non protein nitrogen, AAs: amino acids, FA: fatty acids, ST: starch, SU: sugars, VFA: volatile fatty acids, abs: absorbed; ME: metabolizable energy; PDmax: genetically determined maximum protein deposition

The inputs of the model are absorbed nutrients (amino acids: AAs, non-protein nitrogen: NPN, fatty acids: FA, starch and sugars: ST+SU, volatile fatty acids: VFA, calcium and phosphorus: Ca and P) and characteristics of the genotype. For growing and fattening animals, the latter ones are the initial body weight or age, the PDmax (upper limit to protein deposition), precocity, mean protein deposition (meanPD), age or BW at PDmax, and feed intake at certain BW: FI at 50 and 100 kg BW for pigs, or 1 and 2 kg BW for broilers. Furthermore, the digestible nutrient content of the mixed feed is also a model input. Either nutrient content and digestibility coefficients, or digestible nutrient content of the mixed feed can be taken from a separate sheet based on table values (AFZ data are available to calculate the digestible nutrient content of a certain diet). Outputs of the model are body protein and lipid mass, body weight, feed conversion, urinary N and P excretion, as well as retained P. Further outputs of the model used in the context of T4.1 are the expected feed intake (FI), average daily gain (ADG), and the nutrient requirements of the animal for the potential PD and P-retention.

3.1. Metabolic model to predict utilization of dietary protein and energy

The mechanistic-dynamic model simulates the partitioning of digestible nutrients and predicts the protein and fat deposition as well as the chemical body composition at any time point. The energy and protein flows are taken from the InraPorc model (van Milgen et al., 2008). This model was developed for pigs. In the Feed-a-Gene project, the pig model has been adapted for broilers. Therefore, a common core is used for both species, however, species-specific parameters as well as species specific equations have been integrated.

3.1.1. Structure of the model

The actual daily protein deposition is driven by ileal digestible amino acid intake with consideration of their availability. Constraints of the protein deposition are the genetic potential of the animal and the amino acid and energy supplies. The core of the model is a Gompertz function for potential protein deposition (potPD) based on current and mature protein mass, when the animal is fed ad libitum with a high quality feed. The ad libitum feed intake is a function of body weight taking into account the phenotypic traits (see later). Because of the difficulty to estimate mature protein mass in young animals, the Gompertz function was parameterized to include the mean protein deposition during the growing and finishing period (which is strongly related to the growth rate) and a precocity (maturity rate) parameter describing the concave shape of the protein deposition curve.

The potential protein deposition (Potential PD, g/d) of the animal is modelled using a modified version of the Gompertz function:

$$\text{Potential PD} = \text{precocity} \times \text{Prot} \times \ln\left(\frac{P_{\text{maturity}}}{P}\right) \qquad \text{(eq.1)}$$

where Prot is the current animal protein mass (kg), precocity is the shape parameter of the Gompertz function (d^{-1}) and P_{maturity} (kg) is the mature protein mass considered as a technical parameter with little practical meaning. P_{maturity} is calculated based on the expected final protein weight for a certain period (which is calculated from mean protein deposition for that period) as follows:

$$P_{\text{maturity}} = P_{\text{final}} \times (P_{\text{final}}/P_{\text{initial}})^{\exp\left(\frac{-\text{precocity}\times(\text{age}_{\text{final}}-\text{age}_{\text{initial}})}{1-\exp\left(-\text{precocity}\times(\text{age}_{\text{final}}-\text{age}_{\text{initial}})\right)}\right)} \qquad \text{(eq. 2)}$$

The actual daily PD is the minimum of potential PD, PD allowed by energy intake, and PD allowed by amino acid intake. The digestible nutrients yield energy for metabolism and they are used as fuels (energy compounds) or substrates for fat deposition. In the energy flow, digestible nutrients are considered on a NE basis (conversion factors are used to determine the NE supply from each nutrient). The species-specific energy conversion factors are shown in Table 1. Available, PD-free net energy (NE) is first used to support the maintenance need and the energy cost of PD. The remaining NE is then available for lipid deposition (LD). PD and LD determine the (empty) body mass through an allometric function.

Table 1

Specie specific energy conversion factors

Values	InraPorc (growing pig model)				Poultry model according to Carré et al., 2014		
	Coef GE	Coef DE	Coef ME	Coef NE	Coef ME	Coef AMEn	Coef NE
	kJ/g						
Crude fat	38.76	39	39	35.01	38.38	37.77	32.43
Crude protein	22.64	23.31	20.34	12.08	20.60	18.36	14.32
Starch	17.54	17.45	17.45	14.32	17.00	16.67	13.28
Sugars	16.71	16.62	16.62	11.94	13.02	12.52	7.932
Residue	18.58	16.61	15.51	8.64	9.93	9.30	12.71

The following species-specific equations are used in the model:

Maintenance energy requirement

For pigs, the maintenance energy expenditure is defined as the fasting heat production (FHP) depending on partial FHPs related to basal and feed intake dependent FHP plus the energy needs for physical activity.

$$NEm = (NE_{activilty} + \frac{FHP_{init} + FHP_{slope} * NEint}{BW^{0.60}} * k_{BR}) * BW^{0.60} \qquad (eq. 3a)$$

where NEm is the maintenance NE requirement, $NE_{activity}$ is the NE needed for activity (calculated as energy expenditure of 4 hours standing), FHP_{init} and FHP_{slope} are parameters being 436.5 kJ/MBW and 0.1754 kJ/kJ, respectively, NEint is the NE intake before 24h fasting, and k_{BR} is the efficiency of net energy used from body reserves according to van Milgen et al. (2008).

For broilers, the maintenance energy requirement is also expressed on a NE basis. However, due to lack of quantitative relationship between feed intake and FHP as well as precise estimate of energy requirement of activity the following equation is used:

$$NEm = ((FHP_{init} * activity_{level}) + FHP_{init} * k_{BR}) * BW^{0.70} \qquad (eq. 3b)$$

where FHP_{init} is a parameter being 460 kJ/MBW and MBW is considered as $BW^{0.70}$ according to Noblet et al. (2015), $activity_{level}$ is set as 33% extra FHP according to van Milgen et al. (2001).

Obligatory urinary energy loss

Feed-a-Gene

Energy loss via urine consists of obligatory urinary energy loss and the energy from excess protein. The latter one is calculated as:

$$\text{energy loss from excess protein } = \frac{\text{excess protein}}{6.25} * \text{EuN} \qquad \text{(eq. 4)}$$

where EuN (endogenous urinary nitrogen) differs for the species, since mammals excrete N mainly as urea, while birds excrete uric acid. EuN is set to be 31.1 kJ/g in pigs (van Milgen et al., 2008) and 33.97 kJ/g in poultry (Lim et al., 1986; Koh et al., 1992).

In pigs, the obligatory urinary energy loss is calculated based as a power function of BW according to an empirical equation from van Milgen et al. (2008):

$$\text{obligatory urinary energy loss } = 168 * \text{BW}^{0.175} \qquad \text{(eq. 5a)}$$

However, in poultry the obligatory urinary energy loss is related to the fasting heat production according to Koh et al. (1992):

$$\text{obligatory urinary energy loss } = \text{FHP} * 0.00275 * \text{EuN} \qquad \text{(eq. 5b)}$$

The equation shows that each kJ FHP is accompanied by 2.75 mg EuN excretion.

Maintenance protein requirement

The faecal endogenous protein and amino acid losses are functions of dry matter intake in both species. However, the values are different for pigs and poultry. Obligatory urinary endogenous amino acids are identical in the pig and poultry model and these losses are calculated on a metabolic body weigh basis. As part of maintenance, there are integument amino acid losses in the pig model and feather losses in the poultry model (see later).

Feed intake function

The ad libitum feed intake (FI) is estimated as a function of body mass (BW, kg) taking into account certain phenotypic traits:

According to Vautier et al. (2011) and van Milgen et al (2015) the so-called Gamma function of maintenance estimates FI the most precisely on a long-term basis:

$$\text{FI } = (a \times (b \times \text{BW} \times \exp(-b \times \text{BW})) + 1) \times c \times \text{BW}^{d} \qquad \text{(eq.6)}$$

The Gamma function is based on the premise that adults eats for maintenance (or that the maintenance energy expenditure equals the energy intake). The Gamma function thus indicates that as BW increases, the animal eats for c x MBW. The value of "c" depends on how energy is expressed (on a NE, ME, DE or even on a feed weight basis) and thus value of c is considered constant for a given mode of expression (e.g. it is 0.75 and 0.8 MJ/kg MBW/d when expressed on a NE basis in pigs and poultry according to van Milgen et al., 2008 and Carré et al., 2014, respectively). The superscript of "d" is a species-specific parameter being 0.6 for pigs (van Milgen et al., 2008) and 0.7 for poultry (Noblet et al., 2015).

Feather development

Feather protein might represent up to 30% of total body protein (Griminger, 1986). Therefore, the protein and particularly the amino acid requirement of feather production has to be taken into account when the pig model is adapted to poultry. It is assumed that the feather growth has priority over the tissue growth, thus it can be considered as an obligatory protein flow (Meda et al., 2015). The feather weight is an allometric function of empty feather-free body weight (EFFBW) and the feather protein mass (featherW) is an allometric function of the feather mass (Gonçalves and Sakomura, 2017). The amino acid composition of feather protein differs from body proteins and contain a relatively high proportion of sulphur amino acids (mainly Cys) and non-essential amino acids. In the model, the amino acid composition of the body and feather protein is set according to Stilborn et al. (1997, 2010) and presumed to be standard for different strains of birds.

$$\text{featherW} = a\_feather * \text{EFFBW}^{\text{b\_feather}} \qquad \text{(eq. 7)}$$

$$\text{feather protein} = a_{fProt} * featherW^{\text{b\_fProt}} \qquad \text{(eq. 8)}$$

The above-mentioned allometric equations describe the feather mass (g) and the feather protein mass (g). The loss of feathers is part of maintenance need and it is a conditional function of age and depends on sex according to Fischer et al. (1981). It is assumed that no feather loss appears before 4 weeks of age, and which feather loss is an allometric function of age.

There are five "free" parameters that can be obtained from the data and modified by the user. All other parameters are assumed constant. The parameters that can be estimated to represent the genotype are three parameters of the growth equation, namely the initial BW (which is used to estimate the initial protein mass $P_{initial}$), Precocity (the shape parameter of Gompertz equation for PD) and mean PD (general potential for protein deposition, which is used to calculate P_{final} and subsequently $P_{maturity}$). Two additional parameters that can be estimated are the parameters "a" and "b" for the feed intake equation.

3.1.2. Model simulation

As mentioned above, the metabolic model predicts the growth performance as well as the chemical body composition of a pig or a broiler over time from dietary inputs. The model has been challenged and, as an example, 4 different scenarios are shown. The feeding strategy is the same in all simulations (Table 2) as well as initial BW (44 g), FI at 1 and 2 kg BW (1.2 - 1.9 MJ/d), and the duration of the simulation (42 days). In this in silico broiler study, 3-phase-feeding is used with two different genetic potential strains differing in precocity (0.04 vs. 0.05) or meanPD (9 vs 14 g/d). The results of the simulations are shown in Figure 2 and 3.

Table 2

Model inputs in the simulation

	Phases		
	0-14 d	15-28 d	29-42 d
AMEn (MJ/kg)	13.00	13.00	13.00
CP (%)	24	22	19
dig Lys (%)	1.56	1.33	1.14
dig Met (%)	0.55	0.47	0.40
dig Thr (%)	0.90	0.80	0.71

The first simulation shows the broiler response in terms of protein and lipid deposition if precocity is different (Figure 2). The output of the simulation stresses that by changing the precocity value, the diet can be limiting for the birds. In case of a higher precocity value (i.e., when the animal is early-maturing), the animal has a more rapid growth rate at the early ages, and the starter diet used in the present simulation was not sufficient to supply enough amino acids for this bird of high genetic potential. The figure emphasizes that the fat deposition and, consequently, the fat content of the body is higher at the slaughter age if the bird is early-maturing. This is a consequence of the approach that fat deposition is an "energy sink" in the model.

Figure 2. Predicted daily protein and lipid deposition with three-phase-feeding when meanPD is set as 11 g/d and precocity is 0.040 and 0.050 shown on the left and right sides, respectively (Dukhta et al., 2018)
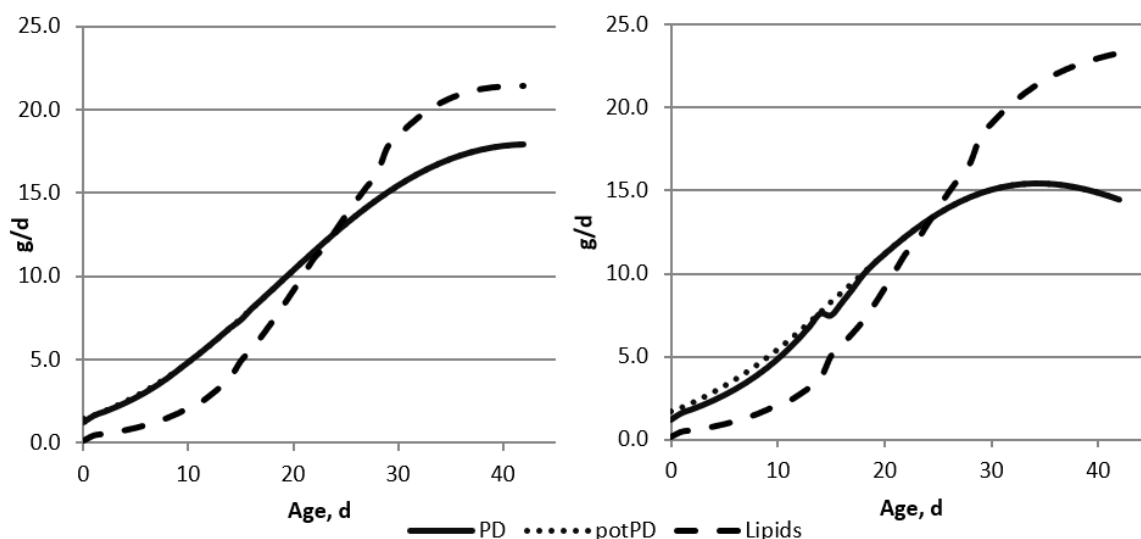

Figure 3 shows the model output if the precocity value is fixed (0.040) and the meanPD is changed from 9 to 14 g/d. The feeding regime is the same as in the earlier simulation (three-phase-feeding). Based on comparison of the scenarios, it can be concluded that the diet was

limiting for the birds having a high meanPD throughout the growing and finishing periods. Protein deposition requires a considerable amount of energy and thus in high genetic potential birds (high mean PD), the energy remaining for lipid deposition was lower compared to the bird of low genetic potential.

Figure 3. Predicted daily protein and lipid deposition with three-phase-feeding when precocity parameter is fixed (0.040) and meanPD is different being 9 and 14 g/d on the left and right sides, respectively (Dukhta et al., 2018)
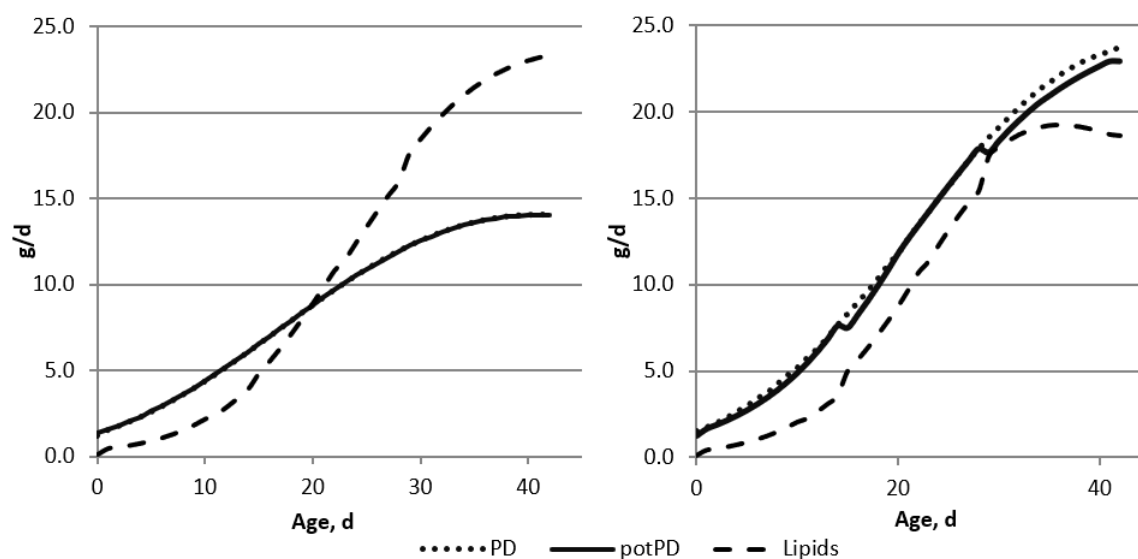
Currently the user-defined input parameters to characterise the phenotype can be estimated from measured data, using an optimization processes (i.e., invert modelling) to obtain best fit of simulated data to the real data. This is done using feed intake and growth data (with indication on feed allowance and feed composition) to determine a posteriori the parameters for the period concerned.

## 3.2. P-module predicting phosphorus utilization and requirement

The InraPorc model does not simulate the P metabolism of the pig. However, there is evidence that a long-term P deficiency reduces the growth rate of animals, while an oversupply results in a high rate of P excretion that is critical from an environmental point of view. Modelling P metabolism allows to improve our understanding on the main factors affecting the P requirement, which has practical importance both from an economic and ecological point of view. Therefore, in the Feed-a-Gene project, it was aimed 1) to develop a model predicting the dynamics of P partitioning and retention in growing and fattening pigs over time; 2) to integrate it into the basic model that represents the energy and protein metabolism and 3) to adapt the P-model for broilers.

3.2.1. Structure of the model

The P-module represents the main fluxes of bone mineralization in terms of Ca and P accretion. Input parameters are related to the diet and include dry matter, the Ca and P content of the feed, the Ca and P digestibility, and to animal traits such as daily feed intake, and protein and fat deposition rates. The model output is the retained P and the digestible P requirement.

The flowchart of the model is shown in Figure 4. The absorbed P is used for maintenance purposes, for soft tissue development as a compound of cell membranes, buffers, energy mediators (ATP, ADP, etc.), and other specific P-containing metabolites, and for bone tissue formation as hydroxyapatite. The efficiency of P utilization is assumed to be 100% for maintenance and 94% for retention (Symeau et al., 2014) irrespective of target tissue such as soft or bone tissue accretion. The surplus P that cannot be retained and the inefficient proportion of P in retention processes is excreted via urine. Urinary endogenous P (part of maintenance) is reported to be 1 mg/kg BW (Jongbloed et al., 2003) in pigs and it is also used for broilers in the model.

Figure 4
Schematic representation of P and Ca fluxes in the model
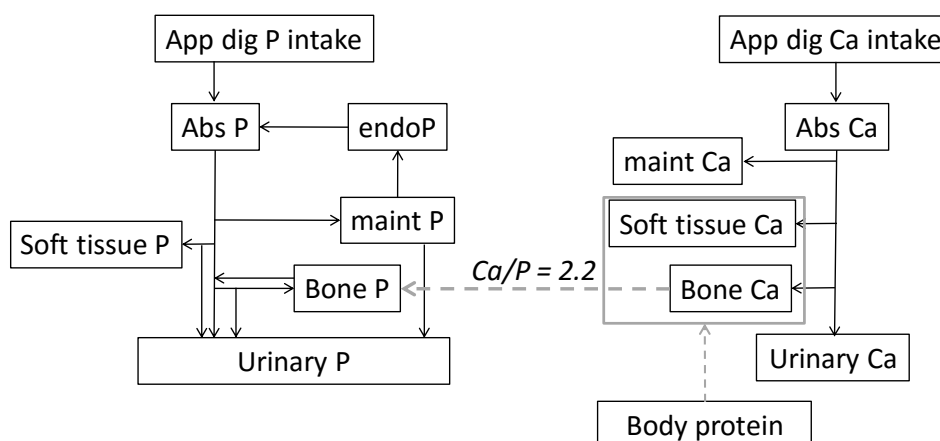
The maintenance P contains the need for recovery of faecal endogenous P loss and obligatory urinary P excretion, and feather P accretion in birds. The endogenous (gut) loss is a function of dry matter intake, while the obligatory urinary P is a function of body mass. Most body Ca and P is located in the skeleton, and the skeleton is also used as a reservoir for these minerals.

The Ca and P content of bone ash is relatively constant (36-39% for Ca and 17-19% for P), so for simplicity reasons, the Ca and P content of bones was assumed to be 37.5% and 18% of ash, respectively. The Ca/P ratio in the bone tissue was set to 2.2, presuming that all Ca and P is present in the form hydroxyapatite ($Ca_{10}(PO_4)_6$). The Ca pool of the body is the skeleton, considering that 99% of the whole body Ca is in bones. Therefore, in case of Ca flow it is assumed that the absorbed Ca (i.e., that is not excreted by the urine as obligatory Ca loss; urinary endoCa) is available for bone mineral formation.

Symeau et al. (2014) assumed that the Ca/body protein ratio (Ca_prot) is constant and the maximum Ca retention is therefore a function of body protein deposition. Due to the standard Ca/P ratio of bone tissue (2.2 g Ca /g P), the potential bone P mass (g) also depends on protein retention:

$$\text{potBoneP} = potPD * 0.99 * \text{Ca\_prot}/2.2 \quad \text{(eq. 9)}$$

Constraints for bone P retention are the potential PD as an animal trait, available Ca and available P. If dietary factors limit the P-retention in the bone, the priority of P-fluxes might be changed. The skeleton is considered as a reservoir for Ca and P. However, in case of severe P and Ca deficiency, the animal should not mobilize all bone Ca and P reserves otherwise it would compromise the structural function of the skeleton. Therefore, in the model the extent of the P deficiency is represented, and it is defined by the so-called relative bone P deficiency. Relative bone P deficiency is the actual bone P mass (g) as a percentage of the potential bone P mass (g).

In vivo studies confirm that pigs and poultry can mobilize up to 50% of the bone reserves of Ca and P. Therefore, it is assumed that 50% of bone P deficiency is the threshold. In a non-critical bone P status (if relative bone P deficiency < 0.5), the soft tissue has priority over the bone tissue, and the absorbed P above the maintenance needs is used to fulfil the P requirement of soft tissues first and the rest is available for bone formation. The P requirement of soft tissues (muscle and backfat in pigs and muscle and fat pad in broilers) can be derived from the soft tissue accretion multiplied by the P content of the soft tissues. The muscle and the fat mass are calculated by allomertic equations taken from Landgraf et al. (2006) for pigs and from Danishman and Gous (2013) and Zuidhof (2005) for broilers. However, the allometric parameters might be different according to genotype or sex. The parameters of the equations can be changed if one has data for describing the allometric function between empty body weight and muscle and backfat or fat pad mass.

If the relative bone P deficiency is high (> 0.5), the bone tissue has priority over the soft tissues to retain the available P above the maintenance needs. Therefore, the absorbed P minus the obligatory urinary P is then available for bone P formation and the remainder of the P is used for soft tissue development. Moreover, the efficiency of recovery of the bone P pool is depending on the rate of P deficiency. Again, the actual bone P retention is the minimum of bone P retention allowed by available P, available Ca, and maximum bone P retention.

According to the literature, changes in bone tissue are not directly proportional to lean growth. This is considered in the present model by separating the soft and bone tissue P pools and considering the bone P as a reservoir until a certain P status. Studies exploring the P requirement of pigs and poultry show that long-term feeding of a P-deficient diet reduces body weight gain. It is known that a P-deficient diet reduces feed intake. However, the reduction in growth rate is not only due to the lower feed intake. If the absorbed P is insufficient to support the maintenance needs and tissue development, the bone P mass might become critical and below a threshold level, soft tissue is no longer given priority. It is presumed that muscle tissue acts as a reservoir for nutrients, such as amino acids and P. The concentration of P in muscle is constant, therefore the development of muscle tissue must be limited by the available P supply. Therefore, the P-module has a feedback to the basic energy and protein metabolism module by correcting muscle growth if the P supply limits the development of soft tissue (Figure 5).

Figure 5

Integration of the energy and protein metabolism model with the P-module
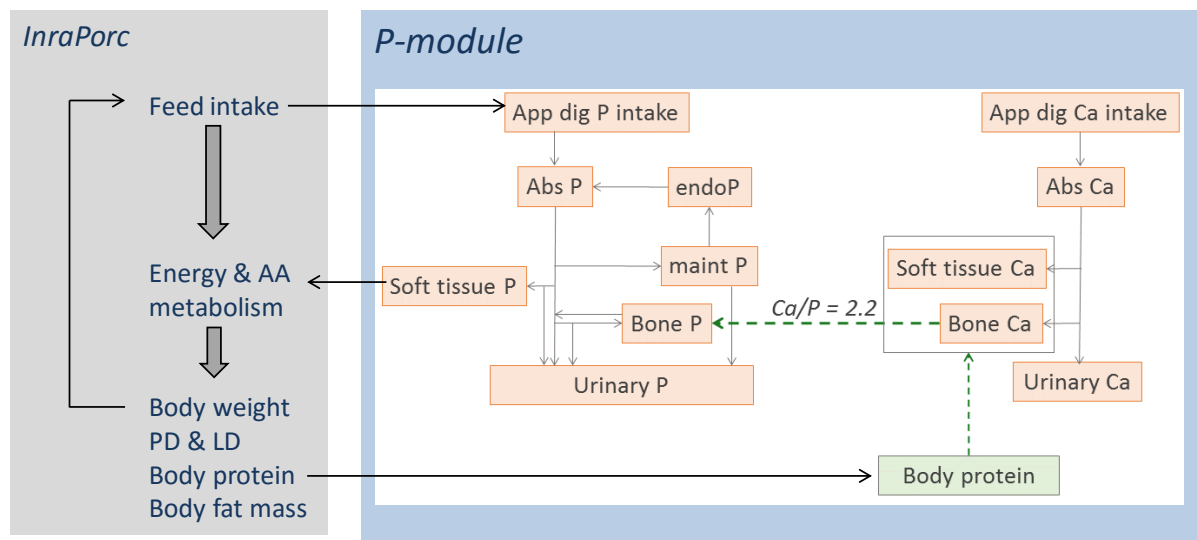
The muscle gain allowed by available P (muscle_gain_avP) is calculated by the following equation:

$$muscle\_gain\_avP = \frac{act\_softP\_ret - BF_{dep} * P\_cont\_fat}{P\_cont\_muscle} \qquad (eq.\ 11)$$

where act_softP_ret is the actual P retention in soft tissues (g/d), BFdep is the gain of backfat in pigs and fat pad in broilers (g/d), P_cont_fat and P_cont_muscle are the P content of fat tissue and muscle tissue (g/g), respectively.

The nutrients (including amino acids and energy) not used for protein deposition due to the difference between the muscle gain allowed by the P supply (muscle_gain_avP) and the muscle gain allowed by the InraPorc based model (driven by energy and amino acid supply and limited by potential PD) are deposited as body lipids. Therefore, in case of a severe P deficiency, the chemical composition of the deposited tissues is changed, and results in a lower body weight gain.

3.2.2. Model simulation

The P module is a useful tool to estimate the P requirement of the animals, and to predict the optimal level of the digestible P in the feed for different strains. An example of a model simulation for broilers is shown in Figure 5. The digestible P requirement is defined as need for digestible P to cover the maintenance P, the potential bone, and the normal (non-limiting) soft tissue P retention. The optimal dietary digestible P content in the diet is calculated relative to the expected (model-derived) feed intake. In the simulation, the feeding regimen is identical

with the earlier example (as shown in Table 2), and two birds differing in growth intensity (precocity is 0.04 vs 0.05) are compared in terms of their digestible P requirement and demand for the digestible P content of the feed. Since the early-maturing birds (precocity = 0.05) deposit more protein and grow more rapidly at the starter phase, they require more digestible P in the starter diet and less P in the finisher diet compared to a late-maturing bird.

Figure 5

Model simulation to estimate the digestible P requirement of broilers (g/d) and the optimal dietary digestible P (g/kg)
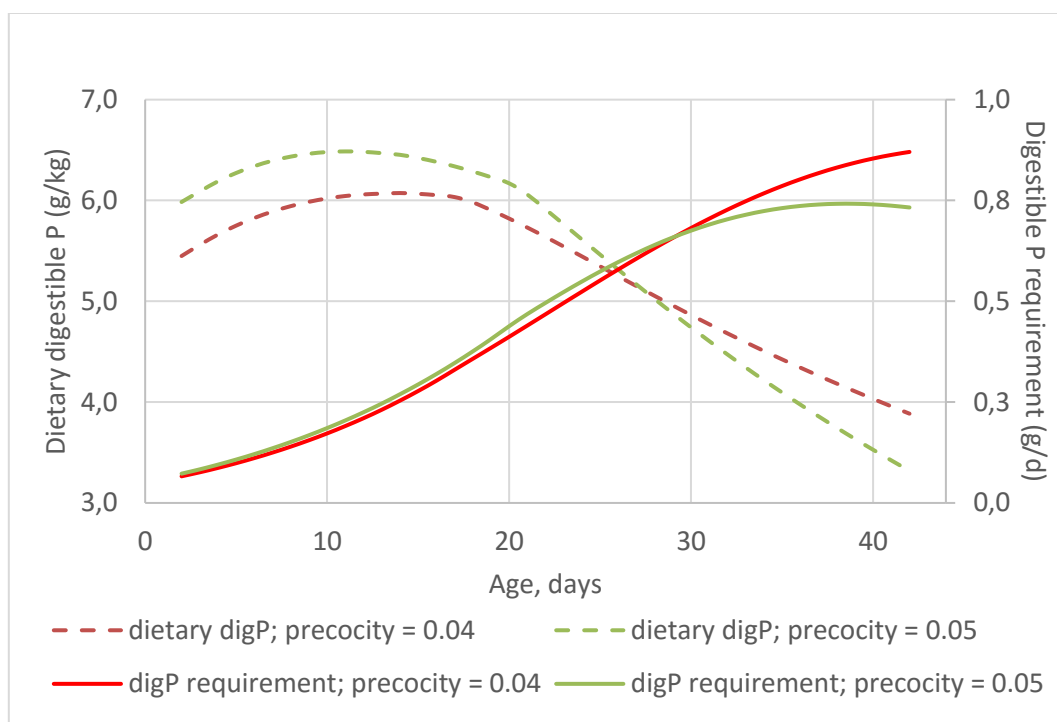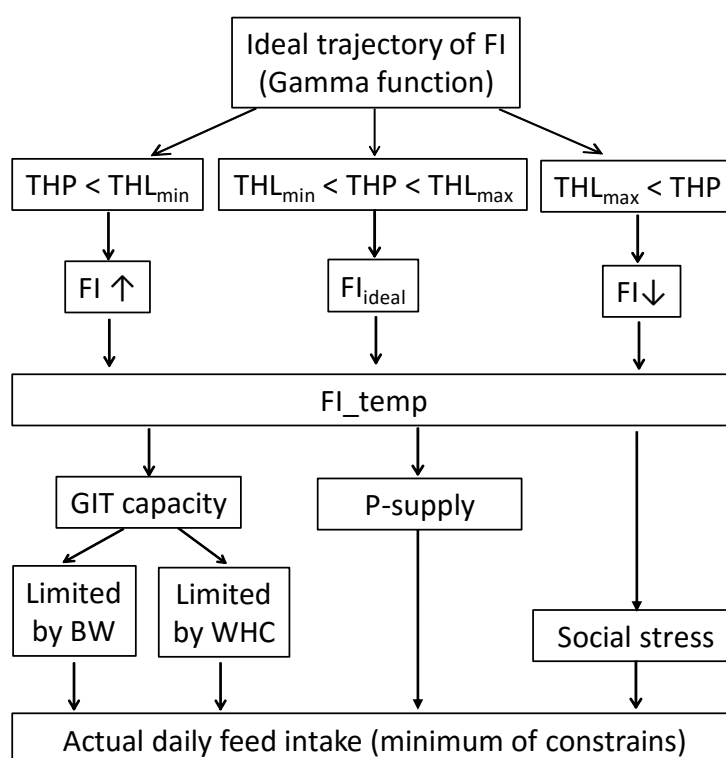
3.3   Feed intake module

In the basic InraPorc model, the amount of ingested feed per day is estimated based on body weight and phenotypic traits. However, it does not consider that dietary and environmental factors might modify the actual feed intake. The developed feed intake module accounts that the following constraints can affect the amount of feed ingested: environmental temperature, capacity of gastro-intestinal tract, stocking density, and P-supply (Figure 6).

Figure 6

Concept of feed intake module

The ambient temperature is one of the major forces modulating the desired feed intake (Black et al., 1986; Emmans, 1987; Quiniou et al., 2001; Prince et al., 1965; Farrell and Swain, 1977; Hurwitz et al., 1980; Howlider and Rose, 1987; Ferket and Gernat, 2006). The animal will try to maintain its body temperature so that its heat production equals its heat loss capacity (HP and HL, respectively). HP is depending on BW and the inefficiency of nutrient conversions of metabolism. Practically it can be calculated by the following equation:

$$HP = MEint - (NE_{PD} + NE_{LD}) \qquad \text{(eq. 10)}$$

where HP is the total heat production (kJ/d), MEint is the metabolizable energy intake (kJ/d), NE_{PD} and NE_{LD} are energy retained as protein and lipid (kJ/d), respectively, all calculated by

the energy and protein metabolism (InraPorc based) model. The HL is a function of BW and environmental conditions (i.e., temperature, humidity, air speed). The representation of the animal's response to these environmental conditions is taken from Ferguson (2006) and Gous et al. (1994). Accordingly, HL consists of sensible and evaporative heat loss (SHL and EHL), where SHL is highest at cold temperatures and decreases with increasing temperature (Reece et al. 1969, Deaton et al. 1969). The EHL is constant for a particular live weight and characterised by minimum and maximum values due to the ability of the animal to store some heat.

Both minimum and maximum EHL (EHLmin and EHLmax; kJ/d) are functions of metabolic body weight in pigs (Ferguson, 2006):

$$\text{EHLmin} = (8 + 0.07 * BW) * 0.0078 * BW^{0.67} \qquad \text{(eq. 11a)}$$

$$\text{EHLmax} = \left((12 + 100 * BW^{-0.33}) * HF * 0.09 * BW^{0.67}\right)/11.568 + \left((45.4 * BW^{-0.13}) * air\_speed^{0.6}\right) * (0.0269 * T^2 + 0.0603 * T + 5.3 - water\ in\ air) * 0.35 * 0.0078 * BW^{0.67}$$
(eq.12a)

where HF is the humidity, T is the temperature (°C), water in air is in g/kg.

According to Emmans (1989), in poultry the minimum evaporative heat loss is estimated to be 20% of the total heat production under thermoneutral conditions (eq. 13), while the EHLmax is constant across all temperatures and is several times greater than EHLmin. The external effects of temperature and ventilation on body heat production is taken from Hauschild et al. (2015) and calculated as follows:

$$\text{EHLmin} = 0.2 * HP \qquad \text{(eq. 11b)}$$

$$\text{EHLmax} = BW * (9.4434 * (Vel - 0.0215) * T) \qquad \text{(eq. 12b)}$$

where Vel is air velocity (m/s) and T is the temperature (°C),

Sensible heat loss (SHL, kJ/d) depends on the temperature gradient between the environmental temperature (T, °C) and the surface of the animal (T_{body}, °C):

$$\text{SHL} = SHL_{slope} * (T_{body} - T) * BW^{0.67} \qquad \text{(eq. 13)}$$

where SHL_{slope} is a rate of heat loss (kJ/°C), which is assumed to be 48 for pig and 33 for poultry (Ferguson, 2006; calculated from data of Farrell and Swain, 1977; respectively).

The minimum and maximum SHL are calculated by taking into account that the body temperature is between 38°C and 40.5°C in pigs and between 41°C and 42°C in poultry (DeShazer et al., 1974; Cooper and Washburn, 1998).

The minimum and maximum total heal loss (MJ/d) is:

$$\text{THLmin} = EHLmin + SHLmin \qquad \text{(eq. 14) and}$$

$$\text{THLmax} = EHLmax + SHLmax \qquad \text{(eq. 15)}$$

The actual FI in the model is changed if the animals are not in thermoneutral conditions. At heat stress, the animals consume less feed to reduce the total heat production. The reduction in FI is identical with the difference between the HP and THLmax (MJ/d).

$$\text{FI}_{\text{heat\_stress}} = \frac{(NEint_{al} - (THP - THLmax))}{NE_{feed}} \qquad \text{(eq. 16)}$$

where $\text{FI}_{\text{heat\_stress}}$ is the feed intake during heat stress (kg/d), NEint_al is the *ad libitum* NE intake, NE_{feed} is the NE content of the feed (MJ/kg).

If the animal is in a cold environment, its HL exceeds the HP. To cope with this situation, feed intake increases to maintain the heat equilibrium. However, in pigs the feed intake can be increased only within certain limits, since the capacity of the gastro-intestine tract (GIT) may limit feed intake. The maximum GIT capacity is given by equation (eq.17) and was proposed by Black et al. (1986). Although new and improved genotypes are used nowadays, it was assumed that the equation is still valid. There are no recent publications showing the physical limit of the feed intake of modern strains in terms of kg/day, since in intensive pig production concentrated diets are fed. However, the animal's response to dietary energy and nutrient dilution may require further attention. The capacity of the GIT depends on BW. However, dietary factors, particularly the so-called water holding capacity (WHC) of the feed has an impact on the actual feed intake. According to Whittemore et al. (2003) and Wellock et al. (2003), the WHC has a negative effect on the feed intake (eq.18). Therefore, to estimate the GIT capacity, two equations are used for pigs:

$$\text{FI}_{\text{GIT}} = \text{if}(T < LCT; \ 0.111 * BW^{0.803}; \ (0.111 * BW^{0.803}) * (1 + (LCT - T) * 0.025))$$
$$\text{(eq.17)}$$

$$\text{FI}_{\text{bulk}} = \frac{0.192 * BW - 0.000299 * BW^2}{WHC} \qquad \text{(eq.18)}$$

It has to be noted that the feed tables usually do not contain information on the WHC. Therefore, eq. 18 can be used only if the WHC of the feed is known.

Figure 7

Simulated actual daily feed intake in pigs upon different ambient temperature (blue line). The dotted line represents the ideal trajectory of feed intake.
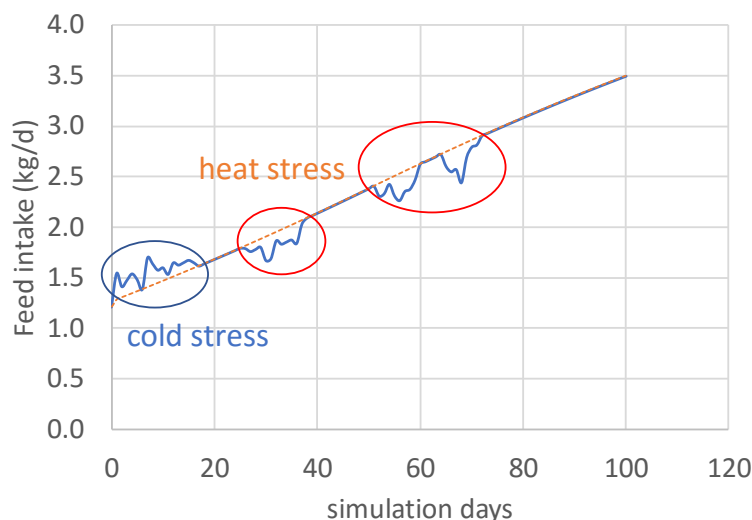
According to a number of studies, modern broilers fed a commercial diet are far from eating to physical capacity (Leeson et al., 1992; Gous, 2013; Nielsen, 2014). Leeson et al. (1992) reported that broiler chickens can increase feed intake by 70% when feeding a low-energy diet compared to control birds receiving a normal diet. Although broilers tend to eat to fulfil their energy requirement and thus target a certain energy intake, there is no evidence that the energy density of the feed is a constraint for them. Consequently, the feed intake capacity is not a limiting factor in the broiler model.

There is no evidence in the literature that a pig will attempt to eat for a mineral, such as P, when this is the first limiting nutrient in the diet (Pomar et al., 2006; Lopes et al., 2009). However, the feed intake of the pig may be greatly depressed for diets severely deficient in P (Mahan 1982; Lopes et al., 2009). Symeou (2014) concluded that the requirement for P to maximize body weight gain and feed efficiency is only 85% of the P needed to maximize bone mineralization. An assumption was made that feed intake is reduced proportionally if the dietary P supply is lower than 85% of the requirement. Therefore, the actual daily feed intake is a function of the digP intake/digP requirement (eq.21):

$$\text{FI}_{P_{suppl}} = \text{if}\left(\text{digP}_{int} < 0.85 * \text{digP}_{requirement}; \left(0.53 \, \frac{\text{digP}_{int}}{\text{digP}_{req}} + 0.526\right) * \text{FI}_{ideal}; FI_{ideal}\right)$$

$$(eq.19)$$

It is well documented in the literature that stocking density has impact on the voluntary feed intake in pigs and poultry, particularly broilers. The NRC (2012) provides an empirical equation estimating the negative effect of space allowance of pigs, and this is used in our model as well.

The equation is based on the premise that the ME intake decreases linearly with a reduction in space allowance compared to the requirement.

$$\text{FI}_{\text{space}} = \big((100 - \text{relSpace}) * 0.252\big)/100 * \frac{\text{MEint}_{\text{sim}}}{ME_{feed}} \qquad \text{eq.20a}$$

where FI_{space} is the FI according to the stocking density (kg/d), relSpace is the relative space allowance of the pigs (% of requirement), $\text{MEint}_{\text{sim}}$ is the simulated ME intake calculated from the Gamma function, and ME_{feed} is the ME content of the feed.

For broilers the stocking density is taken into account by the following equation that was calculated from data of Shawany (1986):

$$\text{FI}_{\text{space}} = (-0.0118 * \text{relSpace}^2 + 2.1477 * \text{relSpace} + 2.4484)/100 * \frac{\text{MEint}_{\text{sim}}}{ME_{feed}}$$

eq.20b

3.4 Fatty acid module

At a normal slaughter weight, the pig carcass contains 200-250 g fat/kg, which is distributed between the subcutaneous, inter and intra-muscular, and perinephric adipose tissues (Desmoulin et al., 1988). The quality of adipose tissues (in terms of nutritional value, organoleptic properties, conservation and processing properties) is related to the fatty acid (FA) composition of triacylglycerols. A maximum linoleic acid content ranging between 120 and 150 g/kg and a stearic acid content of at least 120 g/kg of total FA is often indicated as a quality reference to the meat industry (Girard et al., 1988). The FA composition is strongly influenced by intrinsic factors like genotype, sex, age, live weight, fatness and depot site of the pig (Girard et al., 1988; Lebret and Mourot, 1998), and environmental factors, especially, by feeding. In fact, daily feed intake, dietary energy and lipid contents, its FA composition and the partitioning of energy between protein and lipid in the body can modulate the FA composition of adipose tissues (Lebret and Mourot, 1998).

Mathematical models, like InraPorc can be used to predict the consequences of nutritional strategies on pig performance and carcass quality based on body weight and feed intake. However, meat quality traits such the estimation of FA composition are not included. Therefore, the aim of the present work is to develop a module of lipid growth and FA composition to complement basic growth models of fattening pigs.

The fat deposition in broilers up to the commercial slaughter weight is less important and the fat accretion in valuable body parts is less significant than in pigs. Therefore, the fatty acid module has been developed only for the pig model and particularly for heavy pigs.

3.4.1. Description of the model

The model is based on that proposed by Lizardo et al. (2002), which was composed of two modules: a basic nutritional model describing pig growth (de Lange, 1995) and a specific model for lipid growth and FA composition. To describe pig growth, the InraPorc model (2003) is now used to replace the previous model of de Lange (1995) and serves as a general framework on

which the lipid model is built (Figure 8). The inputs of the so-called FA module are identical to the inputs of the post-digestive nutrient partitioning model but additionally the FA composition of the feed is also required. Feed intake, nutrient utilization, protein and lipid deposition as well as the lipid mass are predicted by the metabolic growth model while the partitioning of FAs and the FA profile of the body cuts are estimated by the FA module.

Figure 8
Flow diagram of the lipid and FA model
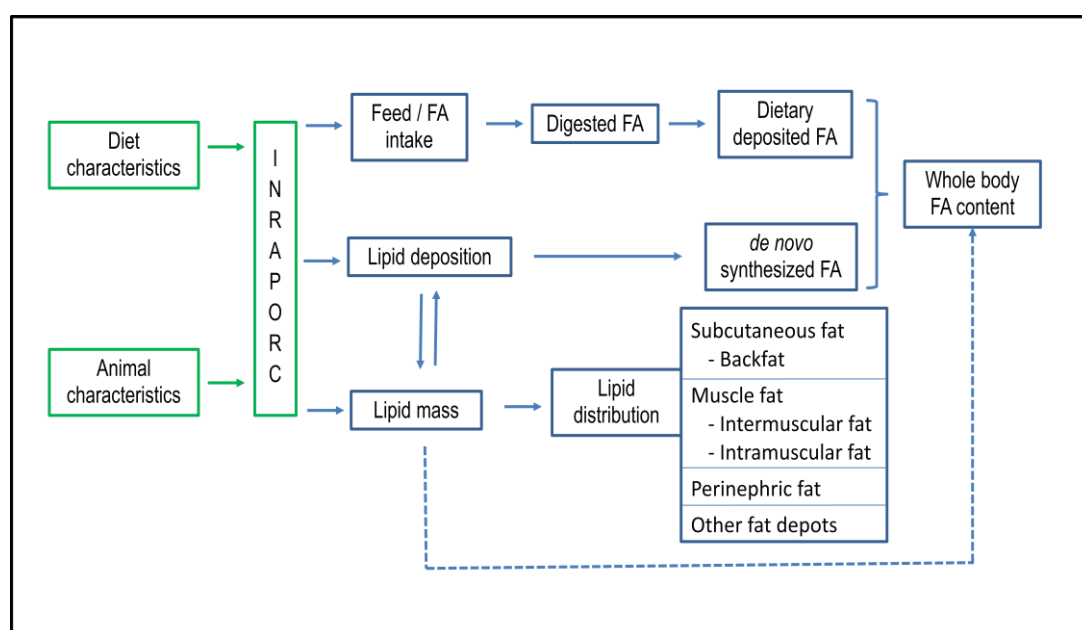
Modelling the fatty acid composition of body lipids

Lipids and fatty acids

Lipids can be extracted from diets or body tissues using different procedures but roughly, 800 g/kg lipid are recovered as FA by gas chromatography. The remainder corresponds to unidentified FAs, glycerol, and the unsaponifiable fraction.

Little information is available on the FA composition of whole body lipids. In contrast, the FA composition of subcutaneous adipose tissue has been extensively studied and backfat cuts represent the most important adipose component of the carcass. When fed a conventional diet, the approximate FA composition of subcutaneous adipose tissue at normal slaughter weight is 0-20 g/kg myristic, 200-300 g/kg palmitic, 10-30 g/kg palmitoleic, 100-150 g/kg stearic, 400-500 g/kg oleic, 50-200 g/kg linoleic, and 10-50 g/kg linolenic acid. The model takes into account these FA separately whereas other minor FA (e.g., lauric, arachidic and arachidonic acid) are considered together in one pool (**minorFA**).

Since pigs have no delta-12 and delta-15 desaturase enzyme activity, the unsaturated linoleic and linolenic acids cannot be synthesized. Therefore, they need to be provided through the diet.

In the model, it is assumed that lipid deposition (**LD**) corresponded to the sum of dietary and *de novo* synthesized FA, adjusted for the FA recovery from lipids (Figure 8).

Deposited dietary fatty acids

For each dietary FA accounted for in the model, a specific ileal digestibility coefficient is used (Jorgensen et al., 1992). These coefficients were 0.91, 0.91, 0.85, 0.86, 0.94, 0.96, 0.94, and 0.95 for myristic, palmitic, palmitoleic, stearic, oleic, linoleic, linolenic, and minorFA, respectively (Table 3). Moreover, it is assumed that ileal digested FA are absorbed, transported, and re-esterified to triacylglycerols without change in molecular structure (Leat, 1983).

Table 3
Major parameters used in the lipid and FA model

Fatty acids	Myristic C14:0	Palmitic C16:0	Palmitoleic C16:1	Stearic C18:0	Oleic C18:1	Linoleic C18:2	Linolenic C18:3	minorFA
Initial at 25kg, %	4.4	32.6	8.5	13.0	25.6	5.5	0.4	10.4
Ileal digestibility,%	91.0	91.0	85.0	86.0	94.0	96.0	94.0	95.0
dietFAstore, %	85.0							
novoFAcomp, %	1.0	24.0	2.0	19.0	54.0	-	-	-

Information about the extent to which dietary FA are deposited (rather than oxidised) is scarce. Based on calorimetry data, Chwalibog et al. (1992) concluded that virtually all dietary lipids were stored, which confirm results of Metz and Dekker (1981) using the slaughter technique that in a normally-fed growing pig, body fat is not mobilised on a day-to-day basis. However, on a balance study carried out by Flanzy et al. (1970) only half of dietary linoleic acid was recovered in the carcass. Acknowledging the discrepancy between these data, and after several blind simulations, it was assumed that 0.85 of absorbed FAs were deposited as is (**dietFAstore**; Table 3). This parameter is like a post-absorption efficiency and it is common for all the FA considered in the model. The complement (0.15) entered a common pool of energy available for anabolic processes or precursors for *de novo* FA synthesis.

De novo synthesized fatty acids

The sum of palmitic, stearic and oleic acid represents 700 to 850 g/kg of the total FA found in adipose tissue. The *de novo* FA synthesis results in palmitic acid (from acetyl-CoA). Stearic and oleic acid result from chain elongation and desaturation of *de novo* synthesized or dietary palmitic acid. The quantity of *de novo* synthesized FA is calculated as the difference between total FA deposition (equivalent to 0.80 of **LD**) and deposited FA of dietary origin. However, little information is available on the composition of *de novo* synthesized FA.

The synthesis of saturated FA implies two collaborative systems. The *de novo* FA synthesis is cytoplasmatic and generates mainly palmitic acid and some minor, medium chain FAs from acetyl-CoA. The second system is mitochondrial and concerns elongation by adding two carbon atoms to the existing FA. Subsequently, FA may be desaturated through activity of endogenous desaturase enzymes (Lehninger, 1981).

A balance trial conducted by Flanzy et al. (1970) with pigs fed a synthetic lipid-free diet demonstrated that the FA composition of lipids in the body weight gain (570 g/d) corresponded to 0.28, 0.18, and 0.53 for palmitic, stearic, and oleic acids, respectively. After doing some simulations based on experimental data, it was assumed that the partitioning of *de novo* synthesized FA (***novo*FAcomp**; Table 3) corresponds to 0.01, 0.24, 0.02, 0.19, and 0.54 for myristic, palmitic, palmitoleic, stearic, and oleic acid, respectively. In the model, the partitioning among these FAs was considered constant throughout the growth period of the animals. Alternatively, FA partitioning could have been represented by separate pools of palmitic, stearic, and oleic acid and material flows between those pools, determined by enzyme activity. However, this later approach makes the model calculation more complicated and there is no relevant data available to quantify the modulatory effect of enzymes.

Development of adipose tissues

In the growing animal, lipids are present in major (i.e., subcutaneous, intermuscular, intramuscular, and perinephric) and minor (omental, mesenteric, and pericardic) adipose tissues (Leat and Cox, 1980) as well as in visceral organs, digestive tract, skeleton, skin, head, feet, and tail (Leat, 1983). Despite the biological importance, some of these depot sites are not considered as part of the carcass or have a low economic value for the meat industry and therefore have not been specifically included in the model.

To describe the lipid growth of adipose tissues considered in the model (subcutaneous, intermuscular, intramuscular, and perinephric) and in the backfat joint, allometric equations were determined relating tissue lipid mass to total body lipid mass (Table 4), based on unpublished results from Le Bourg (1999) and those of Karege (1991).

Table 4

Partitioning of total lipids from EBW (EBW_tL) into main adipose tissues and backfat cut

Subcutaneous tissue	$SCut = 0.1213 \times EBW\_tL^{1.0688}$
Intermuscular tissue	$InterM = 0.0186 \times EBW\_tL^{1.1786}$
Intramuscular tissue	$IntraM = 0.1299 \times EBW\_tL^{0.8174}$
Perinephric tissue	$PrN = 0.00153 \times EBW\_tL^{1.3546}$
Backfat cut	$BFat = 0.0197 \times EBW\_tL^{1.1535}$

The FA composition varies considerably between adipose tissues (Marchello et al., 1983; Bout et al., 1988) and even between different sites of the same tissue (Marchello et al., 1983). Intrinsic development of the tissue (Kouba et al., 1999) combined with energy available for FA deposition during growth was assumed to explain differences in FA composition between tissues. For example, perinephric tissue develops relatively late and it was hypothesized that its constituent FAs are mainly those ingested or synthesized in the finishing phase.

Initial body lipid and fatty acid composition

The FA composition of different tissues in pigs at slaughter depends on the FA deposited during growth as well as on the initial FA composition. Based on data of Karege (1991), it was assumed that the lipid mass of the initial 25 kg piglet was distributed between subcutaneous (0.45), intermuscular (0.11), intramuscular (0.15), and perinephric tissue (0.03). The remaining fraction (0.26) represents tissues of lower economic interest. No information was available concerning the partitioning of FA between adipose tissues in piglets. Consequently, it was assumed that the initial FA composition was similar for all adipose tissues and identical to the backfat FA composition of 80-day old piglets (Camara et al., 1994). This corresponded to 44, 326, 85, 130, 256, 55, and 4 g/kg for myristic, palmitic, palmitoleic, stearic, oleic, linoleic, and linolenic acid, respectively (Table 3). The remaining 104 g/kg was considered as the **minorFA** fraction. Nevertheless, if an initial body FA is provided then the model can assume it for simulations.

3.4.2. Evaluation of the model

In order to evaluate the model, some literature data concerning the influence of dietary fats on whole body FA composition were used. Despite a large number of publications on this subject, there are only few reports containing all the information that is required to use the model (i.e., diet composition, feed intake, growth performance between 25 to 100 kg, and particularly whole body FA composition). Studies included are those of Tibau et al. (2002), Kloareg et al. (2007), Duran-Montgé et al. (2010), Skiba et al. (2015), and Raj et al. (2017). Growth duration, the upper limit of protein deposition (PDmax) and average daily feed intake of each dietary treatment were empirically adjusted to match the reported average daily growth rate and total

feed consumption. To simplify the approach, predictions of palmitic, palmitoleic, stearic, oleic, linoleic, and linolenic acid contents, as well as per FA families and whole body FAs were evaluated.

The comparison between literature data of whole body FA composition and the corresponding predictions by the model are presented in Figures 9 and 10.

The observed FA content in backfat ranged from 182 to 287g/kg for palmitic, 13.1 to 34.1 g/kg for palmitoleic, 98.6 to 178 g/kg for stearic, 331 to 510g/kg for oleic, from 53.4 to 271g/kg for linoleic acid, and from 3.7 to 139 g/kg for linolenic. Predicted values varied between 149 and 270 g/kg for palmitic acid and mainly agreed with observations ($R^2 = 0.79$). Similar results were obtained for palmitoleic acid, which varied from 12 to 30 g/kg ($R^2 = 0.79$). Although no systematic deviation from the observed values was observed for stearic acid (88-164 g/kg), predictions were not very accurate ($R^2 = 0.44$). Predictions for oleic (289-564 g/kg), linoleic (62-350 g/kg) and linolenic (5.24-231 g/kg) acids were more accurate ($R^2 = 0.77$; $R^2 = 0.72$, $R^2 = 0.96$, respectively).

Summarizing, the model is based on a metabolic (dietary and *de novo* synthesized FA) and spatial (allometry) distribution of FA deposition. It is hypothesized that differences in FA composition between tissues can be explained by differences in tissue development combined with differences in the origin of FA. There are few data sets available that allow a full evaluation of the retained hypothesis. Considering the economic importance of backfat and the volume of data concerning its FA composition, this tissue can be used to test the above-mentioned hypothesis.

Figure 9. Comparison between literature data and model predictions of pig whole body fatty acid composition. Each graph corresponds to 20 dietary treatments (Tibau et al., 2002; Kloareg et al., 2007 ; Duran-Montgé et al. 2010 ; Skiba et al. 2015 ; Raj et al. 2017).

Figure 10. Comparison between literature data and model predictions of pig whole body fatty acid composition. Each graph corresponds to 20 dietary treatments (Tibau et al., 2002; Kloareg et al., 2007 ; Duran-Montgé et al. 2010 ; Skiba et al. 2015 ; Raj et al. 2017).
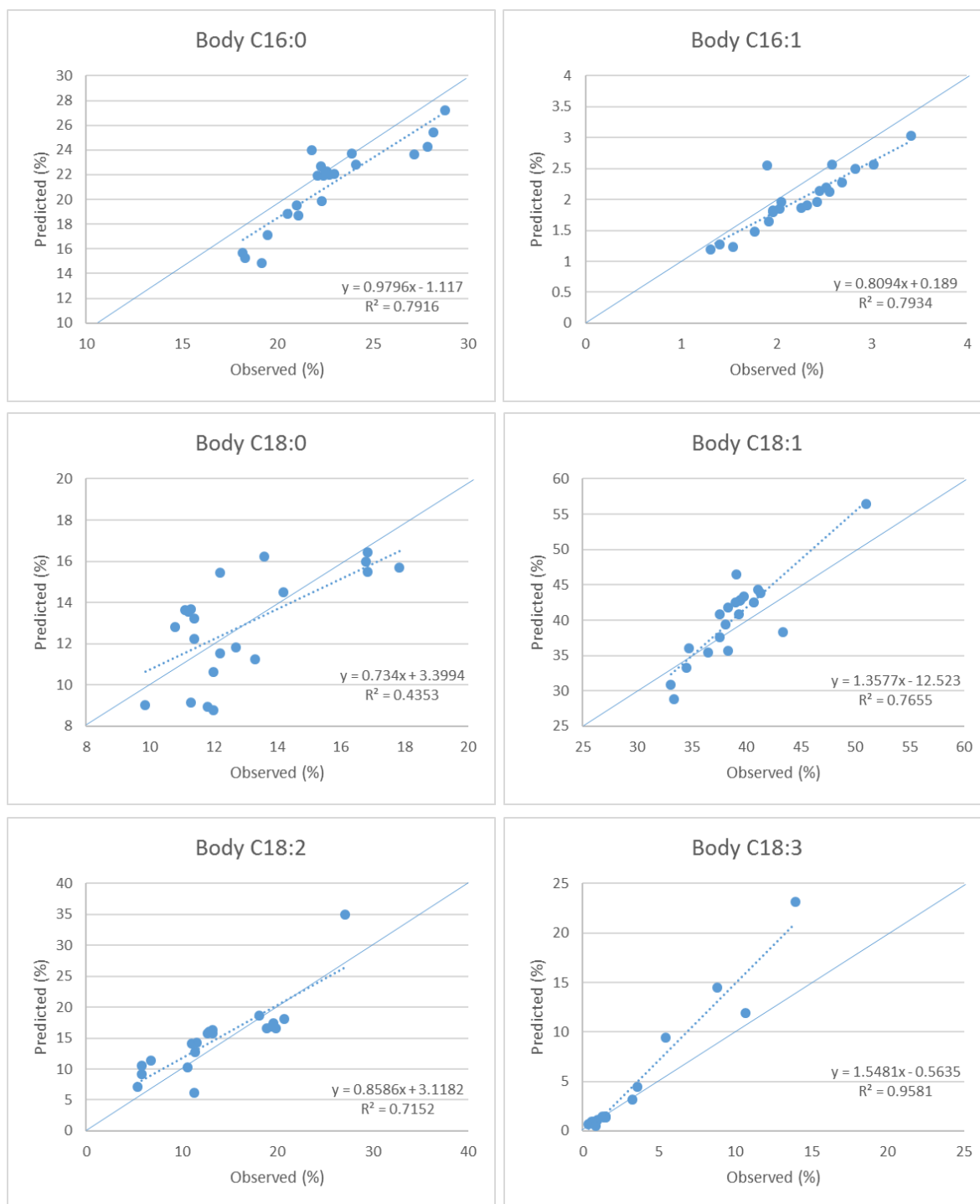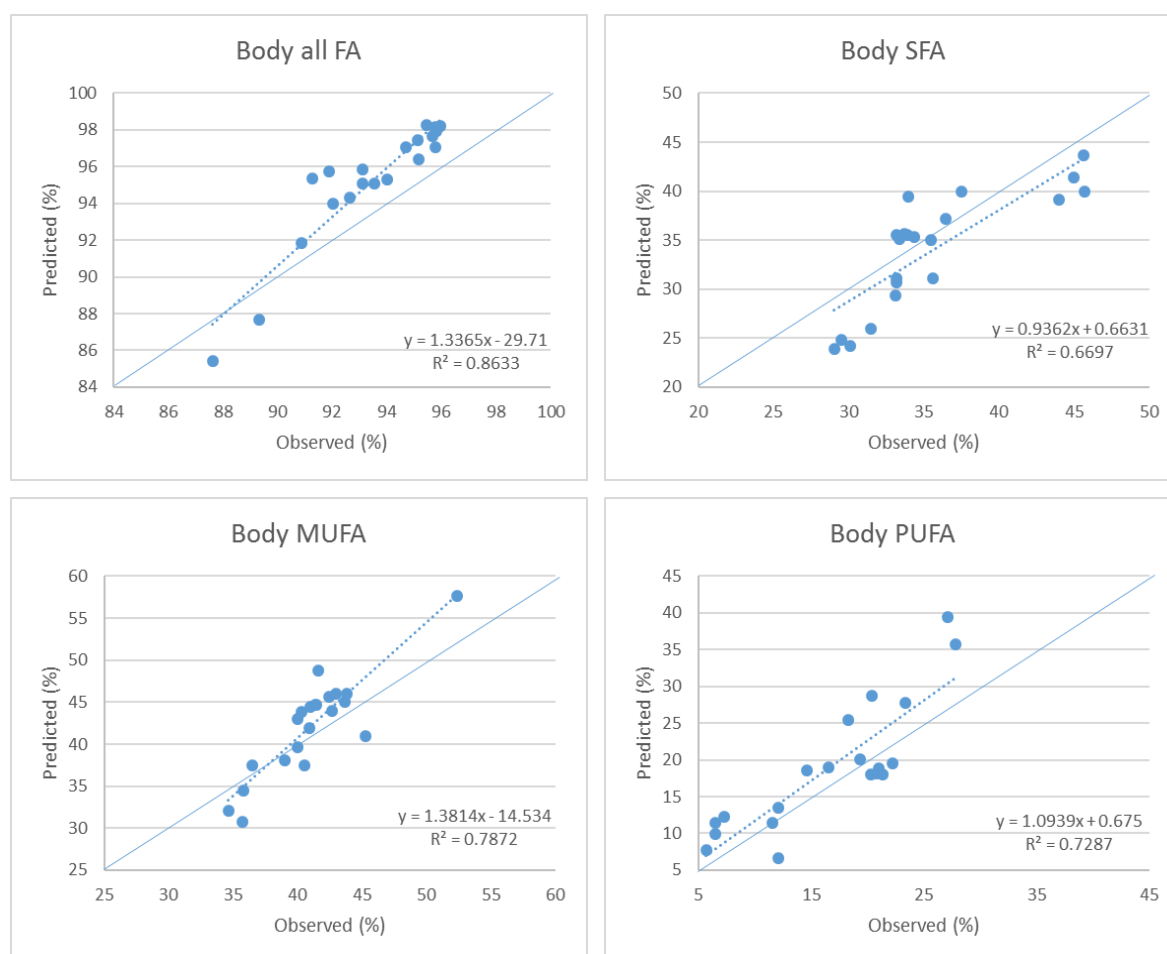

4. Conclusions

The model as described in deliverable D3.1 has been improved by integration of new modules to the basic model, which was able to simulate the energy and amino acid metabolism of growing and fattening pigs. The improved model predicts P metabolism and retention, and it gives a more precise estimation on feed intake according to relevant environmental factors and simulates the fatty acid composition of the body fat at different anatomical parts. The pig model has been adapted to broiler chicken.

The nutrient partitioning model for pigs and broilers is available for the DSS development in Task 3.5. The models simulate the post-digestive utilization of energy and amino acids, as well as the Ca and P metabolism, and predicts the growth performance and changes in chemical body composition of the individual animals and birds over time.

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