DOCTORAL (PhD) DISSERTATION

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HUNGARIAN UNIVERSITY OF AGRICULTURE AND LIFE SCIENCES

2023

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GENERIC DYNAMIC MODEL TO SIMULATE PERFORMANCE AND BODY COMPOSITION OF BROILERS

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KAPOSVÁR

2023

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1. LIST OF LEGEND AND ABBREVIATIONS

AA(s) – amino acid(s)

AA_{f_loss}– sum the AA loss attributed to feather protein loss

$AA_{endogen}$– sum of basal endogenous AA loss

$AA_{urinary}$ – sum basal turnover of protein excreted via urine / obligatory urinary loss

activity_level – activity level in % of FHP

AME – apparent metabolizable energy

AMEn – apparent metabolizable energy corrected for zero nitrogen retention

AID – apparent ileal digestibility

a_eBW – a coefficient in allometric function of eBW

a_Bwater_f – a coefficient in allometric function of eFFBWater, females

a_Bwater_m – a coefficient in allometric function of eFFBWater, males

a_FP_f – a coefficient in allometric function of FP, females

a_FP_m – a coefficient in allometric function of FP, males

a_FW_by_eFFBW_f – a coefficient in allometric function of $FW_{(i+1)}$, females

a_FW_by_eFFBW_m – a coefficient in allometric function of $FW_{(i+1)}$, males

ag_ad – parameter “a” in feed intake curve (ad libitum)

Age_init – initial age at start of the simulation, days

Age_final – final age at the end of the simulation, days

b_Bwater_f – b efficient in allometric function of eFFBWater, females

b_Bwater_m – b coefficient in allometric function of eFFBWater, males

b_eBW – b coefficient in allometric function of eBW

b_FP_f – b coefficient in allometric function of FP, females

b_FP_m – b coefficient in allometric function of FP, males

b_FW_by_eFFBW_f – b coefficient in allometric function of $FW_{(i+1)}$, females

b_FW_by_eFFBW_m – b coefficient in allometric function of $FW_{(i+1)}$, males

bg_ad – parameter “b” in feed intake curve (ad libitum)

BP – empty feather-free body protein

$BP_{initial}$ – initial empty feather-free body protein

BPD – empty feather-free body protein deposition

BPD_freeNE – protein deposition-free net energy

$BP_{maturity}$ – empty feather-free body protein at maturity

BP_{final} – expected final empty feather-free body protein

BL – empty feather-free body lipid

$BL_{initial}$ – initial empty feather-free body lipid

BLD – empty feather-free body lipid deposition

BW – body weight

BWG – body weight gain

BW_init – initial body weight

c – parameter "c" in feed intake curve (multiples of maintenance)

Ca – calcium

CFI – cumulative feed intake

d – parameter "d" in feed intake curve (power of metabolic BW in NE system)

DE – digestible energy

DFI – daily feed intake

EAA(s) – essential amino acid(s)

eBW – initial empty body weight

eFFB – empty feather-free body

eFFBash – empty feather-free body ash

eFFBW – empty feather-free body weight

eFFBwater – empty feather-free body water

eUA – endogenous uric acid

eUE – endogenous urinary energy

HI – heat increment

HP_{act} – heat production related to activity

FHP – fasting heat production

FI – feed intake

FI_1 – net energy intake at 1 kg of body weight

FI_2 – net energy intake at 1 kg of body weight

FCR – feed conversion ratio

FMIS – farm management information system

FP – feather protein

FP_{dep} – feather protein deposition

FW – feather weight

FW_{dep} – feather weight deposition

GE –gross energy

GIT – gastrointestinal tract

ID – ileal digestibility

kBR – the energy efficiency of using body reserves

ME – metabolizable energy

meanBPD – mean empty feather-free body protein deposition

MsChick – Model Simulation for Chicken

MSPE – mean square prediction error

N – nitrogen

NE – net energy

NEI – net energy intake

NEPD – net energy of 1 g of protein deposition

NIRS – near-infrared spectroscopy

ObligUrinELoss – obligatory urinary energy loss

P – phosphorus

potBPD – phenotypic potential of empty feather-free body protein deposition

RFID – radio-frequency identification

relMSPE – relative mean square prediction error

SID – standardized ileal digestibility

TID – true ileal digestibility

TMEn – true metabolizable energy corrected for zero nitrogen retention

TAN – total ammonia nitrogen

TP – total protein

VarUrineLoss – amount of energy in 1 g of urinary endogenous N

UrinaryEloss – urinary energy loss from excess protein

UrinE – daily energy loss by urine

2. INTRODUCTION

> "…the intention and the result of a scientific inquiry is to obtain an understanding and control of some part of the universe. ... No substantial part of the universe is so simple that it can be grasped and controlled without abstraction. Abstraction consists in replacing the part of the universe under consideration by a model of similar but simpler structure. Models, formal or intellectual on the one hand, or material on the other hand, are thus a central necessity of scientific procedure" (Rosenblueth and Wiener, 1945)

Livestock products are formed as the results of conversion of feed substances into the animal's body. During lifetime the accretion and partitioning of nutrients by alive organisms lead to the process of growth and development. Development, by definition, may include physical growth, however, it involves the improvement in both structural and functional complexity. The growth is usually quantitative, whereas development is fundamentally qualitative.

Nutrition has a quite profound effect on growth and development as ingested nutrients contribute to and become incorporated into not only the structural components of animals, but they are also key players in the physiological and biochemical formation of tissues and organs (McFarland, 2003). The increase in body weight during growth is imperatively determined by the protein synthesis. The protein content of the diet (with particular amino acid pattern called "ideal protein") in relation to the dietary energy is the main factor determining the amount of fat deposited – up to a certain point the greater the protein-to-energy ratio, the lower the fat content in the animal's body.

Taking into consideration biological and physical laws, an understanding of the matter and energy flows and its partitioning in the animal body over time can be improved. A living organism constantly interacts and, thus, exchanges matter and energy, with its environment as energy may appear in different forms, *i.e.*, heat (Guggenheim, 1967). Like all energy transformations, the energy consumption and expenditure by the animal organism are subjected to laws of thermodynamics. Those state that, firstly, the energy content of the universe is constant, *i.e.*, translated into the practical terms of daily animals' diets: *energy consumed equals to energy expended plus energy stored*. And, secondly, that in the living systems, energy and mass are controlled by each other. Progressively, *mass becomes energy and energy becomes mass*, and this process of energy transduction takes place through *metabolism*, in particular catabolism and anabolism (Bawden and Robinson, 2015).

Being a central and integral part of the scientific methods, mathematical modeling of individuals may be adequate for expressing and understanding growth and mechanisms behind it. Models can be used as simplifications of reality by means of representations of applying concepts with structuring data and prior knowledge (*i.e.*, operational models and research models). Thus, by being constructed in different ways and representing biological functions at different levels, models design and help an observer to understand how the system works and to predict its behaviour (Danfær, 1991; Frigg and Hartmann, 2006; France and Kebreab, 2008). By describing nutrient flows and thus the animal response to certain circumstances, the nutritional models can be used to simulate an individual animal or group responses to different nutritional regimens (Black, 2014). Prediction of animals' growth based on modelling of feed utilization process or, conversely, while defining the nutrients requirements of the expected growth and providing the necessary amount and quality of nutrients, is one of the most important preconditions for the sustainable and economical manufacturing of high-quality animal products (Babinszky *et al.*, 2019). Hence, modelling is a high-potential tool gaining more and more application not only in research but also in practice nowadays.

3. LITERATURE OVERVIEW

3.1. Use of modelling

3.1.1. Mathematical models in precision livestock farming and precision animal nutrition

Meat production and consumption have tripled in developing countries in the last two decades due to their rapid economic growth (Meat and Dairy Production, 2023). It has been mainly attributed to the poultry and pig sectors since meat production of those species requires a relatively short time and they have high feed efficiency compared to other farm animals (OECD-FAO, 2017-2026). It must be noted, however, that they compete with human nutrition in terms of using grains and protein feeds while producing high biological value and nutritious food products.

In global, animal health and welfare, product quality and security, the environmental impact of animal farming, consumer and citizen expectations are crucial in high-quality animal origin food production. Precision livestock farming (PLF) or "Smart Farming" is often referred to as the solution to those challenges because it seems promising to provide an increasing amount of food with a low environmental impact and waste (Halas and Dukhta, 2020). Given the society's demand for more sustainable productions, there is a need to look for specialized employees and sometimes there is a lack of skilled workers willing to perform even simple tasks. In fact, agriculture production is still the key in rural development. Adoption of PLF systems has increased in the last decade, however compared to precision crop production, it is still in the early phase of its development. The principle of precision agriculture is to use real-time, reliable information to support the transition towards maximizing efficiency and sustainable production. Thus, PLF relies on real-time monitoring and management system that focuses on improving the life and welfare of the animals by warning when problems arise, but also helps in organizing on-farm routine (Berckmans, 2015). Progress in PLF has been made possible by the significant improvements achieved in computer processing power and the availability of different sensor technologies. Precision feeding (PF) has been called information intensive nutrition (Sifri, 1997), since the animals are fed according to their actual requirement that is depending on multiple factors, including the genetic and environmental conditions. The PF relies on feeding techniques to match nutrient supply precisely with the nutrient requirements of individual animals. For that purpose, mathematical models are used to estimate nutrient requirement of animals, and also models are applied to predict expected performance of the herd or individuals. By integrating growth models into PLF systems greater economic returns can be achieved, while reduced nutrient excretion to the environment, and improved efficiency of resource utilization can be realized (Zuidhof, 2020).

PLF is an innovative and integrated production approach based on utilizing advanced technologies and up-to-date scientific knowledge of animal sciences (Berckmans, 2004). Precision feeding lays the groundwork for addressing key issues in today's intensive livestock farming, which are: (*i*) reducing feeding cost by improving feed and nutrient efficiencies; (*ii*) improving production system sustainability by increasing profitability and reducing environmental footprints; and (*iii*) increasing food safety through traceability.

Nowadays farming has evolved from simple farm recordkeeping into sophisticated and complex information systems. Different software are available collecting and handling the real-time data that are used in daily management and practical or strategic decision making. The animal is equipped with a radio-frequency identification (RFID) sensor (Ruiz-Garcia and Lunadei, 2011), and this sensor can be used to identify the animal at, for instance, the feed station that assigns an individual ration of feed (Muntz et al., 2020). Those software are being an integrated part of the so-called farm management information systems (FMIS, Tummers *et al.*, 2019). The concept is more developed for the fattening pig where each pig is fed individually. The deterministic nutritional model for pig seems more easily to apply compared to broilers, as nowadays the average bird of the flock is considered by nutritionists. Nevertheless, there are developments for broiler chicken wearing the RFID sensors for studying their feeding behaviour are conducted (Berger *et al.*, 2021).

Modern livestock farming has adopted innovative technologies to improve the biological efficiency of animal production and animal feeding, and for that purpose different mathematical models have been applied (Halas and Dukhta, 2020). By using these models, it has become possible to simulate and predict, for instance, how the animal responds to certain diet in ideal environment or when disturbances happen. The optimal nutrient supply can be determined by the repeated simulation of the animal response to different diets and feeding regimen. Besides simulation of the growth performance in response to different nutritional inputs, and out of considering the fact that animal experiments are costly and time-consuming, the animal response's models may be used to test hypotheses and thus evaluate different theories about the regulation of growth examining the closeness of predictions to experimental observation (Gous, 2007*a,b*; Griffiths, 2010).

3.1.2. Types of models

There are different types of models, based on certain criteria models can be either static or dynamic, either empirical or mechanistic, and either deterministic or stochastic. A practical example of the *static* models would be nutritional table values. Such datasets represent the state of the system for only one certain period over time. Since they estimate the energy and nutrient requirements for livestock species at certain BWs, values generated by those models have been applied in diet formulation. Moreover, static models were developed to describe the growth of animals or animal body parts (Huxley and Teissier, 1936). Though, with the introduction and increasing of computers use during the late 1960s and 1970s, the number of equations included in models grew substantially.

At the same time and since then, the modern nutritional research investigated the animal response to energy and/or nutrient intake and their partitioning within the body generating a huge amount of data. This allowed to develop various mathematical models to help understanding of the animal performance as well as to predict the nutrient requirements of animals applying a more *dynamic* approach, when time was described explicitly – outcomes were predicted over varying periods of time using varying repetition intervals (Black, 2014).

Many of the earlier animal simulation models were based largely on regression equations that described associations between two or more variables. In so-called empirical models, only mathematical-statistical relationships are represented by the equations. Such models developed by breeding companies – that have been used in breeders' guidelines – are typically based on empirical relations between animal performance (*e.g.*, BW, FI, backfat sickness, breast muscles weight) to age. For the sake of reliability, the empirical models must be based on large datasets that might be updated regularly to account for the rapid genetic improvement. However, differences in production conditions may require different empirical equations. In fact, the underlying biological mechanisms behind growth are not explored in empirical models. Predictions from these empirical models were frequently poor when applied to situations outside the range from which the original data were collected (Black, 1995). Thereby, to enable an understanding of the effect of nutrition on performance and underlying mechanisms of biological processes, a more mechanistic approach was required with an explicit representation of nutrients use (*e.g.*, the efficiency of amino acid utilization) and partitioning (*e.g.*, between body protein and lipid). Many of dynamic mechanistic models contain combinations of empirical and mechanistic equations to describe the growth process over time. It is based on either the laws of physics and chemistry or on equations with known characteristics derived specifically to represent the perceived mechanisms of a range of animal systems, including nutrient metabolism and energy transactions in individual organs or whole animals using biochemical pathways (Black, 2014).

Most of the current animal models are *deterministi*c – representing the outcome for the one average animal as a mean of the group of the similar animals, rather than being *stochastic* – demonstrating a natural variability within a population.

3.1.3. Model development

Model development usually starts with the graphical representation of the model concept. In growth models, the flowchart of the pathways of nutrients' use is set, and the main transactions are represented. Thus, although in the flowchart not all transactions are indicated, the level of detail is worth being decided at the early stage of development. The animal can be considered as a physiological system with measurable characteristics (physiological data), like body weight, capacity for protein deposition, the amino acid composition of the body protein, *etc.*, and biological processes (physiological pathways), such as the utilization of digested protein to body protein, the energy requirement for maintenance, *etc.* The first step in the modeling process is to collect basic data from literature or from available datasets to generate the physiological dataset and to describe the physiological pathways with particular algorithms. Similar pathways are generally described with the same type of algorithm in which the partial coefficients may be different. The algorithms are usually not complicated and can be taken from any field of science. The so-called calibration or parametrization of the model is the process that results in the best fitting of the simulation to the tested dataset. In the course of parametrization, the different model parameters are adjusted, and the best combination of the parameter values are searched. Those parameters are involved in this process that have some "valid" variance. The values that have biological, physiological, or nutritional relevance like energy content of protein and lipids, amino acid content of body protein, Ca/P ratio in bone *etc.* are not changed during the calibration, but, for instance, the allometric coefficients describing the relationship of water to protein or the energy requirement for maintenance and/or for activity may be adjusted. There are two steps of parametrization: 1) the model inputs are changed one by one by checking whether the outputs are realistic, 2) once the first parametrization is done, the so-called key parameters are adjusted. The key parameters are the ones that can be freely set by the user – in this step the combinations of the key parameters are optimized that results the best fitting of the model output to the dataset that is used in the model validation.

Traditionally, these two steps are repeated many times until the system can be described at some uniform level of detail (Black, 1995*a*). When the model development completed, the evaluation of the model should be done with independent dataset. Due to the fact that the research data might be perturbed, as well as the model was developed in a certain range of circumstances, the refinement of the model can be a never-ending process. At a certain level of precision – that might be subjective – the model development should be closed.

3.2. Evolution of the models

3.2.1. Growth curves and their biologically meaningful interpretation

Models, as an abstraction of reality, can be complex or simple. They may contain multiple equations or only one. Growth curves are equations that have been used for a long time in biological sciences. The phenomenon of the growth attempted to be mathematically characterized by the collected cumulative data marked as size (either weight or height, on the y-axis) plotted against time (x-axis). Along over time, the arrayed points on the coordinate axis appear into a sigmoidal curve (S-function) with a relatively slow initial growth rate increasing to a maximum and then slowing down to approach an upper limit. Several equations have been proposed in the literature mainly based on the Gompertz (1825) as well as logistic (Verhulst, 1845), von Bertalanffy (1938) and Richards (1959) as single functions fitted to an S-shaped growth pattern (Tjørve and Tjørve, 2017). Sigmoid curves are able to represent that growth occurs up to so-called maturity point (the upper limit of the sigmoid curve) and since that the growth process terminates by only one equation. The growth rate, characterized by a varying velocity over the physiological age, has a bell-shaped curve (the 1st derivate of the cumulative growth S-function) as shown in Figure 1. It should be noted that the function works irrespective of specie, the time scale might be different, but the shape of the curves is the same, for example, in pigs and broilers. S-shaped tendency has been historically proven to work for describing of the weight and height or body parts growth in plants as well as for that in avian, mammals and human species (Bridges, 1986; Lampl, 2012).

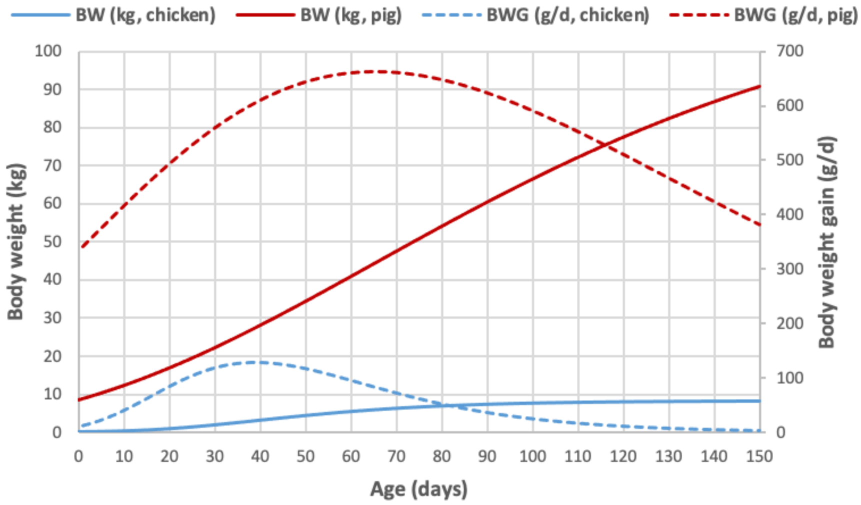


Figure 1. Simulation of broiler chicken (blue) and pig (red) body weights (BW, kg, S-function, left axis) and body weight gains (BWG, g/d, bell-shaped curve, right axis) over 150 days

In nutritional models Gompertz function has been used the most frequently. There are different formulas of Gompertz that is practically an exponential equation. In academic sector the following formula is mainly applied: $y = y_0 e^{\frac{r}{\alpha}(1-e^{-\alpha x})}$, where *y* is the depending variable (*i.e.*, body weight, protein mass, size of population, number of cells), y_0 is the initial state at t=0 (weight, number of individuals in the population, or number of cells *e.g.* in a cancerous tissue), *r* is the rate of growth or proliferation, specifically called precocity in nutritional growth models, and α is a parameter modelling the inhibition to the growth.

The popularity of the equation – according to Wellok *et al.* (2004) – may be due to the fact that the Gompertz function is suitable as a descriptor of potential growth in non-limiting conditions by using the minimum parameters and holds over a very wide range of degree of maturity. The values of its parameters for a particular kind of pig, or other animal, can be estimated quite simply from data obtained under conditions that at least approximate to being non-limiting. The values for Gompertz function are often compared by various authors for evaluating the overall growth or body chemical components in broilers or laying pullets (Sakomura *et al.*, 2006, 2011; Silva *et al.*, 2016; Nogueira *et al.*, 2021).

Researchers have investigated for years the question on how growing and developing alive system reacts to energy and nutrients intake. Pioneers of quantum mechanics likened living organisms, in physical terms, to eddies in a stream of energy – "Living things are open systems operating within open systems, needing maintained supplies of energy and materials, and the means to dispose of waste products and corpses…" (Sherrington, 1940). From the time that Hammond (1932) and McMeekan (1940) noted the orderly progression of growth of tissues (bone, followed by muscle, followed by fat deposition) for sheep and swine, respectively, there were established the two main aspects of growth: (1) the efficiencies of a particular conversion process, compared to (2) the rate at which these processes occur (Brody, 1945). Animal husbandry scientists became curious about the relative rates at which muscle and fat were being produced. These principles of progressive growth of the skeleton, followed by growth of muscle and, finally, accumulation of fat provide the basis for understanding of the declining growth efficiency as animals mature because more energy is required to accumulate fat than to accumulate muscle. The body chemical and physical composition systematically changes during the growth, and these changes in the proportion of various body components have become studied at more detailed levels over the last century (Mitchel *et al.*, 1926). In animal husbandry science, an organism has become perceived as a purposive system of some kind and in some state (Emmans and Oldham, 1988).

Dumas *et al.* (2008) in his review indicated that feed evaluation systems rather than growth modelling engrossed the mind of nutritionists, meaning that animal growth equations were introduced and developed by biologists rather than nutritionists *per se*. The biologically meaningful interpretation regarding the relationship between growth and maturation rates came into light onwards. A fixed point of inflexion being a limitation for variation in the slope of the curves and feature of the growth trajectory as well as the dependence of those on age, sex, breed, and type of animal, were introduced into animal science.

Eventually, nutritionists focused on a task to understand better the animal response to a certain feed and the underlying mechanisms that occur in certain environments. During this work, and among others, mathematical modeling was used as a tool to explore the gaps in knowledge of physiological phenomena. As a result, it became feasible to predict the growth and the change of body composition in time when fed different nutrients, but those models must be more complex containing many equations. The process, often called "simulation modelling", can involve one equation or the integration of many equations (Black, 2014).

3.2.2. Computerized models, their interconvertibility and application

In the 1970s and 1980s, mathematical modelling of animal growth became to more mature phase in terms of using computer programs to solve set of equations that grasp principal concepts of the protein and energy flows behind the growth process. It became clear that representation of the biological systems by its nutrient flows in combination with fundamental biological knowledge, when incorporated into simulation models, could be used to assist decision making on farms. The outcome of an event could be predicted before it has been observed, and the input and/or components of the modelled system representing concepts of the mechanisms could be easily changed. These predictions could be used to help managers make decisions about the most profitable strategies to adopt.

The mechanistic-dynamic deterministic description of protein and lipid deposition as affected by protein and energy supply in growing pigs developed by Whittemore and Fawcett (1974, 1976) showed how ideas and data from different disciplines could be brought together to simulate the pig growth. It marked the start of the development of computerized models for monogastric animals. Further, there have been developed numbers of mathematical models, and those models were focusing on different phenomena with different levels of aggregation: production, digestion, or metabolism.

The so-called growth models simulating animal performance commence with a description of the animal, including an estimate of its genetic potential to deposit protein and – in some model – the fat (energy), and using nutrient content of the fed diet. Some more complex or holistic models also use the social and climatic environment, as well as health status of the animals as input parameters. The daily FI is predicted either from simple algorithms or a complex set of equations (Poppi 2008; Black, 2009). Knowledge on the digestibility of dietary nutrients was crucial since feed evaluation systems used in the practice are based on digestible nutrient content. Estimation of digestibility is based on using either simple algorithm (Graham *et al.*, 1976), but also complex models of digestion has been developed particularly for ruminants (Black *et al.*, 1981; Dijkstra *et al.*, 1992; Baldwin, 1995; Nagorcka *et al.*, 2000), pigs (Bastianelli and Sauvant 1997; Rivest *et al.*, 2000), and poultry (Roger *et al.*, 2018). In those models, individual nutrients that can enter the metabolism are predicted. Nutrient partitioning models are usually use digestible nutrient content of the feed as input. The difficulty in merging the digestibility and the growth models is that the time step used in characterizing the two phenomena is different. In case of digestion models the processes should be explained on time interval of minutes or seconds, while that is too small-time step in a growth model, where 1 day is the common time step.

A number of growth models have been adopted to user-friendly software and thus are available for practice. In the coming section, some of them are overviewed. They, in general, use the same or similar concepts to represent the partitioning of energy and protein (AUSPIG, EFG software, INAVI, InraPorc, Avinesp) and some of them can be integrated into Smart Farming system.

AUSPIG (1991) computer simulation model is based on a mechanistic model of Black *et al.* (1986) which combines many of the production variables that interact in complex ways to predict the energy and amino acid utilization for a pig growing under a defined set of physical and management conditions. It simulates the growth performance of a pig from weaning to sale and determines the nutrient requirement of the growing pig for maximum growth (Smits and Mullan,1995). The continuously updated AUSPIG model is in use in Australian precision farming system (Black and Bánházi, 2022).

The EFG software (developed by Emmans, Fisher and Gous, 1995) is based on combination of the feed formulation program using linear programming, a broiler growth mechanistic model, and an optimization algorithm. EFG software calculates the impact of all ingredient combinations on FI and optimizes the feeding strategies in meat type chicken. The model was based on the theory proposed by Emmans (1981) that animals strive to attain a desired lipid-to-protein ratio at maturity. That model was the first one transposed to another specie, the poultry model was adapted to pigs. Also, in 2003, the EFG software has incorporated an amino acid (AA) optimizer module.

The INAVI broiler model (Quentin, 2004; Méda *et al.*, 2015) describes the use of ingested energy for maintenance, and for protein and lipid deposition, while accounting for the first limiting AA. The growth is considered as a consequence of ME used by the animal (*i.e.*, the difference between ME intake and heat production) with the introduction of two parameters describing the efficiency of ME use as NE (*k* NE/ME) and converts energy into BW gain via the energetic value of deposition. Total growth can also be seen as the sum of the growth of several compartments (protein, and its allometry to fat, ash, water) as proposed by Emmans (1995), in time step of 1 hour. The actual FI is estimated from the comparison between calculated and reference heat production based on the premise that an animal regulates their metabolism in order to maintain the heat equilibrium. Inputs change the energy flows inside the simulation submodule using accessible response laws. The users are, therefore, able to adapt the model to their own data by changing the inputs.

InraPorc is a model (van Milgen *et al.*, 2008) and a software tool that allows users to work with the model structurally very similar to that developed by Whittemore and Fawcett (1974), where

BWG is modelled as a function of protein and lipid weight gain. Under nutritionally non-limiting conditions, daily FI and protein deposition are modelled independently. The DFI, as one of the major driving forces, is represented as a function of BW in multiples of maintenance, and the parameters of the equation is part of animal traits, while protein deposition is defined as a Gompertz function, both of which have to be parameterized by the user. The energy not used for protein deposition and maintenance is available for lipid deposition, and the lipid deposition is thus considered to be an energy sink (van Milgen *et al.*, 2008; 2015).

The Avinesp model and software (Hauschild *et al.*, 2015) estimates the response of an average chicken to a given feed and environment. It considers the supply of several EAAs – both in broilers and laying pullets – in relation to the potential protein deposition in feathers and feather-free body, as well as applies an effective energy system, proposed by Emmans (1994). It is assumed that the animal will try to eat the amount of feed to fulfil its requirement needs for the first-limiting nutrient in the feed on offer (Emmans, 1997). In a thermal-neutral environment, it is assumed that an immature animal needs ME energy not only for maintenance, which includes some physical activity, but also for protein and lipid retention to achieve at a certain age based on Gompertz equations. The Avinesp model's general structure was adapted for chickens based on proposal for pigs of Ferguson *et al.* (1997).

The software of Avinesp model with a user-friendly interface is probably the first one used on everyday basis nowadays by nutritionists for chickens. In case of the swine sector, the InraPorc is available more than 15 years for pig nutritionists. In general, the comparison of growth rates and the description of live weight and chemical and physical body tissue deposition evolution as a function of age have been most intensively applied in the animal production field to compare, and maximizing productivity while reducing costs and acting in accordance with environmental legislation (Gonçales, 2017; Vargas *et al.*, 2020; Berger *et al.*, 2021).

Because of the conceptual similarities with respect of nutrient use for protein and lipid deposition, the models have been parallel developed for different farm animal and were proven to be interconvertible as the stoichiometry of the underlying metabolic pathways is independent of the species: for pigs (Whittemore, 1983; Black *et al.*, 1986; Moughan *et al.*, 1987; Ferguson *et al.*, 1997; de Lange *et al.*, 2001; 2003; Halas *et al.*, 2004; van Milgen *et al.*, 2008), for sheep (Graham *et al.*, 1976), for beef and dairy cattle (Oltjen *et al.*, 1986; Baldwin *et al.*, 1987a, 1987b, 1987c; Nagorcka and Zurcher, 2002), preruminant calves (Gerrits *et al.*, 1997a, 1997b), and for poultry (Emmans, 1981; Emmans and Fisher, 1986; Emmans, 1989; Johnston and Gous, 2006). Much less, but still several models simulate the requirements for macrominerals like calcium (Ca) and phosphorus (P) (Etches, 1987; Tolboom and Kwakkel, 1998; Kebreab *et al.*, 2009; Halas *et al.*, 2017; Lautrou *et al.*, 2020). Those are also useful for predicting P metabolism in pig and laying hen, but according to our knowledge there is no simulation model estimating the P utilization in broilers. Also, there is a lack of complete model predicting Ca and P retention implemented into an energy and protein partitioning model particularly in poultry. However, in case of a wide range of dietary P supply when the P is limiting not only the bone mineralization, but the soft tissue development may be compromised, and therefore the simulation of Ca and P partitioning should be done in an integrated model.

The use of computer simulation models in agriculture has become widespread as researchers, advisers and farmers had more interactions to improve the efficiency of animal production and the need to improve efficiency continues. Recent development in computer technology has provided the potential to increase the accessibility of research knowledge to a wider audience. This is even more obvious nowadays when IT technology and predictive models support our daily life. Thus, professional models like those ones that predict the animal response to a certain feed or feeding regimen can be used either in extension service or in the farm routine. However, for that purpose the models should be made accessible and applicable for the practice. Mathematical models for long were developed in specific informatics environment, and due to the limitations of the access and use of those programs, their application was limited. Practice needs easily understandable and accessible programs; thus, the models need to be transposed to stand-alone programs that do not require specific programming knowledge. The software allows the user to try and use the model without knowing the internal equations.

The mathematical models have been developed by different research groups focusing on a specific livestock species. However, in practical animal nutrition, for a long time, the use of models was rather limited in daily use for different reasons. First, mechanistic models are comprised of a number of linked equations that require integration in a computer program to make the calculations on a day-to-day basis. Even though the model description (*i.e*., the equations and model logic) may have been published, it may require considerable effort to put all the pieces together and it often turns out that a few pieces are missing. Also, some models have been made available as commercial software tools and could be used in decision-making (Oviedo-Rondón, 2014), however the biological mechanism behind these models may not be publicly available.

3.3. Principles of the modeling approach in the present work

3.3.1. Validity of trans-species approach

The comparative anatomy originated with discussion on dolphin embryos as well as the comparisons between the skeletons of birds to the skeletons of humans by the research of Belon (1555). That could be the starting point for comparative physiology and nutrition too. A comparative approach is recognizing that there are considerable differences in nutrient digestion, metabolism and requirements among various mammalian and avian species. However, on a molecular level, the similarities in metabolic processes among animals are far greater than the differences, reflecting their common evolutionary history. The most common circuit between species is that to attain its potential growth path any organism needs nutrient resources and energy from its feed and an appropriate environment for heat dissipation (Cheeke and Dierenfeld, 2010).

To compare chicken versus pig, it is worth mentioning that both species are omnivores and autoenzymatic digesters (digestive processes carried out by enzymes that the animal secretes into the digestive tract), both having simple digestive tracts even if birds have two-part stomach, a glandular portion known as the proventriculus and a muscular portion known as the gizzard. Those phenomena and some differences in metabolism have a profound effect on nutrient digestion and how (in which form) nutrients enter and become excreted from the metabolism. In brief, the anatomical differences of the digestive tract in poultry compared to pigs are having crop, proventriculus and gizzard, as well as the caeca (two bags versus one in pigs) and the cloaca. From a digestion point of view, it may be also worth mentioning that glucose and amino acids can be absorbed in the hindgut of chicken due to the presence of gut villi. That is more limited in pigs also due to the more developed microbiota in the large intestine which easily utilizes those nutrients. Due to the more active hindgut microbiome, the short-chain fatty acid supply is higher in pigs compared to chicken that definitely has consequences on energy metabolism. Also, the end product of the protein metabolism in birds is uric acid, while urea in pigs that repeatedly stressed when the two species are compared. As concerns fat metabolism, the *de novo* fat synthesis in broilers occurs mainly in the liver, whereas in pigs principally in adipose tissue (O'Hea and Leveille, 1968; Leveille *et al.*, 1975). Thus, it is an important issue from modelling point of view, regarding the impact of those differences on the general behaviour of animal response to different feeds and on nutrient partitioning during growth.

In reproduction, the difference is evident, where poultry lays eggs with a hard shell, pigs' embryos are developing in the uterus. Thus, females of avian species must provide all nutrients for the development of an embryo in advance, whereas mammals supply the developing embryos and the maternal tissues from nutrient uptake and/or their own tissue storages during the gestation. Therefore, an egg must contain all the nutrients in the right quantity and balance, to allow the embryo to grow into a developed bird at hatch. The piglets are not that independent from their mother as chicken, and *postpartum*, sow milk must contain all the nutrients needed to support the rapid growth of a young animals as it is the sole source of food at the beginning of their life.

At last, the bird's body is covered by many different types of feathers, while pigs have light hair coverage, which causes differences in the thermoregulation process and heat production. Although the fact of visual differentiation as an enormous range in mature body weights, size of individual organs, rate of tissue accretion and whole-body composition, the animals share much more in common, in general. To collate swine and poultry performances, the flow and the digestion processes of the ingested feed might be overviewed and compared following its pathway over the gastrointestinal tract (GIT). A comparative understanding of the GIT of pig and chicken, which is particularly crucial to effective application of nutrition, was executed by Moran (1982) as shown in Figure 2.

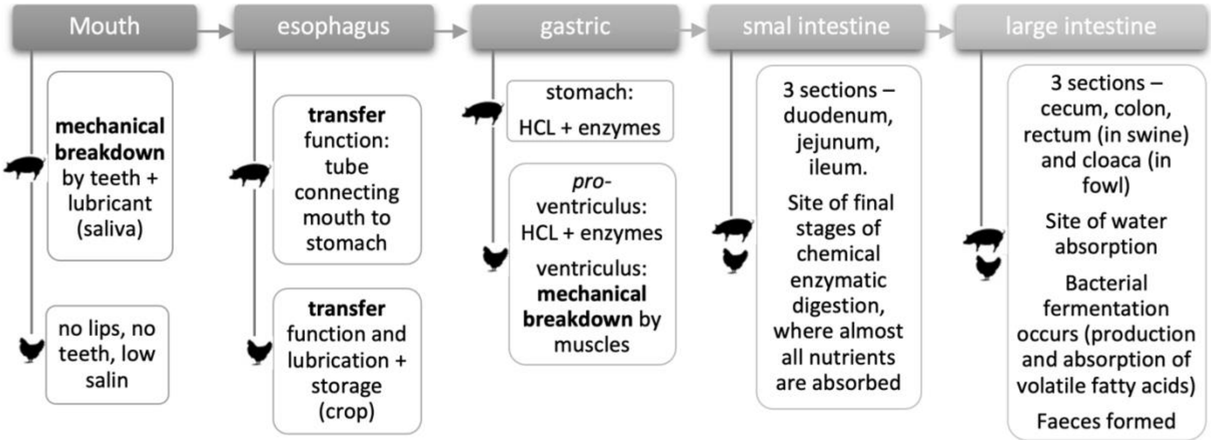


Figure 2. Differences and similarities over the gastrointestinal tract in pig and chicken (Morgan 1982)

Compared to mouth and snout in pigs, birds' digestive tract starts with a beak and has no teeth. Further in digestive tract after esophagus (transfer function) pigs have a stomach as a single muscular organ responsible for storage, initiating the breakdown of nutrients, and passing the digesta into the small intestine. Poultry's oesophagus is relatively long and large in diameter providing both transfer and storage functions (crop). The mucous glands are found in the oesophagus as well as at the interface between the oesophagus and crop, but not in the crop diverticulum. GIT of birds is followed by proventriculus, an analogue to real stomach in pigs, and hind part of the stomach – ventriculus or gizzard – specially modified for grinding food as functional analogue of the teeth. The gizzard's muscles are protected by a tough layer made of the carbohydrate-protein complex koilin, thus birds feel to pick the small stones for better grinding the particles of feed into the GIT. Beyond the gastric apparatus the avian digestive system shows less striking deviation from the general vertebrate pattern (Moran, 1982; Lewis and Southern, 2000; Sturkie, 2012; Marshall, 2013).

Chicks have a very similar small intestine compared to that of pigs. A duodenum, jejunum, and ileum are defined, although these segments are not as histologically distinct. The proximal small intestine receives bile from the liver and digestive enzymes from the pancreas, and the absorptive epithelial cells are decorated with essentially the same set of enzymes and transporters as in pigs. The mucosa of the small intestine "envelops" the nutrients released by the hydrolytic processes (glucose from starch; amino acids and peptide from proteins and fatty acids and monoglycerol from lipids) and from here they may be absorbed into the metabolism (Gray, 1992). On the way between the ileum and a relatively short colon, chicken has two caeca instead of one. Termination of the GIT is presented by the rectum in swine and cloaca in fowl. Cloaca combines the function of the rectal ampoule and urinary bladder, found in pigs as separated. Cloacal contraction moves all accrued faeces and urine out together (Moran, 1982).

The growing evidence exists of a connection between good animal performance and microbiota composition in the hindgut (Rinttilä and Apajalahti, 2013; Wang *et al.,* 2020). The disappearance in the hindgut, whether of carbohydrates or proteins, concerns 10 to 20% of the whole phenomenon of absorption all along the gut. The microbial fermentation of digesta to recover available nutrients, particularly energy around 5-15% of maintenance requirements for poultry as well as swine. However, the method employed by the large intestine to recover nutrients is strategically different between both species: fermentable substrates concentrate in the caeca of fowl whereas swine employ extensive microbial exposure through the entire colon with all indigesta after a short residence in the cecum. Both locations foster fermentation by exchanging microflora extensively embedded in surface mucin (Moran *et al.,* 2022). The mucin synthesis regulation is in concert with microbial colonization of the gut in mammals and they are important components of the innate immune system (McGuckin *et al.*, 2011). Whereas in poultry, the developing microbiome and diet are the two primary sources of antigens encountered by gut associated lymphoid tissue in the first day post hatch (Friedman *et al.,* 2003).

For both species, the feedstuff digested by the small intestine provides the greatest proportion of dietary nutrients for the body, with far lesser amounts being subsequently recovered by the large intestine (Just *et al.,* 1981; Riesenfeld *et al.,* 1980) by absorbing and metabolizing bacterial fermentation products, lactic and volatile fatty acids (VFA). The absorptive surface not only relates to the luminal surface area of the small intestine but also to the characteristics (*i.e*., length, width, and density) of villi and microvilli. Chickens have a 1.2-fold larger total absorptive surface area per unit of body weight than pigs: 43.3 versus 36.7 cm^2 per g body weight (Chivers and Hladik, 1980; Mitjans *et al.,* 1997).

The contribution of the large intestine in the whole digestion is not the same for carbohydrates or nitrogenous matter and seems rather more efficient for the former than for the latter – the major dietary carbohydrate, absorbed as glucose almost completely in the lower jejunum. The undigested residues reach the hindgut in large quantities when excessive levels are present in the diet, a more or less intense bacterial breakdown occurs, with the production of VFA. The principles of protein digestion in poultry are very similar to those in pigs. In chicken only the proventriculus of the gastric region is secretory and initial proteolysis under acid conditions occurs there and in gizzard, while in pig it is happening in stomach. However, according to Chen (2017), broilers showed a higher (*i.e.,* 2-10 %) ileal protein digestibility than pigs for most cereal grains and vegetable protein sources since broilers have a greater size of the GIT relative to their body than pigs. Protein digestion requires adequate interactions between digestive enzymes and dietary protein, however, a fast passage rate of digesta along the GIT, in birds, therefore, might hinder protein digestion. On average, pigs have a longer retention time of digesta in the stomach than poultry in the small intestine (Weurding *et al.*, 2001; Wilfart *et al.*, 2007; Liu *et al.*, 2013). Dietary protein can also be fermented by the commensal microbiota in the GIT, which mainly occurs in the colon of pigs and the caeca of poultry. Dietary protein degraded in the hindgut by microbial fermentation does not significantly contribute to AA supply for both animals and therefore does not directly affect the nutritional value of protein sources.

To conclude, from a modelling point of view the entire digestive tract is relatively simple in both species in terms of the organs involved. Digestive organs are connected in a continuous musculo-membranous tube with certain regions that have different structure and functional elements providing optimal conditions for the digestion and absorption processes. After ingestion and digestion of a feed by an animal, the absorbed nutrients enter the metabolism. The energy of ingested feed becomes available only after the macronutrients contained in it (carbohydrates, fat, and protein) are transformed into less complex structures by underlying a series of reactions during the digestion process: carbohydrates (starch and sugar) to simple sugars such as glucose; proteins to amino acids and peptides; and fats to fatty acids and other compounds such as glycerides. Thus, the simple compounds are used in the animals' metabolism to build the main components of their own body after the adjustment for net absorption and urinary losses – some of the mass of feed is lost for example as a result of incomplete digestion (faeces), non-balanced metabolism (urine) or CO_2 as a product of respiration (Emmans and Oldham, 1988; Rubinstein-Litwak, 2003).

The principles of nutrient use mechanisms are general and when a trans-species approach is used the common points and the specie specificities have to be highlighted. Feedstuffs' nutritional compounds go through a complex series of chemical processes before contributing to the animal body as "growth", and the regulation of energy intake by birds has many of the features observed in mammals. Either pig or chicken, as well as any other animal, attempts to consume a sufficient amount of energy from feed to be able to meet its nutrient requirements meant to satisfy the maintenance and production needs. Productive processes include the synthesis of new tissue (made of protein, water, ash, and fat) in growing animals as well as reproduction in mature animals. In the adult animal of constant body weight, the balance between energy intake and its output is in equilibrium. During growth, the balance is positive, *i.e.*, resulting in body weight gain. The balance is negative when energy expenditure is greater than intake (Blaxter, 1989). While nutrients are converted to gain or other animal products, the nutrient transactions are never 100% efficient and there is also some obligatory loss. In course of nutrient metabolism heat is producing, that is from energetic point of view the inefficient part of energy transactions. Heat is a result of processes related to nutrients utilization (catabolism) and synthesis (anabolism) for maintenance and production.

The environmental conditions in which the animals are kept are of high importance as an efficient animal performance is only possible when heat production is not unfavourably affected by housing conditions or climatic environment (Verstegen *et al.*, 1995). On another hand, metabolism per gram tissue or BW is regressively related to the size of the animals. In relative terms, metabolic rate is less for the pig being a larger animal. The smaller animal – like chicken – operates at higher metabolic rates and, therefore, it consumes more oxygen to meet its energy demands and maintain its homeothermic body temperature. In a perspective of energy exchange, this is partly due to the fact that loss of energy as heat is proportional to the surface area, whereas heat generation is proportional to an animal's body volume. A small animal has more surface area in relation to its volume than a larger animal does (Kardong, 2018).

The energy accretion and partitioning by the alive organism are guided by the same rules of energy transformation, therefore, there is a possibility to develop a generic model with species specifications of energy pathways and transactions to be taken into the account.

3.3.2. Energy utilisation and energy partitioning

The concept of dietary energy flow is valid for all homeothermic animals as well as humans. This is a great example of how a certain phenomenon can be described with a trans-species approach. The energy intake as feed can be considered as an enthalpy of combustion of the dry matter of the feed consumed, it is expressed as gross energy (GE) of feed (Kleiber, 1961). Digestible energy (DE) is the GE of the feed minus the heat of combustion of the energy lost in faeces. The DE intake may be calculated from the digestible nutrient intake, and indigestible energy is a major variable in the evaluation of feed ingredients. Since birds excrete the faeces and urine in a mix, there is no exact data on dietary DE content of poultry feeds. Yet, it may be assumed from the digestible nutrient intake or easily and safely measured in crates, estimated from *in vitro* methods, as well as simply appraised from feeding tables or from a digestive model (Bastianelli *et al.*, 1996; Roger *et al.*, 2018). By definition, metabolizable energy (ME) is DE minus the heat of combustion of the urinary energy and of gases produced in the intestinal tract. ME is divided further into net energy (NE) and heat increment (HI). HI is the heat produced by the digestion and metabolism of nutrients, and by fermentation in the intestinal tract. Besides being considered as energy waste, together with a remaining energy, it is foremost used to meet the requirement for maintenance (NEm), including the energy needed to sustain life and to maintain body temperature. And, if the supply of NE is greater than the energy required for maintenance, it is used for production (NEp, growth, or reproduction). Hereby, heat production (HP) is the sum of the HI and NEm. The comparison of theoretical schemes for ingested feed's energy utilization and its partitioning into the animal's body for both species is illustrated in Figure 3.

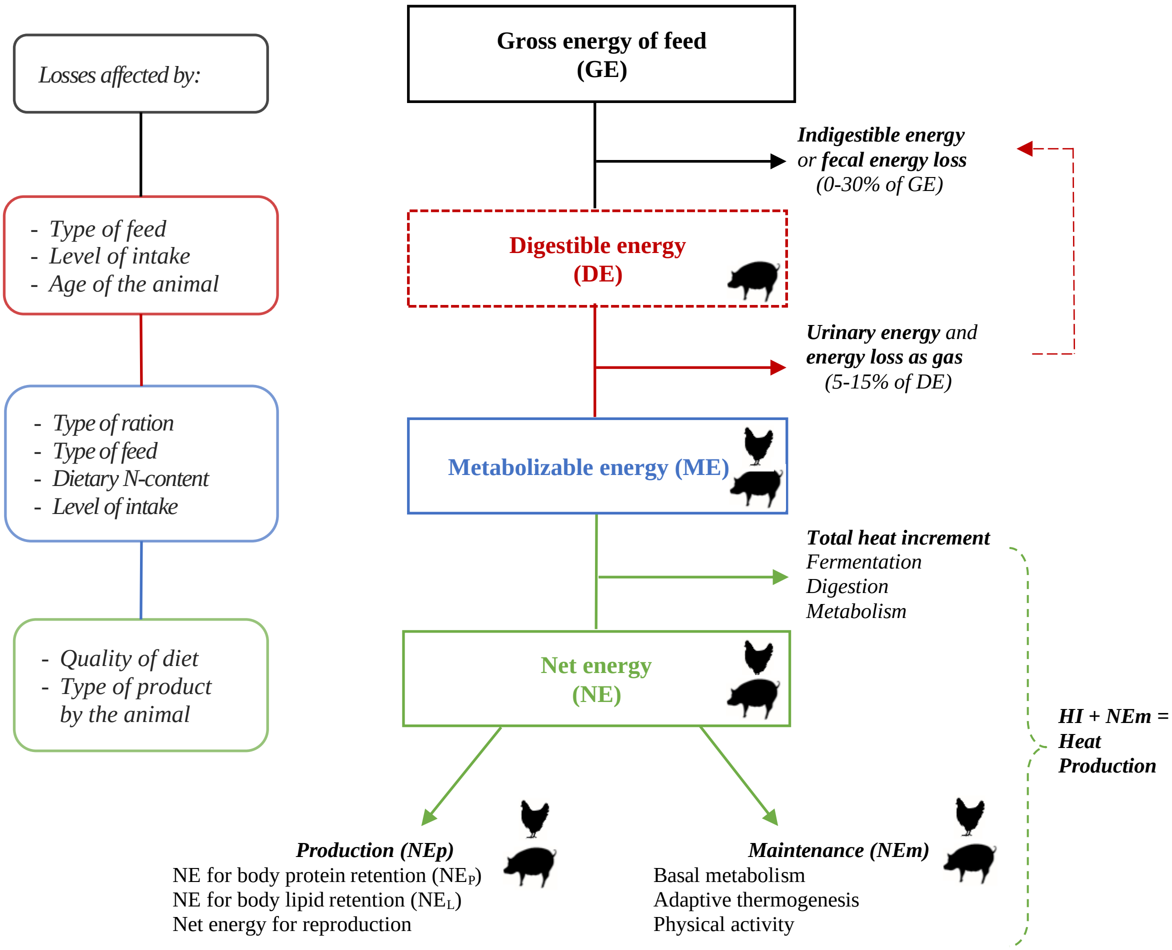


Figure 3. Schematic representation of energy partitioning comparison for pig and chicken

DE is used in pig nutrition in few countries, but ME and NE are also used in many countries. In poultry, there are four types of ME value defined: the apparent and true metabolizable energy (AME and TME) and the apparent and true metabolizable energy corrected for zero nitrogen retention (AMEn and TMEn). Though these four types of ME value are in use, it is not always obvious which type is being reported and additional confusion occurs because values of a particular type may vary depending on the assay procedures used in their derivation. The AME is termed "apparent" because in this system some of the energy that is of non-dietary origin is not considered in the calculation routine. This part consists of endogenous origin materials like gut cells and mucins. TME is expressed GE of the feed minus the GE of the fecal and urinary excreta of feed origin, and by definition a correction should be made for endogenous energy losses. Although, ME corrected for zero nitrogen retention (AMEn, TMEn) is widely used in most countries, the correction is based on the premise that the energy evaluation should precisely estimate the energy yielding capacity of the feed rather than its impact on protein gain. However, considering that in producing animals the

N-retention is positive the reliability of correction for zero N-retention is often debated (Ewan, 2000; Leeson and Summers, 2000; Latshaw and Moritz, 2009).

3.3.3. Net energy system in poultry feeding

NE is, by definition, the most precise energy evaluation system, since it estimates the "energy yield" of the feed that is used directly for maintenance and production. Noble *et al.* reviewed (2010; 2013) that for any animal species and at any stage of production, NE system would be a closest estimate of the "true" energy value of a feed than DE or ME. It seems substantial that the same energy system is used for expressing the diet energy values and for the animal energy requirements. Experiments indicated that the energy cost of growth or the daily energy requirement of an animal are independent of diet composition when expressed on a NE basis, and results have clearly demonstrated its superiority in the case of pigs (Noblet *et al.*, 1994).

Due to technical difficulties for evaluating energy in pigs and poultry as the absolute energy values, the measurement of NE is rather complex and requires specific equipment and expertise (Noble *et al.*, 2021). However, the NE of a compound feed can be calculated by using of tabular values of ingredients or estimated by empirical equations based on chemical parameters and/or the *in vitro* digestibility of organic matter, as well as by near-infrared spectroscopy (NIRS, Paternostre, 2022).

On another hand, even though determination of dietary NE is the final objective in energy evaluation of feeds, most attention should be paid to the accurate estimation of DE or ME values. Intake of digestible nutrients and energy as well as metabolizable energy is the most important factors of variation of the net energy value of poultry or pig feeds. NE as a percentage of ME content corresponds to the efficiency of utilization of ME for NE (*k*). The *k* value is often given a subscript to indicate the fate of the used or retained energy: k_m – maintenance; k_p – protein deposition; k_f – fat deposition; k_o –egg production in laying hens or k_l – lactation in sows. Because of the different energetic efficiencies of the chemical transformations involved in these processes, *k* for a given feedstuff can vary, depending on intake and on the physiological state of the animal.

Caro *et al.* (2018) stated that using NE system makes also possible to overcome the problem related to the variations in HP between ingredients of feeds thus it helps to adapt the feed composition to the climatic conditions for raising the animals. This issue becomes more important with the rapid increase of (monogastrics) animal production in the warmer parts of the world.

The interest in using NE instead of DE or ME in swine nutrition comes from the fact that the NE/DE or NE/ME ratios are affected by the extent of fibre digestion, as the main source of variation in NE content of feeds relies on the levels of digestible and indigestible nutrient contents (fibre or components that change digesta viscosity). In poultry, the extent of fibre digestion is very low

(Jamroz *et al.*, 2001; 2002), which might decrease variations in NE/ME ratios and, thus, reduce the interest of a NE system. However, NE is obviously a completer and more direct indicator of the animal's feed use mechanisms than ME, but it is more prone to variability for real biological reasons (MacLeod, 2002). Therefore, despite all the advantages for swine, in poultry nutrition the NE system remained little or even not used recently.

Lately, both broiler and layer stocks being produced by a limited number of multinational breeding companies and subject to similar husbandry methods. Thus, their NE requirements are relatively consistent and, given the range of feeds normally included in poultry diets, the efficiency of ME utilization does not vary to any great extent at thermoneutral conditions. However, modern poultry production is highly competitive, and it has been indicated that different energy substrates may be used with different efficiencies (Gonçalves *et al.*, 2020). In particular, ME supplied as fat is used more efficiently than ME supplied as carbohydrate or protein. As a result, there has been renewed interest in NE systems for poultry, which might include equations for predicting NE values from ME values (De Groote, 1974; Pirgozliev and Rose, 1999; Noblet *et al.*, 2010; van der Klis *et al.*, 2010; Swick *et al.*, 2013; Carré *et al.*, 2014; Noblet, 2015; 2021), although, the number of studies devoted to NE calculation is much more limited in poultry than in pigs.

Based on the theory of energy flow it is reasonable to conclude that diets formulated on NE basis can give a significant advantage over those formulated on ME. The reliability is strengthened by the fact of the true additivity of NE values in feed formulation (Choct, 2004). Broiler studies – conducted by Carré *et al.* (2013; 2014) – supplied reliable data to develop equations for NE. Those data allowed both AMEn and NE values to be predicted and evaluated. The experiments included measurements on using 30 different diets and performing body analyses measuring protein and lipid depositions from 21 to 35 days. According to the high variability in nutrient content of feeds it was feasible to obtain conversion factors to determine the NE supply from each macronutrient. Carré *et al.* (2014) deduced that the NE/AME efficiency ratios assigned to dietary components were 85, 79, and 68.7 % for ether extract (lipid), starch, and crude protein, respectively. With regard to poultry, the ranking between nutrients for NE/ME is similar to what is observed in pigs (Noblet *et al.*, 1994) but with smaller differences between nutrients (Table 1.)

Wu et *al.* (2019) generated equations predicting NE, and NE/AME using AME value and chemical composition of feeds, which were further validated on a separate set of diets with high correlation (r = 0.99) and accuracy. In the experiment the 25- to 28-day-old broilers were fed 19 diets formulated with varying nutrient composition. The NE/AME ratio was 0.89 for oil, 0.72 for canola meal, and 0.80 for grains in broiler feeds, while for laying hens, according to Barzegar *et al.* (2019; 2020), the NE/AME ratios were 0.92, 0.62, 0.75, and 0.74, respectively, for the canola oil, SBM, corn, and wheat. These data also indicate that the nutrient content, particularly the protein and fat content, has a significant impact on HI, therefore use of NE system is more precise and reasonable.

Table 1. NE/ME (AME for poultry) efficiency ratios comparison for ether extract (lipid), starch, and crude protein (CP)

Publication	Lipid	Starch	CP
De Grote, 1974 (broilers)	90	75	60
Noblet *et al.*, 1994 (pigs)	90	82	60
Van Milgen *et al.*, 2008 (pigs, InraPorc)	89	86	59
Carré *et al.*, 2002 (broilers)	84	78	68
Carré *et al.*, 2014 (broilers)	85	79	68
Wu *et al.*, 2019 (broilers)	84	79	50

NE has a great potential and thus it should be implemented in poultry. Application of NE in practical feeding likely makes improvement in accuracy of poultry nutrition and profitability of the sector (Noble *et al.*, 2021). NE system seems to be good enough as a tool for energy evaluation, nevertheless in a combination with a dynamic approach (in terms of precise estimation of requirement day-by-day as growth is dynamic by nature) it opens the new perspective of feed evaluation system and maximally support the application of precision nutrition for a poultry.

3.3.4. Protein utilization and amino acid partitioning

Protein is a major constituent of the biologically active compounds in the body, and it assists in the synthesis of body tissue for its renovation and growth. It is an important nutrient for growing animals affecting its performance, total feed cost and nitrogen (N) excretion. The N excretion is derived from the difference between the protein intake and retention. If dietary protein is inadequate, there is a reduction of growth and/or productivity, leading to withdrawal of protein from less vital body tissues (like muscle tissues) for maintaining the functions of more vital tissues (gut, viscera). Whereas the protein oversupply is costly both biologically and economically and leads to the excessive N excretion with a potentially negative environmental impact (van Milgen and Dourmad, 2015).

Dietary proteins, simply put, are macromolecules mainly composed of amino acids (AAs), which are building blocks for proteins in the body. There are 20 AAs in animal body proteins, and all are physiologically indispensable, while nutritionally, these AAs can be divided into essential (EAA) – those that animal cannot be synthesized at all or rapidly enough to meet metabolic requirements (semi-essential), and nonessential (NEAA) amino acids – those than can be synthesized *de novo* from other AAs.

The presence of adequate amounts of NEAA in the diet reduces the necessity of synthesizing them from EAA. The AA requirement of an animal includes requirement for maintenance for recovering endogenous gut loss, integument (feather and hair) loss, as well as urinary endogenous losses (AAs for numerous metabolic functions other than protein deposition) and for production of animal protein (*i.e.*, growth as a tissue accretion, reproduction as foetus or egg development and lactation).

The AAs such as Lys, Met, Thr, Trp, Phe, His, Val, Ile, and Leu are dietary essential or indispensable AA for the pig and chicken as these animals do not have the metabolic capacity to synthesize the carbon chains of those AA. The carbon chains of Ser, Gly, Arg, Ala, Pro, Glu, Gln, Asp, and Asn can be synthesized *de novo*. Although the pig has the potential to synthesize these AAs, it does not mean that the synthesis capacity is sufficient to fulfil the requirements. Arginine is often considered as one of the non-essential AA pigs (except in the young ones) as in ureotelic animals, such as mammals, the metabolism of Arg is related to the urea cycle and can be synthetized from ornithine, ammonia, and the amino nitrogen of aspartate. However, Arg is an essential AA for birds, uricotelic organisms, as urea cycle in avian species is not functional due to the lack of carbamoyl–phosphate–synthase–I and low activity of arginase and ornithine transcarbamoylase (Khajali and Wideman, 2010; Freedland, 2012).

The dietary NEAA and EAA are necessary for the survival, growth, development, reproduction, and health of animals. Because body proteins are in a dynamic state, with synthesis and degradation occurring continuously, an adequate intake of dietary AAs is required. AA requirements are quantitatively determined by the phenotypic potential to deposit protein or to synthesize egg protein. This means that actual AA requirements occur at the tissue level. Table 2 demonstrates the AA profile of empty feather-free body, feather, and endogenous gut and urinary losses, as well as coefficients of AA efficiency in feather-free body protein deposition. Though, AAs provided by the dietary protein have to be digested, absorbed, and transported to the target tissue and they may be (partially) catabolized before reaching the target tissue. Consequently, there is a potential discrepancy between the supply (*i.e.*, the AA content in the feed) and the demand for AA (*i.e.*, those ready to be deposited in protein).

Digestion, absorption, and utilization processes in the body can affect bioavailability of the ingested nutrients. An interest in AAs bioavailability in feedstuffs has increased during the last decades, partly due to the development and increased use of more rapid digestibility assays that have permitted more research to be conducted.

Measures of ileal digestibility (ID) are used routinely as estimates of protein quality and AA bioavailability in pig and poultry feedstuffs. Values for ID may be expressed as apparent (AID), standardized (SID), or true (TID). Values for AID are calculated simply by deducting the total ileal outflow of AA from dietary AA intake. In this term the calculation does not consider the source of

Table 2. Essential amino acid (AA) content of empty feather-free body protein (BP), and feather protein (FP), as well as coefficients for basal endogenous AA losses from the gut ($AA_{endogen}$, g/d), the urinary AA losses due to basal protein turnover ($AA_{urinary}$, g/d) and coefficients of AA efficiency in feather-free body protein deposition (k_{AA})*

	g/g of BP[1]	g/g of FP[1]	$AA_{urinary}$ (g/d)[2]	$AA_{endogen}$ (g/d)[3]	k_{AA}[2]
CP	1.000	1.000	0.3611	5.237	0.85
Lysine	0.0684	0.0217	0.0239	0.233	0.77[4]
Methionine	0.0196	0.0052	0.0070	0.087	0.64
Cystine	0.0097	0.0683	0.0047	0.161	0.37
Tryptophane	0.0100	0.0074	0.0035	0.117	0.70
Threonine	0.0388	0.0449	0.0138	0.442	0.73[4]
Phenylalanine	0.0367	0.0465	0.0137	0.301	0.82
Tyrosine	0.0294	0.0332	0.0090	0.326	0.67
Leucine	0.0686	0.0751	0.0271	0.403	0.76
Isoleucine	0.0372	0.0431	0.0124	0.273	0.67
Valine	0.0387	0.0572	0.0164	0.334	0.73
Histidine	0.0248	0.0098	0.0102	0.125	0.93
Arginine	0.0618	0.0683	0.0010	0.275	0.77
Met+Cys	0.0880	0.0269	0.0117	0.124	0.78[4]

* [1] taken from the studies of Wecke *et al.* (2018a), except for tryptophan – Stilborn *et al.* (2010); [2] Taken from InraPorc (Van Milgen *et al.*, 2008); [3] taken from Adedokun *et al.* (2011) and Adeola *et al.* (2016); [4] taken from the studies of Sakomura *et al.* (2015).

AAs in the digesta which is the sum of endogenous losses ($IAA_{endogen}$) and non-digested dietary AA. The $IAA_{endogen}$ may be separated into *basal losses*, which are not influenced by feed ingredient composition, and *specific losses* induced by feed ingredient characteristics such as protein content, presence of anti-nutritional factors, and dietary level of fiber. Once the AID values are corrected for total $IAA_{endogen}$, then values for TID are calculated (Ravindran and Bryden, 1999; Stein *et al.*, 2007). Lack of additivity of AID values in feed formulation may be overcome by correcting AID values for basal $IAA_{endogen}$ only, which yields SID values. It is suggested that SID values are used for feed formulation. It is advisable that basal $IAA_{endogen}$ are measured in digestibility experiments and that these losses are reported with SID values, which is a common practice to express AA feed values and requirements (Donkoh and Moughan, 1994; Lemme *et al.*, 2004).

AA profile is a practical tool to formulate on each EAA and to safely reduce dietary crude protein (CP). It is important to formulate diets that meet energy and AA requirements while at the same time minimizing the excretion of excess energy and N into the environment. To achieve this goal, the digestion and utilization characteristics should be taken into consideration (Lemme, 2009; Kong and Adeola, 2014). Due to corrections for endogenous losses, both the AA value and the AA requirement are greater in a SID system compared with an AID system (van Milgen and Dourmad, 2015). The common approaches for reducing N excretion – that is favourable from both, economic and ecological points of view – are using synthetic AAs with reduced dietary crude protein content and/or adding enzymes to eliminate the anti-nutritional effects such as that of non-starch polysaccharides in poultry diets (Waldroup *et al.*, 2005; Nahm, 2007; Namroud *et al.*, 2008), as well as using phase feeding (Pope *et al.*, 2004; Méda *et al.*, 2011; Lin *et al.*, 2017).

3.3.4.1. Amino acid utilization and ideal protein concept

The profile of digestible EAAs entering the small intestine is the most important factor affecting the efficiency of protein utilization, which depends to a large extent upon the AAs composition of the diet. The closer the AA composition of the diet matches the animal's requirement, the more efficiently the dietary protein is utilized (Schutte *et al.*, 1994). From biological point of view not only the number of absorbed AAs, but the utilization of individual AAs is a key in protein deposition. The utilization coefficients for different AAs are assumed to be constant in broilers, being in the range of 0.73-0.98, in most nutritional model (Hurwitz and Bornstein,1973; Smith, 1978; Fisher, 1973; Fisher, 1994; de Lange *et a*l., 1995; van Milgen *et al.*, 2006; Nonis and Gous, 2008), which probably not the case because the closer the number of absorbed AAs gets to the requirement, the more of them will be oxidized (Lemme, 2003). Also, the effect of age on the efficiency of AA utilization is still not clarified. Since there is a continuous and dynamic protein turnover it is difficult to differentiate the AA utilization for maintenance and for production. To make it simple, in most modelling work the efficiency of AA utilization is applied only to AA used for protein deposition and not to those used for gut endogenous losses and integument. Thus, the SID AAs are assumed to be used with an efficiency of 1.00 (100%) for maintenance purposes. In the Table 2, the $AA_{urinary}$ and most of k_{AA} values are from InraPorc model, and these data are very important in modeling, despite the lack of information on those values for poultry in the literature.

An important progress in recent decades for pigs and poultry nutrition research was the development of the ideal protein concept (optimal proportions of EAA in the feed). The concept has been proposed in the late 1950s by nutritionists at the University of Illinois (Glista *et al.*, 1951; Fisher and Scott, 1954) for chicken and swine diets based on the belief that all NEAAs were sufficiently synthesized in animals. Based on the above-mentioned phenomena of the protein metabolism it is evident that the AA requirement is not just quantitatively but qualitatively should be completed.

The term ideal protein refers to a situation where all essential AAs are co-limiting for performance, so that the AA supply exactly matches the AA requirement. The requirements for AAs in ideal protein are expressed relative to Lys (*i.e.*, Lys = 100%). This expression is very useful from a practical point of view as Lys is typically the first-limiting AA in diets for pigs. Lysine has therefore received most of the nutritionists' attention and considerable research has been carried out to describe the change in Lys requirements during growth, gestation, lactation, or egg laying. Lys was chosen as the reference AA for poultry as well because it is relatively simple and straightforward used for protein accretion, thus, requirement is only affected very little by other metabolic functions (*i.e.*, maintenance requirement) or feathering as this is the case for Met+Cys. Since Lys is almost exclusively used for protein accretion, relatively high proportions of Met+Cys are required for feather growth and maintenance. Being that later is a function of BW, it increases with age. This underlines the advantage of Lys vs. Met+Cys as the reference amino acid for poultry (Lemme, 2003). Nevertheless, Lys is a limiting AA in reduced protein corn-soybean meal broiler diets, and the analysis for Lys is uncomplicated as there are no metabolic interactions between Lys and other AAs, in contrast to Met that can be converted to Cys (Baker and Han, 1994; Boisen *et al.*, 2000; Baker *et al.*, 2022; Lemme, 2003; Aggrey *et al.*, 2018; Whitacre and Tanner, 2018).

3.3.4.2. Amino acids to energy ratio in broiler diets

The protein deposition is a highly energy-demanding process. Available AAs can be used primarily for protein synthesis if energy for deposition is available. The underlying mechanism behind protein synthesis explain clearly why dietary Lys to energy ratio is crucial in broiler production. The simultaneous presence of AAs and energy as glucose in organs and tissues increase protein retention in both growing pigs and broilers (van den Borne *et al.*, 2007; Liu *et al.*, 2013). This could be explained by sparing AAs from being catabolised to produce energy in organs and tissues when sufficient glucose as an energy substrate is available (Chen, 2017). Moreover, the postprandial increase of glucose in the blood is commonly accompanied by an increased postprandial plasma insulin concentration. Insulin stimulates protein deposition and inhibits protein breakdown in muscle tissues (Bigot *et al.*, 2003).

Over age the requirements of digestible Lys increasing and for AME decreasing. Thus, supply of digestible Lys and energy is in disparity with their requirement over most of the production. Also, the magnitude of over and under supply of digestible lysine and energy is greatest within the first half of the production cycle, – a critical time for development and growth. With the nutrient requirement not precisely met throughout the production, a depression in growth (in the case of under supply) or inefficient use of nutrient (in the case of over supply) is probable, and costly for industry. Therefore, the precision feeding concept of increasing dietary phases by blending rations to meet the daily energy and lysine requirements may improve production and reduce feed costs while increasing the environmental load (Moss *et al.*, 2021).

3.3.5. Role of the phosphorus in the body, its utilisation and partitioning

Besides chemical composition of the feed, such as energy and AA contents of the diet, the calcium (Ca) and particularly phosphorus (P) can be limiting for growth performance as well as in reproduction. The major store of Ca and P is the skeleton where the cationic and anionic forms, respectively, of these minerals connect to form hydroxyapatite $Ca_{10}(PO_4)_6(OH)_2$– the primary mineral salt in bone. It confers rigidity on the bone matrix with Ca and P ratio about 2.21:1–2.46:1 with an average of 2.32:1 (Han *et al.*, 2016), although other less stable (amorphous) calcium phosphates may also be produced (Glimcher, 1984). In each physiological state, there is a recommended Ca to P ratio that enables the highest growth performance and bone mineralization. More than 70% of ash in the animal body consists of Ca and P, with about 99% and 80%, respectively, present in the bones. The bone store of Ca and P can be available during disturbances in mineral homeostasis, and it protects internal organs such as the brain, heart, and lungs (McDowell, 2000).

Ca is the most abundant mineral in the body, is indispensable for bone mineralization and eggshell formation, nerve impulse propagation and muscle contraction, and blood coagulation (Klasing, 1998). Whereas P, being the 2nd most abundant mineral and it is crucial for the body homeostasis as a key component of nucleic acids, mediator of energy metabolism (through adenosine triphosphate and creatine phosphate), buffer agent, and a major mineral component of bone but also integrated in phospholipid membrane (Li *et al.*, 2016). P equally important roles in both soft (lean) and hard (bone) tissues. Its total amount presents approximately 20% in soft tissues and exchanges of P between two pools can protect the animal from P deprivation (Suttle, 2010). Bone and lean tissues have different roles in P metabolism. Bone P has a kind of structural function and serves as a reservoir for Ca and P that can be mobilized up to a certain limit. Whilst the concentration of P in muscle and viscera is constant as P in soft tissues has a functional role.

The animal body contains 4-7 g P/kg, depending on species and stage of growth (Humer *et al.*, 2015). The animal growth, health, and well-being rely on prudent P supply which is, however, a non-renewable resource with some current global reserves that may be depleted in further decades (Cordel *et al.*, 2009). Thus, in swine and poultry diets, P is the 3rd most expensive nutrient after energy and protein (Létourneau-Montimy *et al.*, 2011; Li *et al.*, 2017).

3.3.5.1. Digestion of phosphorus

Cereal and legume grains are the major component of non-ruminant diets and have very low concentrations of Ca, but high P concentrations. However, most of dietary P is bound by phytate (phytic acid) and is considered not biologically available. The endogenous mucosal phytase in monogastric organisms appears incapable of hydrolyzing sufficient amounts of phytate-bound P and, thus, due to lack of adequate endogenous phytase activity in digestive physiology and metabolism of monogastric species, P concentration in their manure is high (Ravindran *et al.*, 1995; Singh, 2008). Consequently, only 20 to 40 % of total P intake is available for further utilization and significant amount of P is excreted (Jondreville and Dourmad, 2005). Therefore, supplementation of exogenous microbial phytase in diets is a common applied method to increase mineral and nutrient absorption and decrease its excretion.

Nevertheless, it is important to differentiate between *digestible P* and *available P*, as bioavailability encompasses digestion, absorption, and utilization of P. Digestible P is the portion of dietary total P that is not recovered in faeces. Available P (avP) is the quantity of P that is absorbed from the diet by the animal, it is also called precaecal digestible P or ileal P digestibility (WPSA, 2013). P bioavailability can differ between broilers, turkeys, and ducks and differences may also exist between broilers and laying hens. As reviewed by Li *et al.* (2016), there are many factors affecting phytate P utilization and P bioavailability, including: experimental techniques; the chemical form of P; dietary concentrations of fibre, Ca, P and vitamin D_3, energy, protein, fat, and vitamin K; the availability and interaction of other nutrients in the diet, feed processing, and particle size; animal physiological and health factors, such as feed consumption, growth rate, sex and age; management factors, including ambient temperature and lighting program. Wang *et al.* (2022) suggested as more reasonable to use the ileal P digestibility of feed phosphates when formulating diets in broiler chicks.

3.3.5.2. Partitioning of absorbed phosphorus

After digestion certain amount of Ca and P will be available for absorption and further utilization. Due to growth, metabolism, and physiological turnover, the organism exchanges and subsequently also excretes P which should be steadily replaced by adequate diets (Humer *et al.*, 2015). Part of P requirement is attributed to maintenance needs and rest is used for growth or reproduction. The maintenance P needs are the sum of endogenous P excretion from the faeces (digestion) and urine (metabolism), and the replacement of P related to feather development and feather loss in birds.

The endogenous P excretion in pigs has been estimated to be approximately 7 mg/kg of BW of which 6 mg/kg of BW are attributed to endogenous fecal P output, and 1 mg/kg of BW is attributed to urinary P (Jongbloed and Everts, 1992). Published data on ileal endogenous P losses in poultry are limited, and the values particularly for endogenous P losses in broiler chickens (as well as for other animal species) vary widely depending on the assay diet used. The ileal endogenous P losses determined with the casein-based diet was reported to be 438 mg/kg DM intake by Mutucumarana and Ravindran (2020) and agree with the finding of Rutherfurd *et al.* (2004) – 446 mg/kg DM intake, using a minimal P diet supplemented with amino acids. Dilger and Adeola (2006) obtained an overall endogenous P estimate of 235 mg/kg of DMI and expressed on an absolute basis with using the average DMI of 372 g per chick, the endogenous P loss of 87.4 mg/d per chick was defined. Van Krimpen *et al.* (2002) reported endogenous P losses to be 14 g P/kg, and 32 g P/kg of dry manure for poultry and pig, respectively.

Mutucumarana and Ravindran (2020) compared the ileal and excreta endogenous losses and concluded that a higher endogenous P in the excreta of birds fed P-free and gelatine-based diets suggests an increased P output via urine when diets contain little or no Ca. A study by Liu *et al.* (2013) has shown that Ca deficient diets lead to lower P retention in broilers.

Ca and, to a lesser extent, P are tightly regulated in plasma, and Ca and P homeostasis in birds appears to be very similar to that in mammals (Proszkowiec-Weglarz and Angel, 2013). The interactions of Ca and P with vitamin D_3 are important when defining the requirements of various classes of pig and poultry for these minerals. Like in mammals, the presence of vitamin D receptors has been documented in various chicken tissues, and these interrelationships determine Ca and P homeostasis, which is regulated by the intestine, bone, kidney, and the parathyroid gland. The Ca metabolism has less control in the gut and greater control in the kidneys (Li *et al.*, 2016). The factors that determine intestinal absorption and reabsorption and kidney excretion go along with endocrine regulation (Vitti and Kebreab, 2010). As absorption and utilization of P in pigs and poultry is related to that of Ca, P and Ca requirements must be studied together. For the retention of Ca and P in the body, both minerals need to be available in bone cells, and a low concentration of one mineral will prevent bone synthesis and cause excretion of the other mineral in the urine (Al-Marsi, 1995; Liu *et al.*, 2013; González-Vega and Stein, 2014).

These factors coordinate the animal-intrinsic responses to balance absorption (gastrointestinal tract), storage (skeleton), and excretion rates (kidneys). P homeostasis also depends on several even contradictory factors such as regulators, transporters, and endocrine and paracrine signals whose endocrine function and integration into networks have not yet been clearly identified (Rosemarin *et al.*, 2021).

Overfeeding of dietary P is quite common on commercial farms, with excesses of 20 to 100% over requirement (Applegate and Angel, 2008; 2014). To minimize oversupply of dietary P, it is crucial to formulate diets at correct Ca/P ratios, and thus to know the digestibility of Ca and availability of P in the ingredients used. It is nearly 30 years since the NRC (1994) last prescribed the poultry requirements for Ca and avP values were given for requirements as well as for ingredients. The Ca/avP ratios recommended were 2.22 to 2.28 Ca to 1 P throughout growth. As reviewed by Proszkowiec-Weglarz and Angel (2013), avP term was used instead of nonphytin P (NPP) from NRC (1977), however, P values did not change: the recommended Ca to NPP ratios in 1977 were 2.22 to 2.67 Ca to 1 NPP depending on growth stage. In the intervening period, broiler and layer genetics have changed greatly, housing and management have improved, and diets have changed. As in other species, though, some over formulation of dietary P occurs in poultry production too, because of the variability in the P content and the (bio)availability of P in different sources for chicken or hen (Knowlton *et al.*, 2004).

4. MAIN CONCLUSION FROM THE LITERATURE

Growth is a complex phenomenon that is highly determined by dietary nutrient supply. One of the greatest challenges in precision livestock farming is to be able to precisely meet the animal's dietary nutrients according to its actual requirements – thus to apply precision feeding. Nutrient requirement is changing as the animal grows over time, depending on feed and genetic potential of the animal, as well as the environment. By considering interactions that occur between many factors, which influence growth and development, simulation models have the capacity to greatly simplify a certain phenomenon what is otherwise a part of a large and complex biological system. Simplification helps us to understand the mechanisms and through that to develop better feeding strategies as well as to define the appropriate environmental conditions.

Modeling captures the main characteristics of the process by introducing the most important and determinant pathways of the system. Thus, growth models in case of two kind of animals such as pig and chicken, can share the same core. And, despite the anatomical differences, there are examples on using generic models in animal nutrition for both species as they display many similarities in their digestive (Létourneau-Montimy *et al.*, 2011; Roger *et al.*, 2018) and metabolic processes (Emmans, 1981; Gous *et al*., 2006). The energy flow model is valid to all animals and even to human, and also the protein evaluation systems are very similar in monogastric animals.

There are some examples that models are interconvertible among species because of the conceptual similarities with respect of nutrient use for protein and lipid deposition. There are a few, but very limited number of metabolic models with a trans-species approach that have proved to be reliable in simulating the animal performance: *i.e.*, Emmans (1981) to EFG (1995), or Emmans (1994) and Ferguson *et al.* (1997) to Avinesp (2015). Those models are, however, not transparent since they are used in commercial animal feeding extension service, thus the developer has no interest in making them (the internal equations) available. Therefore, the hypothesis of the present work is that an available, well-defined dynamic mechanistic and deterministic pig model core can be used in development of a broiler model. In the course of the model development, there is a need to develop specie specific equations when the pig model is transposed to poultry. Furthermore, if reliable Ca and P partitioning model is ought to be developed, it should be integrated into the energy and protein metabolism model. According to our knowledge that integrated model has not been developed yet for poultry.

A generic dynamic mechanistic model will help to understand the nutrients partitioning and their interactions, and can be used as a tool in education and practice to develop sustainable feeding strategies.

5. OBJECTIVES OF THE DISSERTATION

The main goal of the dissertation is to develop a generic, dynamic mechanistic and deterministic model that is able to simulate the rate of changes in nutrient partitioning and performance of domestic chicken (*Gallus gallus domesticus*) at different age over the certain period of time. Based on the conceptual similarities of nutrient use mechanisms in pigs and poultry, our hypothesis is that a model core valid for growing and fattening pigs can be used as a starting point for a broiler growth model. Thus, the further aim was to evaluate the extent and how reliable a publicly available and widely used growth model for pigs can be transposed to broiler chickens.

The purpose of the metabolic model is to give a “calculation engine” for predicting the actual animal production in response to different nutrient supplies. To make a comprehensive simulation model not only the protein and energy partitioning, but the mineral, particularly the Ca and P partitioning must be integrated, since in practical conditions dietary available P can be limiting in growth and production. Also, P partitioning module can be a useful tool to estimate the P requirement of the animals precisely, and to predict the optimal level of the digestible P in the feed for different sexes or strains. Thus, the specific objectives of this dissertation are:

1. To develop a post-digestive metabolic dynamic mechanistic model by using a generic approach to nutrient partitioning for broilers, predicting the chemical body composition without major changes in the core structure of the pig model.
2. To conduct sensitivity analysis and to challenge the broiler model with experimental datasets in order to study the model behaviour and its reliability.
3. To extend the energy and protein metabolism model with a module that is able to simulate the P partitioning thus the P retention and excretion in broilers from digestible P intake.
4. To provide case studies on the benefit of model application related to environmental footprint of broiler production.

6. MATERIALS AND METHODS

6.1. Model description: Energy and protein partitioning

There are number of models predicting energy and protein utilization in pigs and poultry. Despite their differences, pig and chicken share many similarities in their physiological processes of digestion and metabolism. 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. Unlike other potential candidates InraPorc model (van Milgen *et al.*, 2008) was fully available and sufficiently detailed 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.

Thus, the InraPorc pig model was used as a starting point, it simulates the utilization of dietary energy and protein in growing and fattening pigs. The amount of ingested feed per day is estimated based on body weight (BW) and phenotypic traits. InraPorc model is based on the idea that protein deposition is determined by the phenotypic potential of the animal when it is fed *ad libitum*. The actual protein deposition will not surpass the phenotypic potential but can be lower due to an insufficient supply of essential amino acids (EAA) or due to a feed restriction. The net energy intake is used for maintenance and to sustain protein deposition, and the surplus energy is used for body lipid deposition. Based on protein and lipid deposition, growth performance is predicted on a daily basis and for the average individual. The same general principle was used in the course of the development of the generic model for poultry (MsChick model) with some specific adaptations for broilers.

Modeling process commenced with studying each equation from the pig model and evaluating the parameter values and conformity to be applied for chicken. Unlike in poultry sector, the (anatomical) body composition is less important for pig producers, therefore most pig models, including InraPorc, estimate the BW and the chemical composition of the body (and the gain) rather than, for example, the yield of ham. Poultry performance studies typically report on breast yield. Therefore, broiler model was developed to be able to estimate not only the body chemical composition but the valuable carcass parts as well.

The partitioning of total protein (TP) into an empty body as the proportion of keratinized protein is quite different in pig's and chicken's bodies. A considerable part of protein is retained in feathers in birds, and the AA composition of feather protein (FP) is quite different from empty feather-free body protein (BP). Feathers may account for up to 30% of TP (Silva *et al.*, 2014), while pigs' hair roughly represents 2% of TP (Bailey and Zobrisky, 1968). In contradiction to the continuous synthesis and degradation of proteins in tissues such as muscle, the protein deposited in poultry feather and pig hair is not a subject to turnover processes, that are known to be associated with the efficiency of AA use and involve an energy cost.

In a generic approach and based on concepts of energy and protein flows, the MsChick model simulates the utilization and partitioning of digestible nutrients (*i.e.*, EAAs, fat, starch and sugars, Figure 4) according to the phenotypic potential of the bird fed *ad libitum*.

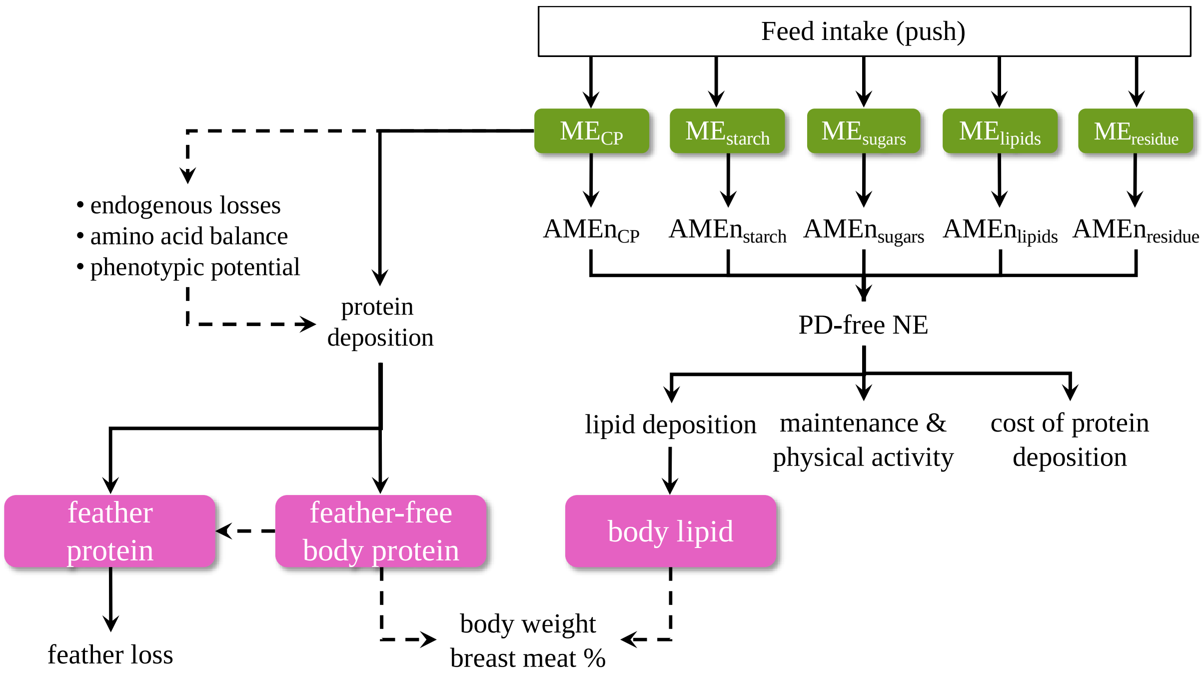


Figure 4. Flow-chart of the model concept on utilization of digestible nutrients including energy, protein (essential amino acids), where: ME$_{CP}$, ME$_{strach}$, ME$_{sugars}$, ME$_{lipids}$, ME$_{residue}$, AMEn$_{CP}$, AMEn$_{strach}$, AMEns$_{ugars}$, AMEn$_{lipids}$, AMEn$_{residue}$ are metabolizable and apparent metabolizable N-corrected energy contents for crude protein, starch, sugars, lipids, and residue; PD-free NE – protein deposition free net energy

The outputs of the simulation are: (1) the prediction of performance as body weight, daily gain and feed conversion ratio over time; (2) the net feather protein, empty feather-free body protein and empty feather-free body lipid gains; (3) the partitioning of digestible EAAs supply in terms of requirements for maintenance, net accretion for BP as well as for FP for feather growth and losses, chemical body composition at any time point, dynamic AA requirement, and N-excretion.

6.1.1. Feed intake (FI)– multiples of maintenances

In the model approach it was assumed that feed intake (FI) is the driving force for growth, it determines the growth but not *vice versa*, and thus the growth rate has no direct effect on FI. The model is driven by daily digestible nutrient (crude protein, starch, sugars, lipids, and residue) supply calculated from daily feed consumption and digestible nutrient content of the feed. The voluntary daily FI as a function of BW considers certain phenotypic traits and defines the energy intake quantity in multiples of energy for maintenance. The approach is based on the premise that while an animal approaches maturity, its *ad libitum* daily FI will approach the maintenance energy requirement, ensuring that lipid deposition will approximate zero alike to protein deposition ensured by a Gompertz function (van Milgen *et al.*, 2006). The function has been shown to be able to estimate smoothly the FI pattern of an average pig (Vautier *et al.*, 2011; van Milgen *et al.*, 2015) and for an average broiler during its growth (Dukhta *et al.*, 2017).

6.1.2. Empty feather-free body protein (BP)

Gompertz function, which is frequently used to model growth, describes protein gain and has been often parametrized to include the mature protein mass. Nevertheless, for the young broilers that are slaughtered nowadays between 35 and 42 days of age, this parameter would be difficult to estimate. Therefore, the same function was reparametrized with calculation of potential mature protein mass: mean BP deposition (*mean BPD*) which is strongly related to the growth rate, and a *precocity* parameter – maturity rate – describing the concave shape of the protein deposition curve, like in InraPorc model (van Milgen *et al.*, 2008). These two parameters do not change over the simulation, but they define the phenotypic potential of the average bird for BP deposition (potBPD) in gram per day.

Beside the phenotypic potential, the actual daily BPD could be limited by digestible EAA or/and energy supplies. However, in case of modern broiler nutrition the energy limitation is not applicable since broilers are fed *ad libitum* with a high-quality feed. Supply of digestible AAs is used for maintenance needs and for protein deposition along the organism's growth. The maintenance needs requirements are based on assumption that there is a constant metabolic activity, and it covers endogenous (originated from the digestive system – abrasion of the gut cells and mucin protein, non-reabsorbed enzyme proteins), urinary (the basal turnover of protein excreted via urine), and feather losses. Thus, nitrogen products need to be restored in order to prevent a negative nitrogen balance with efficiency of 100% and assumed to have a priority over the protein deposition needs. The efficiency coefficient indicates a relationship between the ingested and retained AAs.

The protein deposition for growth depends on the EAAs supply, which remains available after considering the needs for maintenance of feather-free body and feather development itself. As well as maintenance protein, the body protein accretion has a certain composition, and thus the daily requirements of the EAAs in the diet are assumed to be derived from those two needs, plus need for FP. Accordingly, the actual daily BPD will be the minimum of potBPD, and BP deposition allowed by dietary EAA intake. The values of EAA maintenance needs, FP, and BP compositions as well as EAA efficiency for BPD were taken from Table 2.

Respectively, BP is a core of the model and its driving force, the chemical and physical compositions are in high correlation to BP.

6.1.3. Feather protein (FP)

The feather weight (FW) initially at 0 day was estimated in proportion to BW initial (kg) in percent as 2.51, 3.26, 2.69 and 3.82 % for Ross males and females, and Cobb males and females, respectively according to Vargas *et al.* (2020). Further, at the end of the day (which is the beginning of the next day) FW was calculated as an allometry function of empty feather-free BW and FP was an allometric function of FW. The feather development is dependent on sex: at the same age females having more feather mass due to a faster feather growth rate compared to males (Gonçalves, 2017; Vargas *et al.*, 2020). The AAs composition of FP differs from BP and contains a relatively high proportion of sulphur AAs (mainly Cys) and non-essential AAs. In the model, the EAA composition of the FP and BP were set from recently published data of Wecke *et al.* (2018*a*) except for tryptophan (Stilborn *et al.*, 2010). It was presumed that genotype, age, and sex have no significant effect on BP and FP protein composition as well as that feather growth has priority over the feather-free body tissues in AA partitioning with metabolic efficiency 1 (or 100%). This later means no protein degradation is assumed in feather protein turnover. Thence, FP deposition is an obligatory protein flow, and the loss of feather is considered in the model as a part of maintenance need. In the first 4 weeks of age, however, no feather loss is alleged. The flux of FP recovery is initiated from the 5th week by a conditional allometric function of age which depends on sex, and calculated from data of Fisher *et al.* (1981).

6.1.4. Empty body weight

InraPorc model estimates empty BW directly from the protein and lipid mass. However, in other poultry models (broiler models of Hurwitz *et al.* (1978) and Emmans (1981), or Avinesp model) it is typically described by the sum of four chemical compartments of feather-free body: body protein, body fat, body water and body ash, plus feathers. It seems just a technical question, but if water (and ash) content is explicitly included in the model, any shift in protein to water ratio – that might occur as a consequence of genetic selection – can be studied. Therefore, in MsChick model all four chemical body constituents are involved in calculation routine. Water plays an important role in animal performance and being the most significant body component in its gain. Besides, together with ash, both are highly correlated with BP.

Empty BW in MsChick consist of empty feather-free body (eFFB) and feather weights (FW). In its turn, to determine FW only FP was considered, feather has a very high and stable protein content. The eFFB is a sum BP, eFFB lipid (BL), eFFB ash and eFFB water. The eFFB ash was assumed to be 20% of BP and constant over time. The EFFB water calculated by allometric equations of BP using reliable experimental data (Vargas *et al.*, 2020). The initial BL content of the as-hatched chick was assumed to be 10% of live weight, according to Noy and Sklan (1999). The valuable body meat parts such as breast, thighs, drumsticks, and wings are in allometry to the BP which is dependent on sex and independent of chicken breed by applying the equations from Danisman and Gous (2013). The edible meat parts include bone and skin and were presented as means of the two parts from each bird.

6.1.5. Representation of energy metabolism

The digestible macronutrients yield energy for metabolism and serve as fuels for maintenance and BPD, furthermore, are used as substrates for the eFFB lipid deposition (BLD). In the energy flow of the model, digestible nutrients are considered on their net energy (NE) basis, despite the fact that poultry nutritionists, in general, use metabolizable energy system. The applied NE approach is based on a conducted study in broiler chickens allowing both AMEn and NE values to be predicted and evaluated. The available NE system of Carré *et al.* (2014) for poultry allowed us to use the same approach in the broiler model as in the pig model. Thus, specific coefficients determined in broilers have been applied (Table 3).

Table 3. Comparison of the specie specific energy conversion factors for pig as used in InraPorc (van Milgen *et al.*, 2008) and for broiler chicken (taken from Carré *et al.*, 2014) as used in the present model

Values	GE	InraPorc (growing pig model)			MsChick (growing chicken model) *		
		DE	ME	NE	AME	AMEn	NE
	MJ/kg						
Digestible crude fat	38.76	39.00	39.00	35.01	38.56	37.96	32.87
Digestible crude protein	22.64	23.31	20.34	12.08	21.18	18.95	14.23
Digestible starch	17.54	17.45	17.45	14.32	16.57	16.22	13.07
Digestible sugars	16.71	16.62	16.62	11.94	13.17	12.63	7.61
Digestible residue	18.58	16.61	15.51	8.64	11.75	11.17	11.07

* Based on equations according to Carré *et al.* (2014).

Under the assumption of controlled conditions (thermoneutrality, *ad libitum* feeding, balanced diet, *etc.*), the maintenance net energy requirement was defined as sum of fasting heat production (FHP, 450 kJ/ $BW^{0.70}$, Noblet *et al.*, 2015) and energy for activity needs, set as extra 33% of FHP in birds according to van Milgen *et al.* (2001). Although in growing animals the

FHP somewhat depends on feeding level prior to fasting (Labussière *et al.*, 2011), due to lack of reliable data the feeding history was not considered as a variation factor for maintenance energy requirement.

The main products of N excretion are – resulting from AA catabolism – urea in mammals and uric acid in birds. Urea and uric acid have different energetic values. Urea has 2 N-atoms and an energy value of 635 kJ/mol, whereas uric acid has 4 N-atoms and an energy value of 1926 kJ/mol (van Milgen *et a*l., 2019). Urinary energy flux (UrinE, kJ/d) – the daily energy loss by urine – related to obligatory urinary energy loss (ObligUrinELoss, kJ/d) and the energy excretion from excess protein. In this term, excess protein means the protein which cannot be deposited since either a limiting amino acid occurs or because it is above the protein supply required for genetically determined maximum protein deposition. The ObligUrinELoss is independent of the protein supply and, in this perspective, it is alike more related to maintenance needs. It has to be noted that N excretion not only implies N and energy loss in the urine, but some energy is also required to synthesize the end products of protein catabolism which is accounted in the model. The ObligUrinELoss was calculated based on study results that broiler chicken excretes approximately 2.19 mg of uric acid per 1 kJ of FHP, while 1 mg of uric acid is about 39 J of endogenous urinary energy (Koh *et al.*, 1992). The urinary energy excreted due to excess protein (kJ/d) was calculated as amount of excess protein in grams divided per 6.25 and multiplied per 32.97 J as 1 mg of endogenous urinary N is about 32.97 J of endogenous urinary energy. From energetic point of view, the deposited protein presumed to be 23.8 kJ for each gram. Thus, the yield of metabolizable energy from excess protein is calculated as the amount of excess protein in kJ/d subtracting excreted UrinE. The conversion of the excess protein to provide energy (ME/NE) is assumed to be independent of specie and thus the efficiency factor of 0.52, used in InraPorc, was adapted. The value indicates that protein conversion to energy is an energy demanding process.

The consumed energy, remaining above the needs for maintenance and energy used for protein deposition (retained energy as protein as well as the required energy support for the deposition), is available for LD in eFFB. The BL serves as an energy sink in the model. Dietary net energy is converted to retained tissues, and the amount of fat tissue is developed with consideration of 39 kJ energy for each gram of LD.

6.1.6. Some further information on MsChick model

The construction of MsChick had commenced with re-evaluating the model parameters some of which relate (1) to down-scaling of a pig to a chicken (*e.g.*, FI and potBPD), (2) to poultry-specific aspects (*i.e.*, feathers, nutrient digestibility, dietary requirement for Arg), or (3) to interspecies differences (*e.g.*, efficiency of nutrient utilization, body composition). All model parameters are listed in Table 1 of Annex A. The model was built in Microsoft Excel software. The amount of daily NE intake (NEI, MJ/d) and FI (kg/d) were estimated by considering the BW at the beginning of the simulated day *i*. It was assumed that BW at the end of the simulated day *i* is equal to BW at the beginning of the next day *i+1*.

There are five initial parameters for the MsChick model that can be modified or updated by the user to represent the phenotype. Three parameters of the growth equation, namely the BW_{init} (1) – initial body weight which is used to estimate the initial BP, *precocity* (2) – the shape parameter of Gompertz equation, and *meanBPD* (3) – a general parameter potential for BP deposition used to calculate final BP as well as BP at maturity (another Gompertz function parameters). The two additional parameters that can be estimated are "*FI_1*" and "*FI_2*" for the FI equation, expressing NE intake (MJ/d) at 1 and 2 kg of BW, respectively. The latter ones can be calculated with known NE content of the diet consumed (the example of calculation logic is shown in Annex A). Also, there are other parameters which might be modified, such as allometry coefficients for eFFB water and allometry for ash instead of linear regression, *etc.*, with more explanation in Annex A.

6.2. Model evaluation: Energy and protein partitioning

6.2.1. Model simulation and output

Before running the simulation, the model was parameterized (calibrated) for the average broiler chicken according to the Aviagen (2017) and Cobb (2015) guidelines on nutrient requirements and performance objectives for males and females (Table 4). The calibration or parametrization of the model is the process that results in the best fitting of the simulation to all points of the dataset. Thus, the different model parameters are adjusted, searching for the best combination of the parameter values. Those parameters involved in this process that has some "valid" variance.

The values that have biological, physiological, or nutritional relevance like energy content of lipids, energetic efficiency of starch, amino acid content of body protein, *etc.* are not changed during the calibration. Nevertheless, for instance, the allometric coefficients may be adjusted according to the valid datasets. There are two steps of parametrization: 1) when the model is fitted to result in reliable output, and 2) once the first parametrization is done, only the 5 initial key parameters are adjusted – in this step the combination of the initial parameters is optimized by fitting to performance of different strains (Table 4).

Table 4. Aviagen (2017) and Cobb (2015) guidelines data of body weight and daily feed intake of males and females used in model calibration

Age (days)	BW (kg)				DFI (kg/day)			
	Ross males	Ross Females	Cobb Males	Cobb Females	Ross males	Ross Females	Cobb Males	Cobb Females
0	0.043	0.043	0.042	0.042	–	–	–	–
1	0.055	0.055	0.056	0.056	0.013	0.015	0.013	0.013
2	0.070	0.070	0.072	0.072	0.016	0.018	0.017	0.017
3	0.088	0.088	0.089	0.089	0.019	0.02	0.021	0.021
4	0.109	0.108	0.109	0.109	0.022	0.023	0.023	0.023
5	0.133	0.132	0.131	0.130	0.025	0.026	0.027	0.027
6	0.160	0.158	0.157	0.156	0.029	0.029	0.031	0.031
7	0.190	0.188	0.186	0.184	0.033	0.033	0.035	0.035
8	0.224	0.221	0.217	0.214	0.038	0.037	0.039	0.037
9	0.260	0.257	0.250	0.244	0.043	0.041	0.044	0.044
10	0.300	0.296	0.286	0.280	0.048	0.046	0.049	0.047
11	0.343	0.338	0.324	0.318	0.053	0.050	0.054	0.054
12	0.390	0.383	0.368	0.360	0.059	0.055	0.059	0.057
13	0.440	0.431	0.416	0.408	0.065	0.060	0.064	0.063
14	0.494	0.482	0.470	0.460	0.071	0.066	0.070	0.068
15	0.551	0.536	0.528	0.520	0.077	0.071	0.077	0.073
16	0.612	0.594	0.590	0.582	0.083	0.076	0.083	0.079
17	0.677	0.655	0.656	0.646	0.089	0.082	0.090	0.084
18	0.746	0.719	0.727	0.711	0.096	0.087	0.097	0.089
19	0.818	0.786	0.803	0.777	0.102	0.092	0.104	0.092
20	0.895	0.856	0.884	0.844	0.108	0.097	0.112	0.098
21	0.975	0.928	0.971	0.914	0.118	0.102	0.119	0.103
22	1.057	1.002	1.058	0.986	0.124	0.110	0.124	0.111
23	1.143	1.078	1.145	1.060	0.130	0.116	0.130	0.116
24	1.231	1.157	1.233	1.136	0.136	0.121	0.136	0.124
25	1.321	1.238	1.321	1.214	0.142	0.127	0.142	0.126
26	1.414	1.321	1.409	1.294	0.148	0.132	0.148	0.134
27	1.509	1.405	1.497	1.378	0.154	0.138	0.154	0.142
28	1.606	1.491	1.585	1.463	0.160	0.143	0.160	0.144
29	1.706	1.578	1.677	1.549	0.166	0.150	0.165	0.151
30	1.808	1.666	1.773	1.636	0.172	0.155	0.171	0.155
31	1.911	1.755	1.873	1.724	0.178	0.160	0.177	0.161
32	2.015	1.844	1.978	1.813	0.184	0.165	0.184	0.163
33	2.121	1.934	2.085	1.903	0.19	0.169	0.192	0.165
34	2.228	2.024	2.192	1.993	0.195	0.174	0.200	0.167
35	2.336	2.114	2.299	2.083	0.200	0.177	0.209	0.169
36	2.444	2.204	2.406	2.172	0.206	0.181	0.212	0.175
37	2.553	2.294	2.513	2.259	0.211	0.184	0.215	0.179
38	2.663	2.383	2.620	2.344	0.215	0.188	0.218	0.184
39	2.773	2.473	2.726	2.428	0.22	0.191	0.221	0.189
40	2.883	2.561	2.832	2.510	0.225	0.194	0.225	0.193
41	2.993	2.650	2.938	2.591	0.229	0.197	0.229	0.197
42	3.103	2.737	3.044	2.671	0.233	0.200	0.233	0.199
43	3.210	2.820	3.150	2.751	0.240	0.200	0.237	0.203
44	3.320	2.910	3.256	2.831	0.240	0.210	0.241	0.203
45	3.430	2.990	3.362	2.910	0.240	0.210	0.245	0.205
46	3.540	3.080	3.468	2.989	0.250	0.210	0.250	0.204
47	3.643	3.158	3.574	3.068	0.249	0.210	0.255	0.207
48	3.749	3.238	3.680	3.147	0.252	0.211	0.265	0.208
49	3.852	3.316	3.786	3.226	0.254	0.213	0.270	0.209
50	3.955	3.394	3.891	3.301	0.256	0.214	0.265	0.209
51	4.056	3.470	3.994	3.376	0.258	0.215	0.265	0.213
52	4.154	3.544	4.095	3.451	0.260	0.215	0.265	0.215
53	4.251	3.617	4.194	3.524	0.261	0.216	0.265	0.219
54	4.346	3.688	4.291	3.597	0.263	0.217	0.265	0.221
55	4.439	3.756	4.386	3.670	0.264	0.217	0.265	0.225
56	4.529	3.823	4.481	3.741	0.265	0.217	0.265	0.225
57	4.617	3.887	4.573	3.812	0.266	0.217	0.265	0.225
58	4.702	3.950	4.662	3.883	0.266	0.217	0.265	0.225
59	4.784	4.010	4.748	3.953	0.267	0.217	0.265	0.225
60	4.863	4.068	4.831	4.023	0.267	0.217	0.265	0.225
61	4.939	4.124	4.912	4.093	0.267	0.216	0.265	0.225
62	5.011	4.177	4.990	4.162	0.267	0.216	0.265	0.225
63	5.080	4.229	5.068	4.230	0.268	0.216	0.265	0.225

where: BW – body weight in kilograms, DFI – daily feed intake in kilograms per day.

The five initial parameters were set for each sex and genotype. The *BW_init*, *precocity*, and *meanBPD* based on observed (recommended in guideline) and predicted values on BW, as well as *FI_1* and *FI_2* based on recommended guideline values on FI, over 9 weeks of age. Practically, it was adjusted by Solver function in Microsoft Excel software. Firstly, the sum of squared estimate of errors for DFI was It was adjusted by Solver function in Microsoft Excel software. Firstly, the sum of squared estimate of errors for DFI was minimized by changing the FI_1 and FI_2 parameters.

Further the sum of squared estimate of errors for BW adjusting the *precocity* and *meanBPD* were minimized, with *BW_init* at the end. An output of the model is presented as a simulated body weight (BW, kg), daily and cumulative feed intakes (DFI, kg/d and CFI, kg) as well as daily depositions for potential empty feather-free body protein (potBPD, g/d), actual empty feather-free body protein deposition (BPD, g/d) and empty feather-free body lipid deposition (BLD, g/d) for an average broiler of a certain strain.

The model simulates the EAAs utilization with consideration of the maximum protein deposition rate during the lifetime (potBPD) and thereby enables estimation of EAA requirements of an average bird at certain point in lifetime. Based on the known EAA requirement and the estimated FI, the model is able to predict the optimal dietary standardized ileal digestible (SID) EAA content at each day of production. The recommended digestible dietary protein content can be calculated by the model as SID protein requirements (g/d) divided by DFI (kg/d).

According to the model equation [eq.1], the actual SID protein requirement (g/d) is defined as a sum of requirements for body protein deposition determined by the genetic potential, protein deposited in feather – both corrected for the extra need attributed to the <1 efficiency – the maintenance needs as obligatory urinary and (gut) endogenous losses, and feather loss. The model calculates SID AA requirements for the essential AAs as well. The equation is identical for protein and individual AAs using specific parameters in the calculation*.

$$SID_{prot\ req} = \frac{potBPD}{k_p} + \frac{FP_{dep}}{k_f} + prot_{m75-g} * BW^{0.75} + \frac{FI_{actual} * DM * prot_{endog}}{100} + f_{prot_{loss}} \quad \text{[eq.1]}$$

*The equation is based on the modified equation of InraPorc (2008), where: $potBPD$ – genetically potential feather-free body protein deposition (g/d), k_p – efficiency of feather-free body protein deposition, FP_{dep} – protein deposition into the feather (g/d), k_f – efficiency of feather protein deposition, $prot_{m75-g}$ – protein losses due to basal turnover (g/d), $BW^{0.75}$ – metabolic body weight (kg), FI_{actual} – actual feed intake (kg/d), DM – dry matter content of the diet (%), $prot_{endog}$ – basal endogenous protein losses (g/d), $f_{prot_{loss}}$ – feather protein loss (g/d).

After all, the model allows not only to simulate the requirements of the EAAs but also to predict the potential nitrogen surplus per day as well as over the feeding period (Dukhta and Halas, 2023).

6.2.2. Sensitivity analysis

The model outputs such as BW (kg), FCR and BP and BL mass at slaughter (kg) at 42 days of age were checked in the course of changing *meanBPD* and *precocity*, *FI_1* and *FI_2*, as well as allometry coefficient of empty feather-free water to empty feather-free body protein. The values of those parameters were changed with ± 10 and 20 %.

Additionally, the traits such as BPD (g/d), BLD (g/d), CFI (kg), excess protein (g/d) eFFBwater (kg) and eFFBash (kg), and breast meat (% of BW) at 35 d of age were checked in sensitivity analysis in response to parameters of *meanBPD*, *precocity*, *FI_1* and *FI_2* and parameter "*c*" in FI curve (multiples of maintenance) with deviation ± 20 % at the. The dietary EAAs were assumed to be not limited.

6.2.3. Model testing with independent datasets

Model evaluation (validation) involves running a model simulation applying the input parameters measured or determined during the calibration process. The graphs of simulated (*in silico*) performance are compared versus the measured (*in vivo*) data.

The outputs of simulation on distinct performance data were compared to measured data available from literature, and the model was run both with simulated and measured daily FI in separate steps. To assess the quality of the model prediction, mean square prediction error (MSPE), was calculated according to Bibby and Toutenburg (1977).

$$MSPE = \frac{\Sigma\,(O_i - P_i)^2}{n}$$

where: O_i and P_i are observed and predicted values; $_i$ = 1, …, *n*, and *n* is the number of experimental observations.

The root MSPE is a measure in the same units as the output and is also expressed as a percentage of the observed mean (relative MSPE, relMSPE). The MSPE can be decomposed into three fractions. Firstly, errors attributing to the overall bias (B%) represent the proportion of MSPE due to a consistent over- or underestimation of the experimental observations by the model predictions. Secondly, a deviation of regression slope from one (R%), being the line of perfect agreement represents the proportion of MSPE due to inadequate simulation of differences among experimental observations. Thirdly, the disturbance proportion (E%)

represents the proportion of MSPE unrelated to the errors of model prediction. The prediction is considered very good if the MSPE is small and if a small proportion of MSPE is explained by B% and R%.

6.2.3.1. Dynamic dataset from in vivo studies

The calibrated model was validated using daily dynamic data from a two separated pen-trials involving Ross 308 broilers and Cobb 500 broilers. Both experiments were carried out in the framework of the H2020 Feed-a-Gene project at INRAE PEAT experimental facility (https://doi.org/10.15454/1.5572326250887292E12).

In the Ross trial day old (as-hatched) broilers received a single starter diet during the pre-experimental period between 1-10 days of age. Birds were kept in pens (42 birds/pen, 50% males and 50% females) and the experimental period started at 11 days of age. Further, for the experimental period each of 16 pens were assigned to control (C) and precision feeding (PF) treatments. Control feeding consisted of two conventional diets for grower and finisher broilers, between 11-22 days and 23-33 days, respectively. The PF group was fed with daily change in proportion of two premixes A and B throughout 11-22 days, and pre-mixes B and C during 23-33 days of age. It was assumed that the mix of each day exactly matches the nutrient requirement of the birds determined by INAVI model. The DFI per pen and the individual BW was measured in each day during the pre-experimental (1-9 days) and experimental periods (12-31 days). The birds were fed *ad libitum*.

The inputs for the simulation related to the diets were: the nutrient content and EAA composition of the feeds offered in the three phases for C group or adjusted daily for PF group from day 11. The model was run with parametrization for males (M) and females (F) calibrated earlier based on Aviagen (2017) recommendation, aiming to evaluate the predicted and observed responses for C diet and PF dietary treatments. In the next step of model testing the simulated DFI curves were replaced by adjusted DFI values. This was performed by using x_1 and x_2 factors in the FI model equations to fit the model input to the *in vivo* measured daily amount.

In the Ross broiler trial chemical body analysis was also carried out 6 times. Thus, the eFFBW of the birds was analysed for the chemical body composition (body protein, ash, water, and fat) and the *in vivo* measures on 5th, 11th, 16th, 23rd and 33rd days of age were compared to simulated body composition from 0 to 33 or 30 days for C or PH group, respectively.

For Cobb broilers the data of BW and daily feed intake were measured by Bird-e – an electronic feed station (https://www.feed-a-gene.eu/media/bird-e-automate-de-consommation-alimentaire-pour-volailles) of individual ration dispenser for poultry that was developed by INRAE in frames of Feed-a-Gene project to collect real-time feed intake and growth data at individual level on animals reared in group and on floor.

In the experiment 80 Cobb 500 male chickens were reared from 1 to 35 days. At 1 day of age, the animals were identified with a wing tag and an electronic Radio frequency identification device (RFID) chip, then weighed and placed in one pen on a floor covered with wooden chips. The pen was divided into two groups with an equal starting weight. In the first part, the animals were fed with a classic corn-soybean diet as used in usual commercial conditions, and in the second part – with an alternative diet including less soybean meal and a higher proportion of alternative feedstuffs such as sunflower, rapeseed, and fava bean. The diets were isoproteic and isoenergetic. A starter diet was given from hatch to 7 days of age, a grower diet was given from 8 to 22 days, and finisher diet from 23 to 35 days. The 5 birds were chosen randomly from each group. Namely, C101, C114, C128, C136 and C162 fed with classic diet and A193, A040, A051, A059 and A073 – fed with alternative diet (more details are given by Berger *et al.*, 2021).

6.2.3.2. Independent literature data

The calibrated model was tested with literature data published in recent years. The trials involved in the evaluation are listed in Table 5. The model was run always from hatch up to minimum 10 days and maximum 7th week of age, depending on the tested period of the experiment duration, as it was described in the experiment from each article. The appropriate values obtained in the specific phase were compared.

The model was challenged with diets containing graded levels of digestible lysine, methionine, or threonine. Furthermore, datasets on broilers fed with low protein diets supplemented with or without amino acids and/or dietary fat were tested. In study of Zhai *et al.* (2016) 320 Ross 708 male broilers were fed 4 different levels of digestible Methionine and Cysteine – 5.39, 6.15, 6.92, and 7.67 g/kg over the 21-42 days of age. In study of Li (2017), the duration of the experiment was up to 8 weeks, and it included starter (0-14 days), grower (15-24 days) and finisher (25-56 days) phases. However, in the results of the experiment the data were compared from week 1 to week 7. The Ross 708 male and female broilers were fed 3 dietary treatments (300 birds per treatments) up to 7 weeks: (1) positive control – 25.19, 22.33, 20.1 g/kg, (2) low crude protein – 19.19, 16.33, 14.1 g/kg, and 3) low crude protein + crystalline amino acids – 20.36, 17.34, 14.8 g/kg, for starter, grower and finisher, respectively. The influence of dietary protein restriction was studied on the growth and development of visceral organs, muscle tissues and bone mass with or without supplementation of crystalline amino acids. The amino acids were L-Threonine, L-Arginine HCl, L-Valine, L-Isoleucine, L-Histidine, L-Tryptophan, L-Phenylalanine, and Glycine. In study of Liu *at el.* (2017a) ten experimental diets with protein concentrations ranging from 154 to 400 g/kg and two lipid levels (46 and 85 g/kg) with identical energy densities were offered to male Ross 308 broilers from 7 to 28 days post-hatch. In study of Liu at el. (2017b) 14 diets with different concentrations of starch (from 313 to 503 g /kg), protein (from 159 to 357 g/kg) and lipid (from 20.6 to 44.3 g/kg) were formulated. Experimental diets were offered to male Ross 308 broilers from 10 to 23 days post-hatch.

Najafi *et al.* (2017) in their study with 288 Ross 308 male broilers offered four levels of dietary Threonine supplementations (6.5-9.7 g/kg of the diet) during the first two weeks of age. The body weight gain (BWG) and feed intake (FI) were measured at 1, 7, and 14 days of age. In study of Lee *et al.* (2018) the 6 experimental diets with different levels of digestible Lysine (9.8-14.8 g/kg) were provided *ad libitum* to 720 one-day-old male Ross 308 up to 10 days of age. On day 0 and 10, the body weight of individual birds and group feed intake were recorded to determine average daily weight gain (ADG) and average daily feed intake (ADFI).

In study of Sigolo *et al.* (2019) 3 dietary levels of Lysine were offered evaluated from day 1 to 14 (starter period) – 12.7, 14 or 15.3 g/kg, day 15 to 28 (grower period) – 11.1, 12.2 or 13.3 g/kg, and day 29 to 42 (finisher period) – 9.8, 10.7 or 11.7 g/kg. Body weight and feed intake (difference of offered feed and refused feed) were measured weekly. ADFI and ADG, were calculated within each treatment for the starter period, grower period, finisher period, and whole study period (day 1–42).

The model evaluation with independent dataset was done in two steps. Firstly, the calibrated model was run with the trial specific nutrient inputs calculated based on the available data from the publications. In the second step, the daily feed intake (DFI, kg/d) was adjusted by multiplication on the coefficients (1 if DFI did not change), to fit the model FI curve to the observed literature data, thus testing the model prediction of performance with the real amount of nutrient intake.

Table 5. Collection of the broiler trials used for the model testing

Author	Year	Title	Number of birds	Number of treatments	Measured parameters	Periods
Zhai *et al.*	2016	Effects of dietary lysine and methionine supplementation on Ross 708 male broilers from 21 to 42 d of age (I): growth performance, meat yield, and cost effectiveness	960	**4** *dig Met 3.04-5.32 g/kg*	FI, kg BW, kg	21-42 d
Li	2017	Growth and Development of Two Broiler Strains with Low Protein and Crystalline Amino Acid Supplemented Diets	450	**3** *CP control 25.19 –20.1 g/kg* *CP low 19.19 – 14.1 g/kg* *CP +CAA 20.36 – 14.8 g/kg*	BW, kg	0-14 d 15-24 d 25-56 d
Liu *et al.*	2017a	Growth performance, nutrient utilization and carcass composition respond to dietary protein concentrations in broiler chickens, but responses are modified by dietary lipid levels	240	**10** *5 dietary protein levels* *154 – 400 g/kg* *2 dietary ether extract levels 46 vs. 85 g/kg*	FI, g BW, g	7-28 d
Liu *et al.*	2017b	An assessment of the influence of macronutrients on growth performance and nutrient utilization in broiler chickens by nutritional geometry	336	**14** *Starch 313 – 503 g /kg* *CP 159 – 357 g/kg* *lipid 20.6 – 44.3 g/kg*	FI, g/bird BWG, g/bird	10-23 d
Najafi *et al.*	2017	Effect of Different Dietary Threonine Levels on Optimal Growth Performance and Intestinal Morphology in 1-14 Days Old Ross 308 Broilers	288	**4** *dig Thr 6.5-9.7 g/kg*	FI, g/d BWG, g	1-14 d
Lee *et al.*	2018	Standardized ileal digestible lysine requirement of male broilers at the age of 0–10 days	480	**6** *dig Lys 9.8-14.8 g/kg*	ADFI, g/d ADG, g/d	1-10 d
Sigolo *et al.*	2019	Effects of dietary surpluses of methionine and lysine on growth performance, blood serum parameters, immune responses, and carcass traits of broilers	270	**3** *Lys12.7 – 15.3 g/kg*	ADFI, g ADG, g	1-14 d 15-28 d 29-42 d

where: BW – body weight; DFI – daily feed intake; BWG – body weight gain; ADG – average daily gain; ADFI – average daily feed intake.

6.3. Model extension: Phosphorus and Calcium partitioning

The main goal was to frame a model with a generic approach for poultry. Thus, the phosphorus (P) module for broiler was developed in parallel with the pig model (Halas *et al.*, 2017) developed to be integrated to InraPorc model, using the same approach for simulation of P partitioning over time.

The P and calcium (Ca) model extension represents Ca and P metabolism and simulates the effect of dietary digestible P supply on P retention and urinary P excretion (Figure 5). The partitioning and utilization of dietary digestible P is based on the premise that animals need Ca and P for maintenance and production.

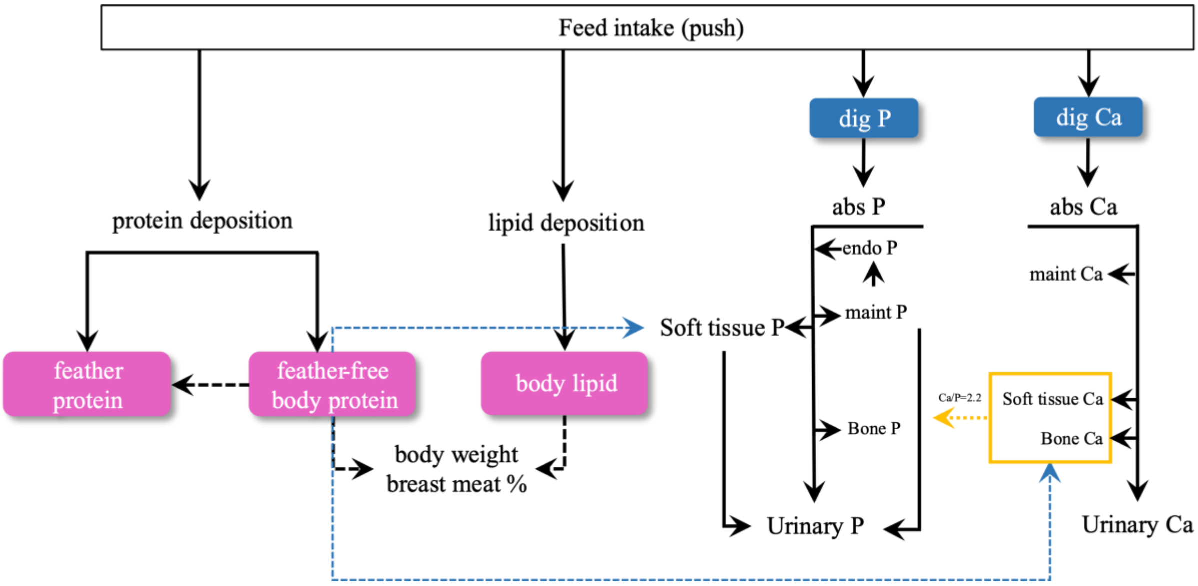


Figure 5. Flow-chart of the model concept on utilization of digestible phosphorus (P) and calcium (Ca)

The ingested digestible P is utilized for maintenance purposes, including to replenish gut and urinary endogenous losses, also used for feather growth, as well as for soft and bone tissues development. The available P (entered the metabolism) in excess over the amount that was used for maintenance and retention is excreted via urine. While integrated, P module has feedback to the basic energy and protein metabolism model by correcting muscle growth if the P supply limits the development of the soft tissue.

6.3.1. P intake and maintenance requirements

Total apparent digestible P intake was calculated as FI multiplied by dietary P content in the diet and P digestibility. The absorbed P corrected with the reabsorption coefficient of faecal endogenous P. Maintenance requirement of available P represented by sum of fecal and urinary endogenous P losses as well as P requirements for feather loss. The faecal endogenous P is a function of dry matter intake, and urinary endogenous P is proportional to BW. The endogenous P excretion assumed to be constant across the growth curve of the chicken.

P requirements for feather development and feather loss were calculated as P content in daily net feather production (FW) and in feather loss respectively, while considering feather P content to be 0.18% of FW (Okareh *et al.*, 2015). In the flows of maintenance and feather development the efficiency of P utilization was accounted with 100%, while the efficiency of P utilization in feather-free tissue retention is assumed to be 94% such as in pig model.

6.3.2. Ca intake and maintenance requirements

Ca partitioning is represented simply in the model. The digestion mechanisms are not considered in our model, and it was presumed that partitioning of the absorbed Ca is analogical for P. The absorbed Ca from the diet is calculated as FI multiplied by dietary Ca content and Ca digestibility. Also, urinary endogenous Ca excretion is proportional with BW, and Ca required for feather development is calculated as sum of Ca in daily net feather production and feather loss, whereas feather Ca content is considered as 0.27% of FW (Okareh *et al.*, 2015; Feedipedia, 2020).

6.3.3. P and Ca partitioning and regulation for growth

The recommended dietary total P and Ca levels are calculated from SID P and digestible Ca requirement divided by digestibility coefficients for P (45%) and Ca (60%) (Rodehutscord *et al.*, 2017; Ingelmann *et al.*, 2018). Those values may be changed by the user if different digestibility coefficients are presumed.

In the model, soft tissue was considered as lean plus fat tissues and viscera, and that it has priority over the bone tissue to utilize the dietary P supply. Lean mass (LM) was calculated as sum of lean in breast, thighs, drumsticks, and wings parts with an arbitrary assumption that lean is 90, 70, 60 and 45 % of the calculated body parts (described in the previous subchapter 6.1.4), respectively. And the P content was assumed to be a mean of 6450 mg/kg in all muscles, for simplification. Viscera mass was assumed to be 28 % of BW (Abdulla *et al.*, 2016), and P content of the viscera pool – mean of total P contents of liver, heart, spleen and gizzard as 6517 mg/kg, according to the study of Li *et al.* (2016). Fat tissue in young chicken (5-6 weeks old) assumed to be represented by fat pad or abdominal fat mass. Fat pad was calculated as allometry based on fat-free eFFB according to Zuidhof (2005) with a total P content 915 mg/kg.

The deposition rates of muscle and fat were calculated as the difference between present day *i* and the previous one (*i–1*). If the simulation runs from day 0, the initial muscle and fat depositions assumed as 1 and 0.001 g/d, respectively. P requirement for retention in soft tissue was calculated as sum of muscle gain and fat pad gain, multiplied by P content in muscle and P content in fat pad, respectively.

Ca retention in soft tissues was calculated considering Ca contents in viscera, muscle, and fat tissues and their mass as 1114 (Awachat*et al.*, 2011), 180 (Çinar*et al.*, 2015), and 100 (assumed based on pig P model, Halas *et al.*, 2017) mg/kg, respectively. Ca available for bone formation remains from the amount of absorbed Ca after excretion of obligatory urinary endogenous Ca losses, Ca used for feather growth and loss. The actual P accretion in bone tissue is dependent on phenotypic potential of maximum protein deposition (potBPD), maximum Ca retention driven by the potential BP mass, and available dietary P.

For determining the available P for bone formation, a so-called relative P-deficiency was defined in the model. That is the actual P content of the bone relative to the maximum protein deposition into the eFFB driven P-retention. If the relative P-deficiency is 50% or lower, the P-flux to soft tissue has no more priority over the bone. Thus, below the threshold level, the P-(under)supply limits the muscle growth. In this case at the end of the simulated day *i* the P-module has response to the energy and protein metabolism model. At the end of day, BP and BL depositions are corrected for the BPD and BLD actual after applying the P-module constrains.

6.4. Model application: Simulating Phosphorus and Nitrogen excretion

It is important to distinguish between digestibility and metabolism processes of dietary N and P as well as to determine the composition and partitioning paths of each nutrient. N and P that are not digested are unavailable for the animal, thus, cannot be used for metabolic processes and will be excreted by faeces. The amounts of absorbed N and P that are oversupplied and cannot be deposited into the body will be excreted by urine (van Krimpen *et al.*, 2013). Thence, precise estimation of undigested and urinary excreted nutrients is essential in the mitigation of a negative environmental impact.

Absorption and retention of dietary P are depending on many factors. One of them is dietary Ca to P ratio since it has a high influence on digestibility of Ca and P, and thus the amount of Ca and P entering the metabolism and being available in the course of bone mineralization. It has been confirmed that in non-limiting P supply the body protein weight is highly correlated with total (body) P mass. However, in P-deficient condition the trajectory still exists but shifts to a lower level (Misiura *et al.*, 2020). Thus, the premise was that maximum potential rate of empty feather-free body protein deposition determined by the genetics (potBPD) must be supported by both optimal AA and P supply, and the available P requirements of a chicken depend on its maintenance requirements and their genetic potential for protein deposition.

6.4.1. *Partitioning of N and P excretion*

The model simulates the utilization of daily digestible protein and available P intake, protein retention in the eFFB and P retention in soft body tissues and bones. Due to the model structure the total N and P excretion and partitioning between faeces and urine can be determined (Figure 6).

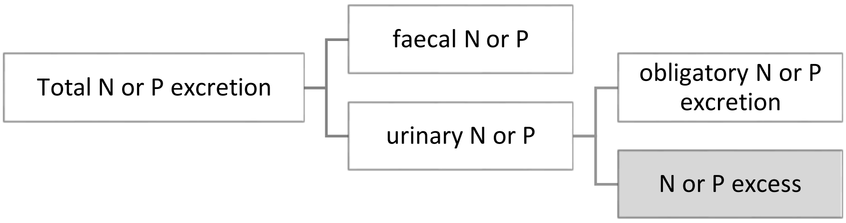


Figure 6. Partitioning of nitrogen and phosphorus excretions

Total N excretion (eq. 2) was calculated as total protein intake minus sum of protein deposited into the feather-free body and feather, divided by 6.25. After subtracting the undigested part, the composition of the urinary N excretion (eq. 3) is considered as a sum of obligatory N loss and N surplus (excess, eq. 4). Total ammonia N (TAN) was assumed to be equal to total urinary N excretion, considering that uric acid and ammonia are the two major N containing compounds in the urine. Obligatory excretion is the part of maintenance and consist of obligatory urinary losses related to the protein turnover, obligatory endogenous losses in the intestine, and efficiencies provision of body and feather protein depositions. Excess N is calculated as digestible N intake subtracting retained N and obligatory N excretion.

$$N_{total\ excr} = \frac{prot_{Int} - (prot_{body} + prot_{feather})}{6{,}25} \quad \text{[eq.2]}$$

$$obl\ N_{excr} = obl_{urinary}\ N_{loss} + endo\ N_{loss} + \frac{(1 - e_{body\ protein}) * prot_{body} + (1 - e_{feather\ prot}) * prot_{feather}}{6.25} \quad \text{[eq.3]}$$

$$N_{excess} = dig\ N_{Int} - ret\ N - obl\ N_{excr} \quad \text{[eq.4]}$$

where: $N_{totalexcr}$ – total nitrogen excretion, $prot_{Int}$ – dietary protein intake, $prot_{body}$ – feather-free body protein content; $prot_{feather}$ – feather protein content; $oblN_{excr}$ – obligatory nitrogen excretion, $obl_{urinary}N_{loss}$ – obligatory nitrogen urinary loss, $endoN_{loss}$ – obligatory endogenous nitrogen loss, $e_{bodyprotein}$ – efficiency of body protein deposition, $e_{featherprot}$ – efficiency of feather protein deposition; N_{excess} – nitrogen excess, $digN_{Int}$ – digestible nitrogen intake, $retN$ – retained nitrogen.

Total phosphorus excretion (eq. 5) was calculated similarly, total P intake minus sum of P deposited into the body soft (muscles) and bone tissues and feather. The composition of the P urinary excretion (eq. 6) is a sum of obligatory urinary endogenous loss, efficiencies provision for P retention into the tissues and P needed for appropriate feathering maintenance. Excess P (eq. 7) is equal to available P intake subtracting retained P and obligatory P excretion.

$$P_{total\ excrtion} = P_{Int} - \left(P_{soft} + P_{bone} + P_{feather}\right) \quad \text{[eq.5]}$$

$$obl\ P_{excr} = \left(P_{soft} + P_{bone}\right) * \left(1 - e_{P\ growth}\right) - U_{endo}P - P_{feather\ depos} + P_{feather\ loss} \quad \text{[eq.6]}$$

$$P_{excess} = avP_{Int} - ret\ P - obl\ P_{ecxr} \quad \text{[eq.7]}$$

where: $P_{total\ excr}$ – total phosphorus excretion, P_{in-t} - dietary phosphorus intake, P_{soft} – phosphorus content in body muscle, P_{bone} – phosphorus content in bones, $P_{feather}$ – feather phosphorus content; $obl\ P_{excr}$ – obligatory phosphorus excretion, $U_{endo}P$ – obligatory endogenous phosphorus loss, $e_{P\ growt}$ – efficiency of phosphorus for growth, $P_{feather\ depos}$ – phosphorus deposited in feather, $P_{feather\ loss}$ – phosphorus lost with feather; P_{excess} – phosphorus excess, avP_{Int} – available phosphorus intake, $retP$ – retained phosphorus.

6.4.2. Application of two feeding scenarios

The calibrated model was challenged with eight phases feeding schedule with more gradual decrease of dietary protein and available P levels during fattening (Table 5). Practically, MS Excel version was run separately with two feeding scenarios: Ross nutrition recommendation (Sc1) having 4 phases and the alternative strategy (Sc2). The ratio of EAAs to protein was assumed to be the same in both simulations, as well as energy content of the diets.

Table 6. Nutrient composition of diets in scenario 1 (Sc1, Ross 308 recommendations) and scenario 2 (Sc2, multiple phases feeding)

	Ross recommendation (Sc1)				**Multiphase feeding (Sc2)**							
	0-10	*11-24*	*25-39*	*40+*	*0-10*	*11-14*	*15-19*	*20-23*	*24-27*	*28-32*	*33-39*	*40-42*
AMEn	12.55	12.97	13.39	13.39	12.55	12.92	12.95	12.98	13.37	13.39	13.39	13.39
CP	23.0	21.5	19.5	18.3	23.0	21.5	20.0	18.0	17.0	16.0	14.0	13.0
digP	4.8	4.35	3.9	3.75	4.6	4.5	4.3	3.9	3.7	3.4	3.1	2.8
digCa	9.6	8.7	7.8	7.5	9.2	9	8.6	7.8	7.4	6.8	6.2	5.6

where: AMEn – apparent metabolizable energy corrected for zero nitrogen balance; CP – crude protein; digP – digestible phosphorus (the amount of dietary P that is absorbed by the gut until the end of the ileum; requirement for digestible P for growing poultry can be calculated by use of the equation: digP = (Pmaintenance + Pgrowth) / feed intake); digCa – dietary digestible calcium.

The actual levels of dietary protein and digestible P were defined based on Sc1 and were kept on the same level when calculating the dietary composition for Sc2. Two scenarios were compared on N and P excretion as well as partitioning of excreted N and P, while keeping the desired level of birds' performance in both cases.

Furthermore, scenario to check the model response to shifts in protein digestibility was also applied in a separate simulation. The digestibility of dietary protein and essential AAs was settled 80% as a default value. The simulations were run with the protein digestibility ± 5%, either at 85% or 75% level. The outputs were checked for N retention and partitioning of excreted N in terms of g/d in each day as well as cumulative total, fecal and urinary N excretion.

7. RESULTS AND DISCUSSION

7.1. Energy and protein partitioning model

7.1.1. Model calibration

The model was calibrated based on datasets from nutrition specifications and performance objectives of Aviagen (2017) and Cobb (2015) broiler breeders' guidelines, for Ross 308AP and for Cobb 500 genotypes, respectively. Thus, the input parameters for calibration – body weight (BW, kg) and daily feed intake (DFI, kg/d) over 9 weeks (63 days) of age – were differentiated by considering different sexes (male and female) and genotypes (Ross 308AP and Cobb 500) as displayed in Table 4. The simulation of performance outputs (Table 7) fitted well to the performance data from the guidelines (Figure 7) with low relative mean square predicted error (relMSPE) being 0.006%, 0.005%, 0.139%, and 0.048% for Ross males and females, and Cobb males and females, respectively (Table 8). MSPE is majorly explained by the disturbance proportion (E%) representing the proportion of MSPE unrelated to the errors of model prediction and less by the overall bias (B%) or the deviation from regression (R%).

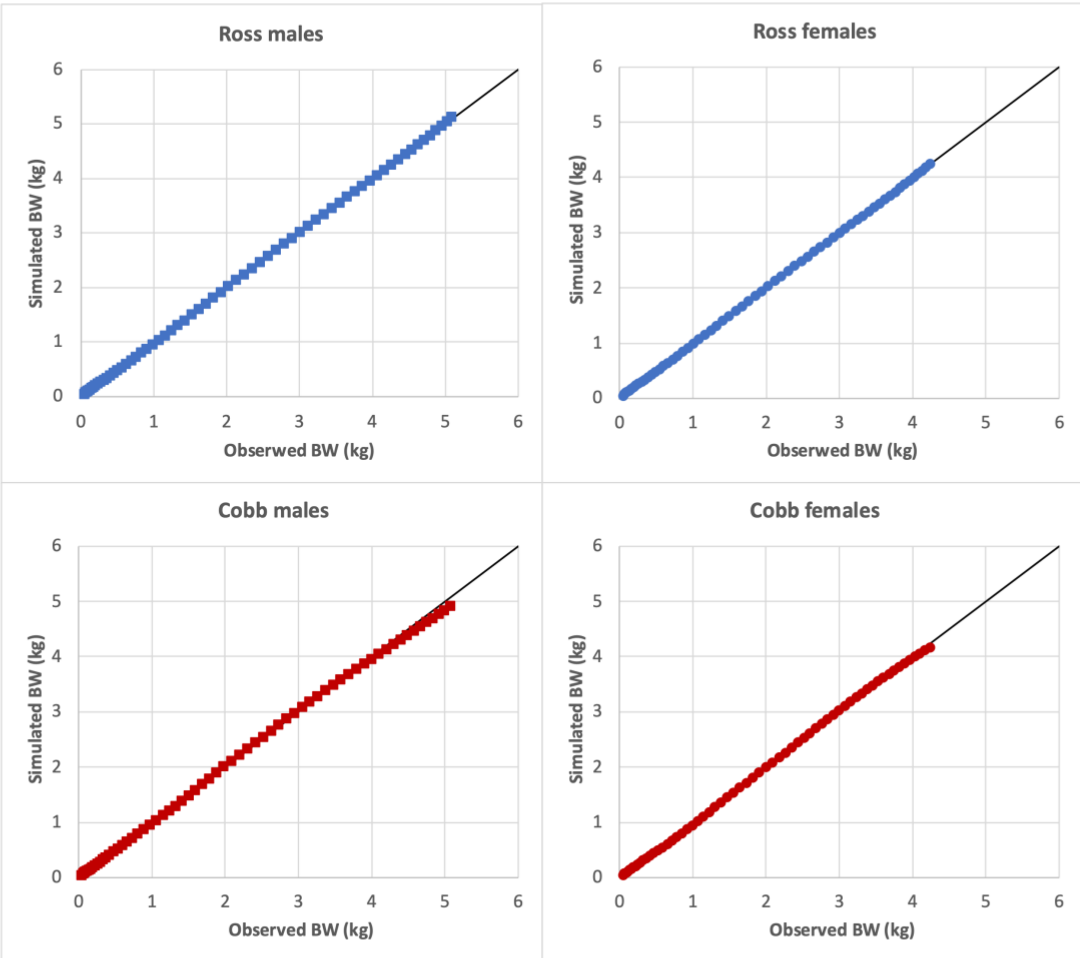


Figure 7. Simulated versus observed data (taken from management guidelines) for Ross and Cobb males and females

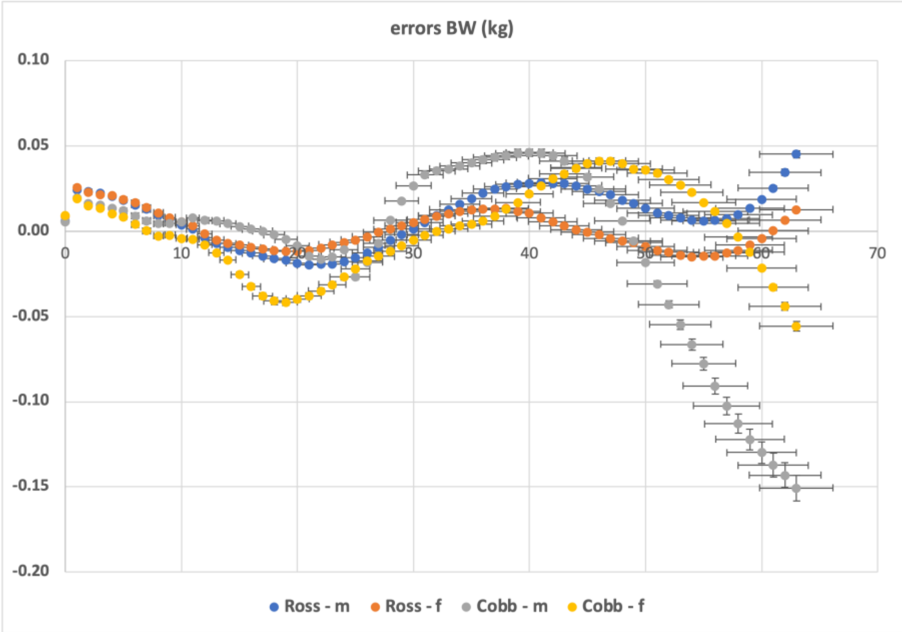
Table 7. Root mean square prediction error (MSPE) and relative MSPE (relMSPE, %) for the simulations over 63 days of age optimized by Solver Excel function

	rootMSPE	relMSPE %	B%	R%	E%
BW – Ross males	0.0001	0.0052	0.0000	0.0000%	100.0000
BW – Ross females	0.0001	0.0048	0.0001	0.0002	99.9997
BW – Cobb males	0.0030	0.1385	0.0062	0.0312	99.9626
BW – Cobb females	0.0009	0.0479	0.0012	0.0006	99.9982
DFI – Ross males	0.0001	0.0872	0.0001	0.0365	99.9634
DFI – Ross females	0.0003	0.1936	0.0400	0.0025	99.9575
DFI – Cobb males	0.0015	0.9057	0.6991	0.1238	99.1771
DFI – Cobb females	0.0004	0.2568	0.0691	0.1191	99.8119

where: BW – body weight; DFI – daily feed intake; rootMSPE – measure in the same units as the output and is also expressed as a percentage of the observed mean as a relative MSPE – relMSPE. B% – represent the proportion of MSPE due to bias, R% – represents the proportion of MSPE due to regression slope, E% – represents the proportion of MSPE due to non-defined error.

Root MSPE is the highest in case of Cobb males following Cobb females simulations. The difference in precision of the simulation is due to the difference in prediction ability of the model for DFI. In case of Cobb, particularly in males the DFI in the last 2 weeks is underestimated and so in females in the last week as shown in Figure 8. The reason of the model underestimation is at least partly due to the fact that the DFI is kept as a standard value in Cobb guideline for males at week 8 and 9 and for females at week 9 (Table 4). Thus, the increase in simulated DFI makes an increasing deviation from the observed values in those weeks. Whereas in case of Ross the values keep more dynamic character. The deviation of the simulated from the observed values are shown on Figure 8.

Besides the highest deviations at the last weeks of prediction, the simulations run for all cases are overpredicting the BW from hatch over the first 10 days. In the beginning of the simulation (2nd day) the overprediction is approximately 25 g, while the trend of the simulated vs. observed figure is decreasing. It corresponds the under prediction of DFI of 2 g (Ross females) up to 10 g around 2 weeks of age (for Cobb males and females). Shortly post-hatch the relative deviation is high, however, the model simulation in long term leads to goodness of fit except for Cobb males. The average deviation of the prediction simulation over 9 weeks is small being -0.73 %, 0.12 %, -0.07 %, and -0.02 % for DFI (not shown in table), and -0.91 %, -0.03 %, -0.13, and 0.08 % for BW, respectively for Cobb males and females, and for Ross males and females. In the 9-week period the deviation of simulated BW from the observation is -12 % for Cobb males, following -2.6 %, -0.6 % and -0.5 % for Cobb females, Ross males and females, respectively.



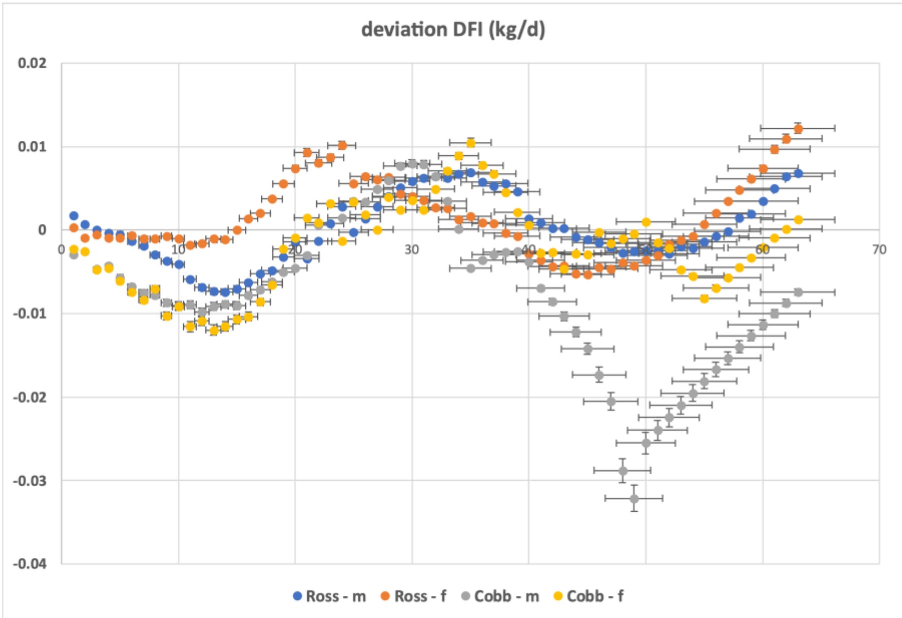


Figure 8. The difference between observed and simulated values for body weight (BW, kg, upper image) and daily feed intake (DFI, kg/d, down image) for Ross and Cobb males and females (deviation = simulated minus observed values)

The relative goodness of fit manner of the simulation confirms that the model algorithms repeatedly run in each time step – actually day by day – are proper. Based on the difference between simulated and observed values shown in Figure 8, it is visible that on the first day of simulation the predicted values are far higher than the observed ones in all strains. Day 0 in the simulation is the initial condition, in case of BW it is the initial BW that was computed in the calibration. The second point in time (day 1) indicates the comparison of the simulation to the experimental data right after the first-time step. Thus, the big difference between observed and simulated data indicates that the model algorithms in this point cannot accurately simulate the growth of the chick and likely the mechanisms behind. It is known that in the first day as-hatched chicken use energy from the yolk sac. That "extra" energy store is definitely not accounted in the model. Furthermore, the relative difference is bigger at the young age because 10 g difference at 50-80g BW is high, while at 1 or 2 kg BW the same difference (10 g) is considered much less error.

It has to be added that some deviation is natural. According to the management guidelines the coefficient of variation in BW is ranged from 6.6 to 9.4% which is typical for a uniform flock (Cobb, 2015; Aviagen, 2017).

The model predictive power is limited by the range of data collected from different literature sources and based on numerous assumptions, which should be replaced in the future with more reliable data from the appropriate trials. The model parameters are generalizing the nutrient partitioning and for instance no extra attention is paid to the first days of the chick when the gut maturation is in progress and that may change the digestion ability of the birds. It has been reported that the digestibility of nutrients is much lower in the first 10 days of life in broilers (Uni *et al., 1995*). Other functions may be age dependent too like efficiency of the AA utilization, but due to the lack of data at the early age of broilers makes it almost impossible to refine our equations at the moment with consideration of the age. It can be experienced that the relative deviation of the simulation from the observation (relative difference in BW and DFI) is decreasing. The 25 g difference of the prediction in a few days old bird weighing 50-100 g is more significant than the 25 g BW deviation in 5-6 or even 8-9 weeks of age when the broilers are 2.2–2.5 or 4.5–5.0 kg, respectively. That may suggest that the model algorithms are typically valid in later ages (roughly from 2-3 weeks of age). The calibration itself is a process that results in the best fitting of the simulation to all points of the dataset (subchapter 3.1.3). The deviation at the beginning of simulation (or anywhere else) can happen, since in the course of the calibration the 5 initial model parameters are adjusted to fit with the smallest root mean square error to the observed dots, and *BW_init* form Table 8 are suggested to be higher from those displayed in Table 4. Other parameters like allometry of chemical body components, digestibility coefficients, efficiency coefficients of energy or amino acid utilization are fixed therefore time dependency of those parameters are not considered in the model. However, due to some studies those traits may be changed with age. In general, the underestimation of the early age performance emphasizes that due to the higher metabolic activity as well as development of functional tissues in early ages, specific equations and more mechanistic approaches may need to adopt in the future model refinement.

7.1.2. Initial parameters

The five initial parameters for both genotypes and sexes are compared in Table 8. The values adjusted by Solver function agree with data in the literature, where *precocity* for empty feather-free body protein deposition (BPD) is mostly higher for females, meaning faster maturity, and varying between 0.031-0.048 and 0.345-0.056 for males and females, respectively. Males, however, have higher *meanBPD*, and this is probable as in the long-term at maturity males having a higher body protein weight compared to females in poultry. NE intake at 1 and 2 kg of BW (*FI_1* and *FI_2*, respectively) are higher for males, and it is feasible since both parameters are proportional to BW at 1 and 2 kg (Gous *et al.*, 1999; Sakomura *et al.*, 2005; Marcato *et al.*, 2008; Sakomura *et al.*, 2015, Silva *et al.*, 2014; 2015; Gonçalves, 2017; Vargas *et al.*, 2020).

Table 8. Comparison of the initial parameters for simulating performance of Ross 308 and Cobb 500 strains proposed by Excel Solver function

Parameter	Ross 308		Cobb 500	
	males	females	males	females
BW_init (kg)	0.049	0.052	0.047	0.051
precocity	0.047	0.049	0.048	0.053
meanBPD (g/d)	9.837	8.468	9.560	8.178
FI_1 (MJ NE/d)	1.232	1.229	1.335	1.281
FI_2 (MJ NE/d)	2.028	1.863	2.070	1.906

where: *BW_init* – initial body weight, *precocity* – parameter describing the concave shape of the protein deposition curve, maturity rate; *meanBPD* – mean empty feather-free body protein deposition; *FI_1* – net energy intake at 1 kg of body weight; *FI_2* – net energy intake at 2 kg of body weight.

The simulation calibrated for Ross males was used to demonstrate the model outputs and sensitivity analysis further.

7.1.3. Model output

Figure 9 demonstrates the body weight (BW, kg), cumulative feed intake (CFI, kg), feed convertion ratio (FCR, kg/kg), actual and potential empty feather-free body protein depositions (BPD actual, BPD potential, g/d) and empty feather-free body lipid deposition (BLD, g/d) over 9 weeks of age. After fitting the initial parameters to the "standards" of guidelines' recommendation on performance objectives, the model highlights the internal phenomena, such as the dynamics of nutrient and energy partitioning over time.

The yellow curve presents the BPD in g/d, showing the highest rate at the end of 5th week, and descending further. As concerns the BLD graph on the Figure 9, it is increasing until 9th week of age and probably reaching its maximum rate further in time. Lipid deposition is undertaking the function of an energy sink and is depending on energy intake from the diet.

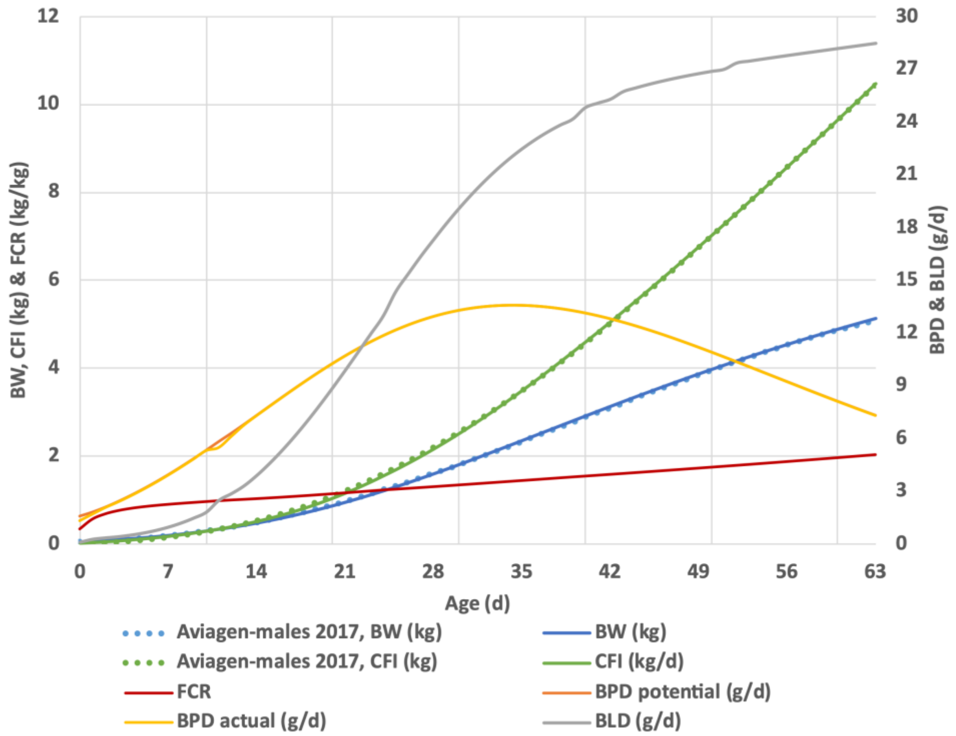


Figure 9. Simulated and observed BW (kg, left axis), DFI (kg/d, left axis). FCR (kg/kg, left axis) and simulated daily depositions (right axis) for potBPD (g/d), BPD actual (g/d) and BLD (g/d) over 9 weeks of age for an average broiler

Wecke *et al.* (2017) reported BW for Ross 308 birds at 36 days of age as 2.437 and 2.499 kg for males and females, respectively. Those values are very close to the model output being 2.458 and 2.215 kg for males and females, respectively. The feather weights were reported as 83.1 and 91.7 g, whereas the model simulated 75.9 and 71.9 g feather for males and females, respectively. The feather cover is proportional to BW and body volume. The diet formulation from the experiment aimed to meet current recommendations of NRC (1994).

According to the model simulation on day 35 there are 13.59 g/d of BPD and 21.51 g/d of BLD into the empty feather-free body for males, whereas 11.68 and 16.86 g/d, respectively, for females. Those depositions correspond to 141.83 g/kg feather-free body protein and 137.79 g/kg body fat content for males, or 144.37 and 138.93 g/kg protein and fat content of feather-free body, for females, respectively.

Marcato *et al.* (2008) published higher values for protein and lower ones for fat, 16.54 and 11.39 g/d for males, 13.8 and 11.5 g/d for females, respectively for BPD and BLD. Wecke *et al.* (2018b) published results for Ross broilers at 5 weeks of age and found 24.2 and 8.3 g/d body protein (including feather) and lipid accretion for males, and 20.7 and 14.0 g/d for females, respectively. As shown in Table 9, the feather protein gain on day 35 was 3.02 and 2.79 (g/d), resulting 16.61 (3.02 + 13.59) and 14.47 (2.79 + 11.68) g/d of total body protein. In terms of whole

Table 9. Model output for the day 35 on empty feather-free body and feather weights, its chemical and physical compartments

Age – 35 days	Ross 308		Cobb 500	
	males	females	males	females
BW (kg)	2.35	2.12	2.33	2.09
eFFBW (kg)	2.11	1.90	2.10	1.87
FW (g)	68.50	72.79	66.72	70.27
FP (g)	60.66	64.36	58.98	61.84
	Mass of chemical components in eFFB			
BP mass (kg)	0.30	0.27	0.29	0.27
BL mass (kg)	0.29	0.26	0.34	0.28
eFFBwater mass (kg)	1.46	1.31	1.41	1.26
eFFBash mass (kg)	0.06	0.05	0.06	0.05
CFI (kg)	3.27	3.08	3.43	3.09
FCR	1.42	1.49	1.50	1.52
BWG (g/d)	110.21	91.18	108.95	91.02
FP (g/d)	3.02	2.79	2.85	2.69
BPD (g/d)	13.59	11.68	13.31	11.55
LD (g/d)	21.51	16.86	21.98	17.94
ExcessProt (g/d)	14.44	11.17	14.51	11.40
	Chemical content of eFFB			
BP (g/kg eFFBW)	141.83	144.37	138.72	143.84
BL (g/kg eFFBW)	137.79	138.93	160.24	150.58
eFFBwater (g/kg eFFBW)	692.02	687.82	673.30	676.81
eFFBash (g/kg eFFBW)	28.37	28.87	27.74	28.77
FP / TP	0.17	0.19	0.17	0.19
FP / BP	0.20	0.23	0.20	0.23
TP / EBW	0.17	0.17	0.16	0.17
Breast meat (% eBW)	21.58	21.12	20.90	20.88
Thighs (% eBW)	8.46	8.53	8.27	8.50
Drumsticks (% eBW)	7.30	7.37	7.14	7.34
Wings (% eBW)	5.73	5.82	5.61	5.80

where: BW – body weight, eBW – empty body weight, eFFBW – empty feather-free body weight, FW – feather weight, FP – feather protein, BP – empty feather-free body protein, eFFBL – empty feather free body lipid, BPD – empty feather-free body protein deposition, LD – empty feather-free body lipid deposition, ExcessProt – excess of the dietary protein at the end of the day, eFFBwater – empty feather-free body water, eFFBash – empty feather-free body ash, TP – total protein (BP + FP), BWG – body weight gain, CFI – cumulative feed intake, FCR – feed conversion ratio.

empty body composition, total body protein content corresponds as 165.25 and 171.68 g/kg of whole empty body and total body lipid content 133.45 and 133.81 g/kg of whole body (BL mass / (eFFBW + FW/1000) for males and females, respectively. Those values, particularly for protein content are low but still in line with literature data (see later).

In conclusion, the model likely somewhat underestimates BPD and overestimates BLD. Misprediction could be adjusted, by changing model inputs, increasing the values of initial parameters e.g., *meanBPD* and *precocity*, while reducing values of *FI_1* and/or *FI_2*. Having the low phenotypic potential and the high dietary energy intake, would consequently bring to the high fat deposition, which considered to be an energy sink for all "not utilized" AAs and energy at the end of the day.

If to dig deeper, the BPD might be under predicted because the initial key parameters were set to combination that is limited by potBPD (phenotypic potential) and not by the dietary available EAAs (particularly from day 15, Figure 10). Also, there is a little glitch at day 11, visible on both figures, Figure 9 and 10. It means that one or several AAs are insufficiently available to fulfil the genetic potential for BPD. Practically it could be explained as dietary AA composition is decreasing not gradually (in phase feeding), compared to the dynamic increase of the energy intake, animal growth and, therefore, its nutritional needs.

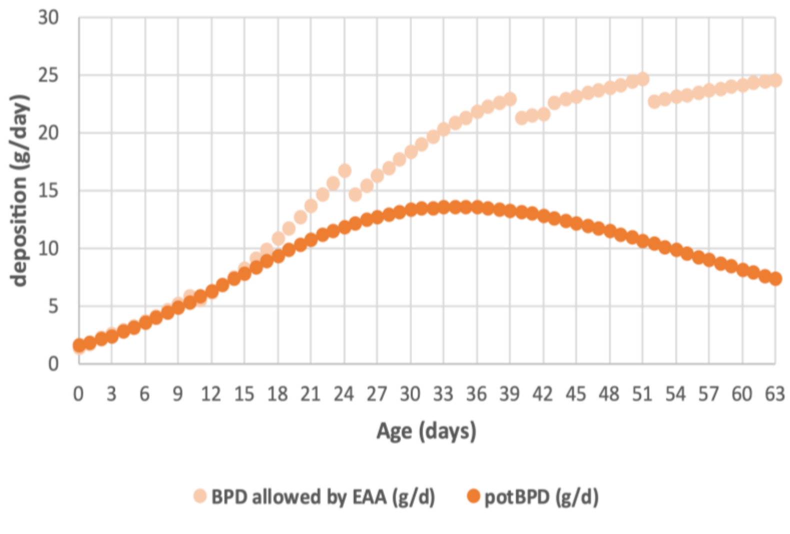


Figure 10. Simulated empty feather-free body protein as phenotypic potential (potBPD, g/d, orange dark dots) and allowed by the dietary SID EAA intake (BPD allowed EAA, g/d, orange light dots)

Secondly, the model "diet" part (*FI_1*, *FI_2*) was fitted to DFI (kg/d) from the guidelines at one step, and the model "animal" part (*BW_init*, *precocity* and *meanBPD*) – to BW (kg), afterwards. It was done back and forward, until the sum of squared estimate of errors either for "diet" or for "animal" became the smallest. Thus, diet parameters and the dietary energy intake was at certain "obligatory" level, when all another "animal" parameters responsible for the dietary energy utilization for maintenance (*FHP*, kJ/d/$BW^{0.7}$), physical *activity* lever (% of *FHP*, *etc.*) were, perhaps, settles relatively too low.

Thirdly, the connection point between "diet" and "animal" parts is related to energy utilization efficiency coefficients, and an animal was considered to stand into a thermoneutral environment. The *c* parameter from net energy intake function *ad libitum* (6.1.1) adapted from InraPorc (eq. 8) indicates that as BW increases, the animal eats for *c* multiplied by metabolic BW.

$$NEint_{al(i)} = (a * \left(b * BW_{(i)} * e^{(-b*BW_{(i)})} + 1\right) * c * BW_{(i)}^{d} \quad \text{[eq.8]}$$

The value of "*c*" depends on how energy is expressed and, therefore, value of *c* was considered constant for a given mode of expression (*e.g.*, it was 0.75 and 0.8 MJ/kg of metabolic BW/d when expressed on a NE basis in pigs and poultry according to van Milgen *et al.*, 2008 and Carré *et al.*, 2014, respectively). Since there was no such a clear value in the literature for poultry, for the model construction it was a presumption to be at the fixed level. There is another parameter – k_{BR} – the energy efficiency of using body reserves (see Annex A), which was adapted from the pig model as 0.7084, and it is indirectly affects the energy left for BLD at the end of the day *i*. The higher the value, the less fat will be deposited.

Finally, the non-initial parameters, which are currently fixed in the model (Annex A) such as allometry coefficients of the compartments (for feather weight and its protein contents, empty feather-body, water, ash, and lipid contents, as well as all the digestibility and efficiencies coefficients, and energy or AA obligatory losses, *etc.*) were assumed or taken elsewhere from the different literature sources. All in all, it was expected to generate some degree of error when extrapolating apart versus collating together the parameters of the algorithms, while modeling the day-to-day steps of nutrient utilization.

Explicitly, there are a very limited number of publications available with dynamic datasets on development of body chemical components differentiating sexes and genotypes from as hatched till maturity. There are only a few recent years' studies published by Gonçalves (2017) and Vargas *et al.* (2020) when animals performances were observed until 16 weeks of age. It is important to stress that in earlier studies the maximum age utilized by authors was 56 days which is only a half-way to maturity. Thus, the obtained parameters should be compared cautiously.

Simulated body chemical composition, as well as valuable meat parts, on the day 35 are presented in the Table 9, and the dynamics of body chemical composition are shown in the Figure 11.

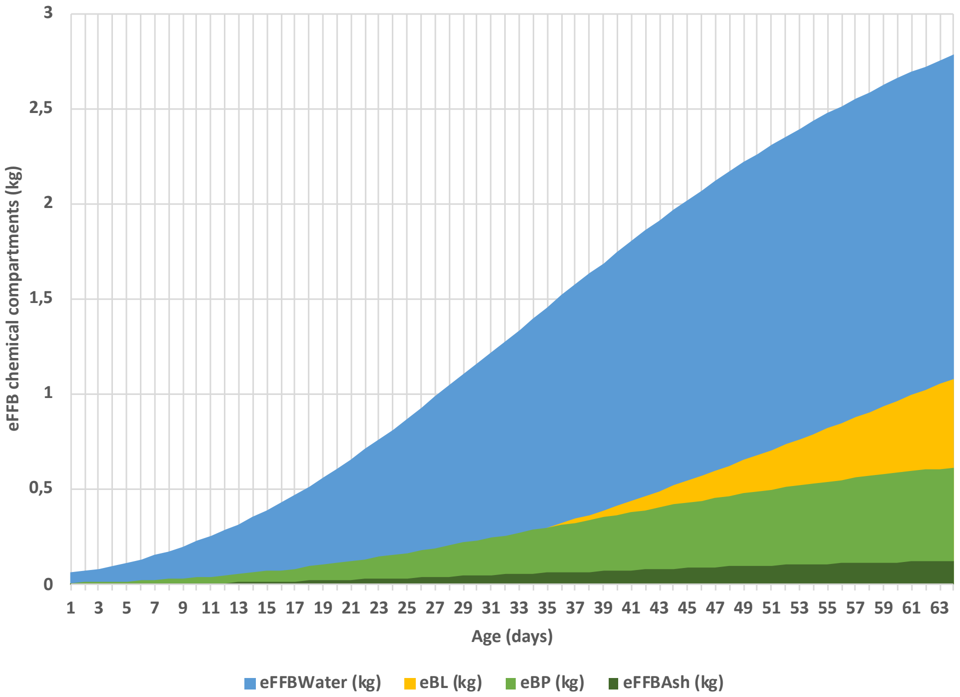


Figure 11. Model simulation of chemical compartments of empty feather-free body (eFFB) as a function of age for an average broiler: eFFB water (eFFBwater, kg), eFFB lipid (BL, kg), eFFB protein (BP, kg), and eFFB ash (eFFBash, kg)

The prediction of BW at 33 days of age for Cobb male broilers being 2.117 kg agrees with Caldas *et al.* (2018) reported as 2.044 kg (with coefficient of variation 7.6 %). The total protein content, water content, lipid content and minerals (g/kg) were 173 (2.6% CV), 707 (1% CV), 90 (14.5% CV) and 20.8 (6.6% CV), respectively, in the reported study. To be able to make a reliable comparison, the model outputs were computed at 33 days of age 161.5, 659.4, 148.7 and 27 for total protein content (BP+FP), water content, lipid content and ash (g/kg), respectively. The datasets published by Caldas *et al.* (2018) besides protein, water, lipid, and mineral contents are, however, include some rest fraction, which is assumed to consist mainly of glycogen and variability of the analysis.

In general, the trend of estimated parameters of empty feather-free body and feather weights, its chemical and physical compartments are in line or near to those published.

Simulated breast meat % (as percent of empty body weight, eBW) values are close to the values from the recommendation for Ross (2017): being for Ross males 22% of 2.2 kg eBW, which is near 22.33-22.53 % of live weight 2.2-2.4 kg. For Ross females it was predicted 23% of 1.9 kg eBW in place of 22.58-23.56% for the live weight 2.0-2.2 kg. For Cobb (2015) genotype the recommendations do not differentiate between sexes, listing about 22.5-23 % of breast meat for 2.1-2.5 kg of live weight. The values predicted by the model (around 23%) are close to the values from the guidelines. The results published by Sakomura *et al.* (2011) are reporting the breast meat at 35 days of age being 22.8 and 24 %, and 23.4 and 23.3 % of eBW of 2.142, 1.830 and 2.193 and 1.911 kg for Ross males and females, and Cobb males and females, respectively.

For other edible meat parts (portions), the simulation is under predicting values for thighs, drumsticks, and wings. In the recommendations for Ross the values are respectively, 13.6, 9.5, 7.8 % for the females of 2.0-2.2 kg of live weight, and 13.5, 10.18, 7.7 % for males of 2.2-2.4 of eBW. Whilst there is no information on thighs, drumsticks and wings yields in Cobb broilers breeder recommendations. Sakomura *et al.* (2011) reported higher values than predicted by the model, respectively for Ross males and females, and Cobb males and females for thighs – 9.5, 9 and 9.6, 9.1 % eBW; drumsticks – 11.9, 10.7 and 10.58, 10.57 % eBW; and wings – 8.4, 7.7 and 7.6, 7.4 % eBW. The allometric regressions equations for each sex (independent from Ross308 or Cobb genotype and feeding level) were applied in the model are based on the studies of Danisman and Gous (2013). However, the authors concluded that in order to improve the accuracy of the prediction of component weights – as influenced by strain, sex, and dietary protein content – the minimum and maximum lipid deposition in these components should be determined in different strains.

The model enables estimation of dietary SID EAA requirements at each day of production of an average bird as shown on Figure 12. It simulates the EAAs utilization with consideration of the maximum protein deposition rate during the lifetime (potBPD). The required dietary AA concentration is the highest at the 1st week of age and decreasing gradually over time. Certainly, the situation varies depending on the fixed rates of the AAs partitioning amongst the feather-free body and feathers, as well as AA established composition of these two protein pools, which is fixed in the model independently from sex and genotype.

The dashed lines are estimating the AA profile of ideal protein (AA requirements expressed in % of lysine). The model simulation confirms the experience that requirements for AA to Lys ratios are not fixed due to undergo dynamic changes during different physiological stages and in response to alterations in genotypes and environmental factors (Wu and Li, 2022). There are some peaks around 42 days for Thr and Met+Cys on the graph and it could be explained by increasing feather (AA) loss, starting from 28 to 42 days of age. At around 42 days of their life, broilers undergo a number of moult periods and feather regeneration (Lopez and Leeson, 2008). Also, it is visible that, for instance, at 42 days of age the Thr:Lys ratio is increased, and the tendency continued with age. Lemme (2003) also reported very similar tendency, since the relative requirement of growth is descending by age while the proportion of maintenance requirement in the total AA need is increasing.

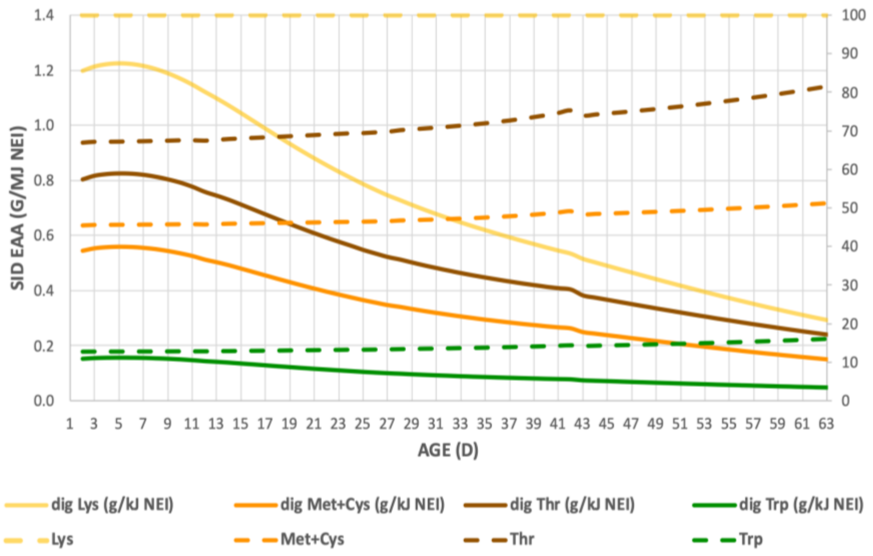


Figure 12. Simulated standardized ileal digestible (SID) lysine (Lys), methionine + cysteine (Met+Cys), threonine (Thr), and tryptophan (Trp) requirements (g/MJ NEI), as well as their Ideal Protein ratio (% to Lys) for an average broiler (dashed-lines)

It is well documented that ideal protein profile is changing during life. That phenomenon is definitely attributed to changes in the proportion of amino acids used from maintenance and deposition, but it may also be related – at least partly – to changes in amino acid utilization. This latter is just a hypothesis that should probably be further investigated *in vivo* and *in silico* too. Yet, the model is based on the presumption that the EAA composition of feather-free body and feather protein pools are considered independent of sex and genotype, as well as that AA efficiency doesn't change over time. There is no evidence in the literature that the efficiency of AA utilization in protein deposition would change with age, however, it is clear and explicitly included in the model that the age of the bird determines the maximum gain of protein. According to the Gompertz function the increasing phase of the protein gain is followed by a decreasing protein growth rate. Thus, the higher rate of oxidation may be obtained in the model in older age but that is not related to the k_{AA} values. When more reliable data are available on the qualitative relationship between age and k_{AA} values, those equations can be applied.

The partitioning of daily standardized ileal digestible (SID) lysine (Lys), threonine (Thr), methionine (Met) and cysteine (Cys), and tryptophan (Trp) requirements into maintenance, protein deposition in eFFB and feathers, and feather loss, is shown on the Figure 13 as grams per kg of the diet over 6 weeks of age. The guidelines recommendation is defined by a right scale and transparent light orange area on the right side of coordinate axis. The requirements simulated by the model are presented on the left side scale in bright colours, subdivided among requirements for BP (orange), FP (yellow), maintenance (green), and F loss (blue).

During the first days of life the requirements' simulation are being non-proportionally high and were omitted as it is related to the initial feather development parameters conditions. However, as it can be seen in the case of simulation for Lys and Thr, at the beginning of grower phase the requirements simulated by the model are higher by those in the recommendations. Nevertheless, from another hand, this issue could rise from the k_{AA} values for Lys and Thr being too high (0.77 and 0.73) or quantity of these AAs (g/g) in BP or FP, as well as the assumption that coefficients $AA_{urinary}$ (0.0239 and 0.0138 g/d) or $AA_{endogen}$ (0.233 and 0.442 g/d) for maintenance needs, adopted from pig values, probably was not precise enough for poultry (see Table 2). Yet, the good point is that these values could be defined via experiment and replaced, and the model helps to identify such missing points.

In the case of Met + Cys, the value is modelled as one AA flow, thus the level and circumstances of convertibility of Met to Cys were not considered. That makes sense, considering that the S-containing AAs are generally given together in practical animal nutrition. Using Met+Cys value would also be justified because the animal body can produce cysteine from methionine and within certain limits the reverse is also true. Also, it is worth mentioning that due to the lack of data, the other essential AAs for poultry such as proline and glycine were not included in the model at the current stage of development.

The recommendation for the phases is presented as stair steps, where the length of each step is defined by the length of the phase and the depth – by the amount of nutrient. If more phases are applied to fit the nutrient supply of the birds to their actual requirement, the use of dynamic models are essential (see further in Chapter 7.3). The development of a dynamic approach in diet formulation is necessary in the transition from phase to phase, which was successfully introduced for pigs (Remus *et al.*, 2020).

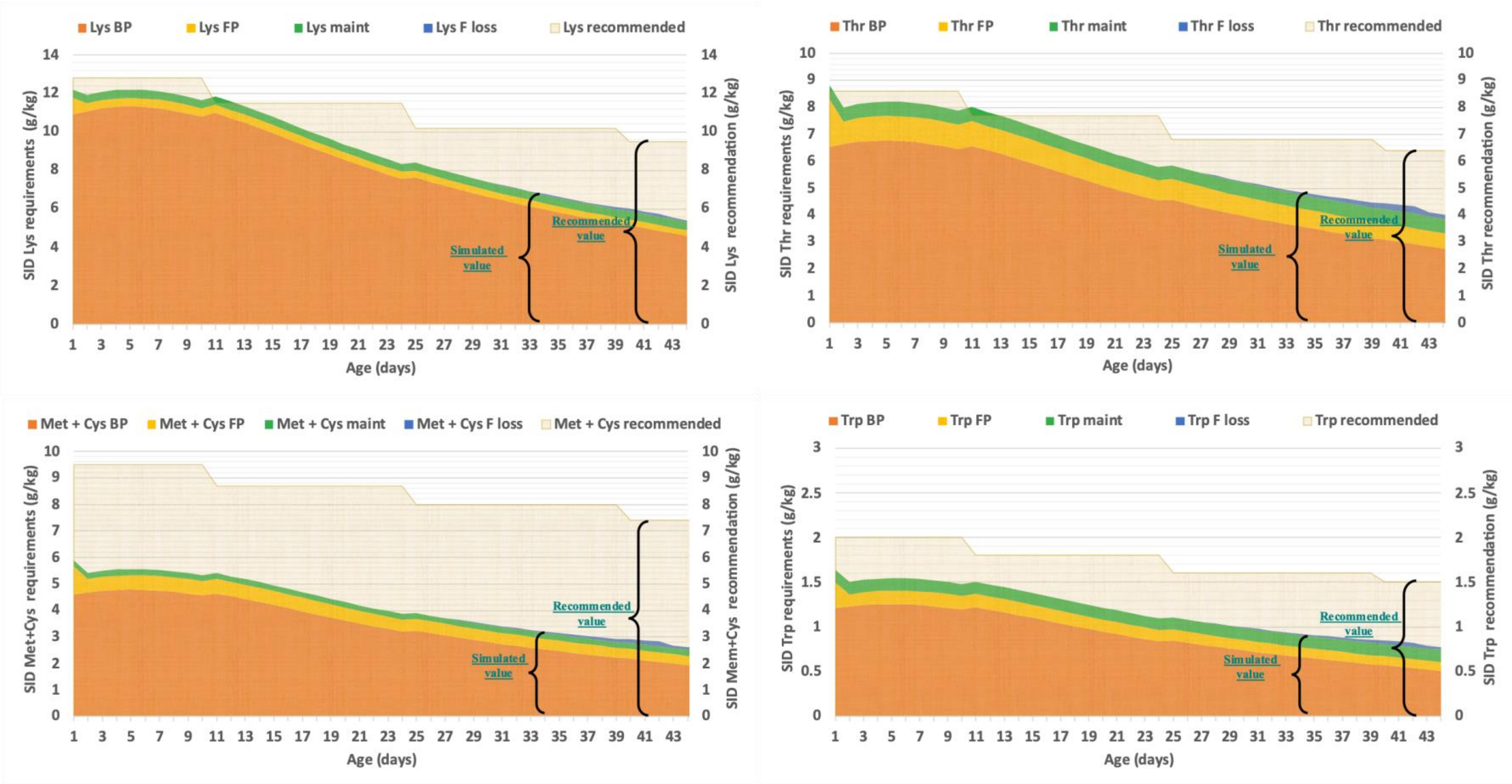


Figure 13. Simulated partitioning of standardized ileal digestible (SID) lysine (Lys), threonine (Thr), methionine + cysteine (Met+Cys) and tryptophan (Trp) requirements in gram per 1 kg of diet (left axis): the empty feather-free body protein (BP), feather protein (FP), maintenance needs (maint) and feather loss (F loss, g/d) versus the recommendations for SID level (recommended, g/kg/d)

7.1.4. Sensitivity analysis

The purpose of the sensitivity analysis is to examine the model behaviour when distinct model parameters are changed. In the course of the process the 4 out of 5 key initial parameters (*meanBPD*, *precocity*, *FI_1*, and *FI_2*) were modified by ± 10-20%. In this thesis due to the limitation of the length of the text, the most important results of the sensitivity analysis are shown. Those ones are presented that are principal parameters in the model. The results of the sensitivity analysis as regards the BW, feed conversion ratio (FCR), protein and lipid mass as affected by the initial model parameters are shown in Figure 14.

The driving force of the model is daily net energy intake, and the model's core is the empty feather-free body protein. If the dietary AA intake of the bird is adequate to fulfil the requirements deternined by the phenotypic potential (as Gompertz function parameters *meanBPD* and *precocity*), the growth trajectory will not be disturbed. Therefore, dietary AAs were settled as not limiting for sensitivity analysis.

These changes in *meanBPD* and *precocity* parameters can influence the output traits of the simulation in direct or indirect ways. By increasing the parameters value, the treats values such as BW and protein mass will increase as well (direct way), while the FCR will decrease (indirect way). It could be explained as following: if BP value has grown, all the treats in linear or allometric relation to BP – eFFBwater, eFFBash, BW, FW, breast meat – will increase as well.

From the Figure 14 it can be concluded that model outputs as BW, protein mass, and FCR are the most sensitive to *meanBPD*. The 20% decrease in *meanBPD* cause 20% reduction in BW at 42 of age, whereas increase of *meanBPD* by 20% gives higher BW by 18.2% (with AAs dietary levels considered as non-limiting). The FCR, respectively, with lowest *meanBPD* increases by 15% and decreases by 8% with highest *meanBPD*, compared to the simulation with initial values. The decrease of *precocity* by 20% caused 13% decrease of BP mass and increase by 20% corresponds 10.6% increase. Respectively, it influences the BW in direct way, resulting in 12.5% decrease and 9.7% increase, respectively with highest and lowest *precocity*. This parameter influences all the traits in a direct way.

The lipid deposition is dependent on energy intake, particularly by parameters *FI_1* and *FI_2*. They are somewhat interconnected, since a bird that eats a lot at the first part of fattening will likely eat more later too. However, the *FI_1* and *FI_2* values can be handled independently in the model. Those parameters are fixing the daily amount of energy to be consumed at certain BW (1 and 2 kg, respectively). Since, the DFI is depending on net energy intake, if to decrease both *FI_1* and *FI_2* the BL and BLD values will decrease. Thus, *FI_1* and *FI_2* have the highest impact on the dietary energy intake over the fattening period, and therefore drastically impact the BL as shown in the Figure 14 as well as on the Table 10.

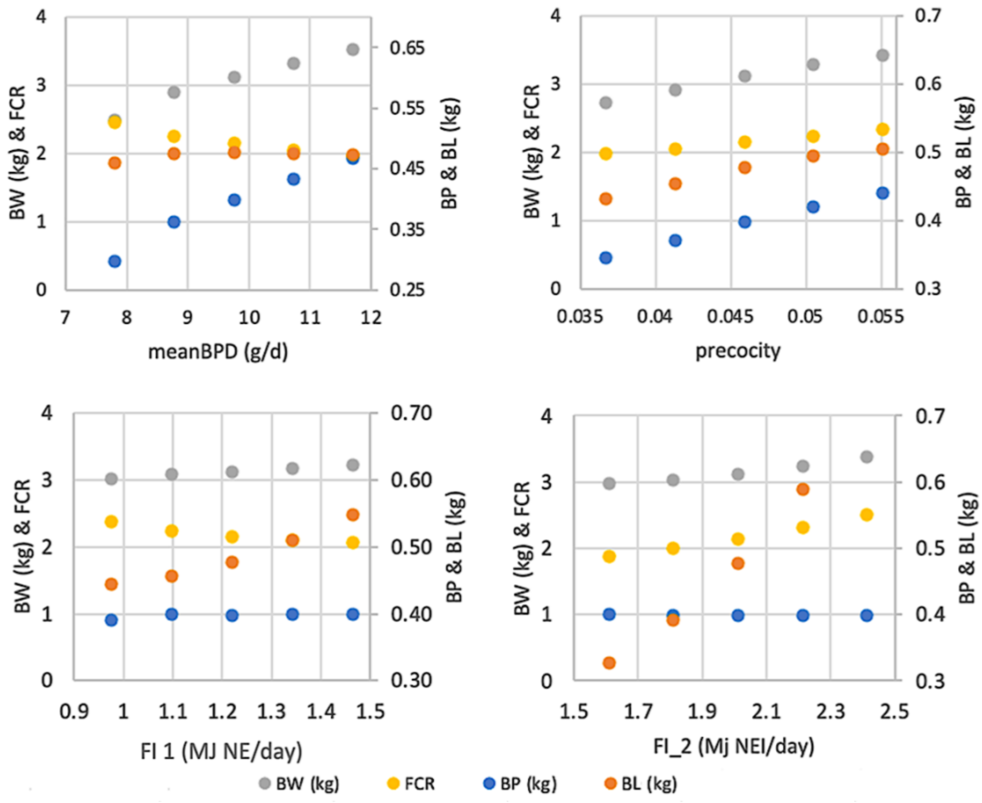


Figure 14. Sensitivity analysis as regards the body weight (BW, kg), feed conversion ratio (FCR), empty feather-free protein (BP, kg) and empty feather-free lipid mass (BL, kg) affected by the initial model parameters (*meanBPD*– a general parameter for potential empty feather-free body protein deposition, *precocity* – the shape parameter of Gompertz equation, *FI_1* and *FI_2* – NE intake (MJ/d) at 1 and 2 kg of BW, respectively

If to decrease the energy content of the diet, thanks to the established energy intake level by *FI_1* and *FI_2*, in simulation the animal will increase the quantity of the diet intake, keeping the BLD (g/d), and thus, BL (kg) almost at the same level. Nevertheless, the manipulations with maintenance parameters – FHP, activity level, k_{BR} – acting in inverse way regarding the BL (kg) and BLD (g/d), with decrease in maintenance energy needs, the amount of fat deposition will increase.

As concerns a tendency for the efficiency values for AA utilisation (not presented graphically), the gradual change in coefficients affects the actual BPD (g/d) in a direct way. Meaning, that if to come back to the Figure 13 and increase the efficiencies for k_{AA} Lys and Thr, there would be no issue of simulated requirements going higher than recommendation values.

Table 10 represents the sensitivity of model outputs when changing specific parameters such as *meanBPD*, precocity, *FI_1* and *FI_2*, and parameter “c” in FI curve (multiples of maintenance).

Table 10. Results of the sensitivity analysis as regards changes in weight, efficiency, and body components in response to 20% changes in the value of selected initial parameters

35 days of age	*meanBPD (g/d)*		*precocity*		*FI_1 (MJ/BW$^{0.7}$)*		*FI_2 (MJ/BW$^{0.7}$)*		*c parameter*	
	-20%	*+20%*	*-20%*	*+20%*	*-20%*	*+20%*	*-20%*	*+20%*	*-20%*	*+20%*
BW (kg)	-13.4	13.4	-16.2	16.8	-5.2	6.1	-1.5	2.7	0.2	1.9
eFFBW (kg)	-13.2	13.1	-16.0	16.4	-5.1	6.0	-1.5	2.7	0.2	1.9
FW (g)	-14.1	14.2	-17.1	17.8	-5.4	6.5	-1.6	2.9	0.3	2.0
CFI (kg)	-7.7	7.3	-13.5	14.3	-15.5	16.8	-3.9	6.7	-1.4	4.0
FCR	7.0	-5.5	3.6	-2.4	-10.8	9.9	-2.4	3.8	-1.7	2.0
BWG (g/d)	-15.8	15.0	-7.3	2.8	1.0	-2.1	-11.6	14.4	-0.4	0.6
FP (g/d)	-15.9	17.0	-9.7	4.8	1.5	-0.8	-11.0	12.6	-0.1	0.7
BPD (g/d)	-21.0	21.0	-8.2	5.1	0.0	0.0	0.0	0.0	0.0	0.0
LD (g/d)	-1.0	-1.6	-8.2	6.3	5.0	-9.8	-51.8	64.1	-1.5	2.9
ExcessProt (g/d)	7.0	-9.7	-11.2	13.5	1.4	-5.0	-46.6	58.3	-1.2	3.8
BP (kg)	-16.1	16.5	-18.1	19.1	0.5	0.8	0.7	-0.1	1.1	1.1
BL (kg)	-3.0	1.9	-11.6	11.3	-38.8	38.4	-14.4	19.6	-4.4	7.2
eFFBwater (kg)	-14.5	14.6	-16.3	16.9	0.5	0.7	0.6	-0.1	1.0	1.0
eFFBash (kg)	-16.1	16.5	-18.1	19.1	0.5	0.8	0.7	-0.1	1.1	1.1
Breast meat % of BW	-10.0	9.5	-10.0	9.6	6.2	-4.8	2.5	-2.8	1.3	-0.3

where: meanBPD (g/d) – mean protein deposition rate, *FI_1* (MJ/BW$^{0.7}$) – expected NE intake at 1 kg of BW, *FI*_2 (MJ/BW$^{0.7}$) – expected NE intake at 2 kg of BW (kg) – body weight, c – multiples of maintenance need in feed intake function, -20% – decrease of the parameter value by 20%, +20% – increase of the parameter value by 20%, BW (kg) – body weight, eFFBW (kg) – empty feather-free body weight, FW(g) – feather weight, CFI (kg) – cumulative fee intake, FCR – feed conversion ratio, BWG(g/d) – body weight gain, FP (g/d) – feather protein, BPD (g/d) – empty feather-free body protein deposition, LD (g/d) – empty feather free body lipid deposition, ExcessProt (g/d) – excess of the dietary protein at the end of the day, BP (kg) – empty feather-free body protein mass, BL (kg) – empty feather-free body lipid mass, eFFBwater (kg) empty feather-free body water mass, eFFBash (kg) – empty feather-free body ash, Breast meat % of BW – percentage of breast muscle meat (including bones and skin) to live body weight.

The diagnostic variables in this respect are BW (kg), eFFBW (kg), FW (g), CFI (kg), of eFFB (kg) and breast meat (%). Those outputs are shown to be affected directly or indirectly in the sensitivity analysis.

It is interesting to underline, that tendencies of model behaviour presented in the Table 10 are following the ones described above. At 35 days age the % values of changes in BW are linearly equal when decreasing or increasing meanBPD, being around 13%. Whereas, at 42 days of age with decrease of meanBPD by 20% the BW decrease by 20%, however with increases of meanBPD by 20%, it increases only by 18%. This could be explained by the age dependency of the max PD and that at 35 days of the BPD graph is at its peak, while at 42 days the amount of BPD grams per day is commencing to decrease.

7.1.5. Model testing

7.1.5.1. <u>Dynamic Ross dataset from the in vivo study</u>

The advantage of the dynamic datasets is that both DFI and BW were continuously measured during the trial, therefore, the reliability of the model in time could be tested. Results show that simulations fit well the observed broilers' performance for each experimental group (Figure 15). However, BW performance was underpredicted for males and there was a maximum relMSPE 1.28 and 1.06% for control and precision feeding groups, respectively (Table 11).

Table 11. Root mean square prediction error (rootMSPE) and relative MSPE (relMSPE, %) for the simulations run with experimental datasets

	rootMSPE	relMSPE %	B%	R%	E%
C-m BW	0.0097	1.2763	0.2476	0.7951	98.9573
C-m DFI	0.0002	0.1956	0.0004	0.7951	99.9966
C-f BW	0.0011	0.1614	0.0000	0.1750	99.8250
C-f DFI	0.0001	0.1630	0.0013	0.0050	99.9937
PF - m BW	0.0081	1.0585	0.2848	0.7139	99.0013
PF - m DFI	0.0002	0.1802	0.0023	0.0069	99.9908
PF - f BW	0.0005	0.0776	0.0075	0.0609	99.9316
PF - f DFI	0.0001	0.1685	0.0044	0.0105	99.9851

where: C-m – males fed control diet, C-f – females fed control diet, PF-m – males fed precision feeding diet, PF-f – females fed precision feeding diet, BW – body weight, DFI – daily feed intake, rootMSPE – root mean square prediction error, measure in the same units as the output and is also expressed as a percentage of the observed mean as a relative MSPE – relMSPE, B% – represent the proportion of MSPE due to bias, R% – represents the proportion of MSPE due to regression slope, E% – represents the proportion of MSPE due to non-defined error.

Also, chemical body analysis was done in 5 time points during the 33 days long study. The simulation outputs were compared with measured values (5th, 11th, 16th, 23rd and 31st days of age) for Ross 308 males and females in control group (Figure 16a and 16b), and for males and females in precision feeding group (Figure 16c and 16d).

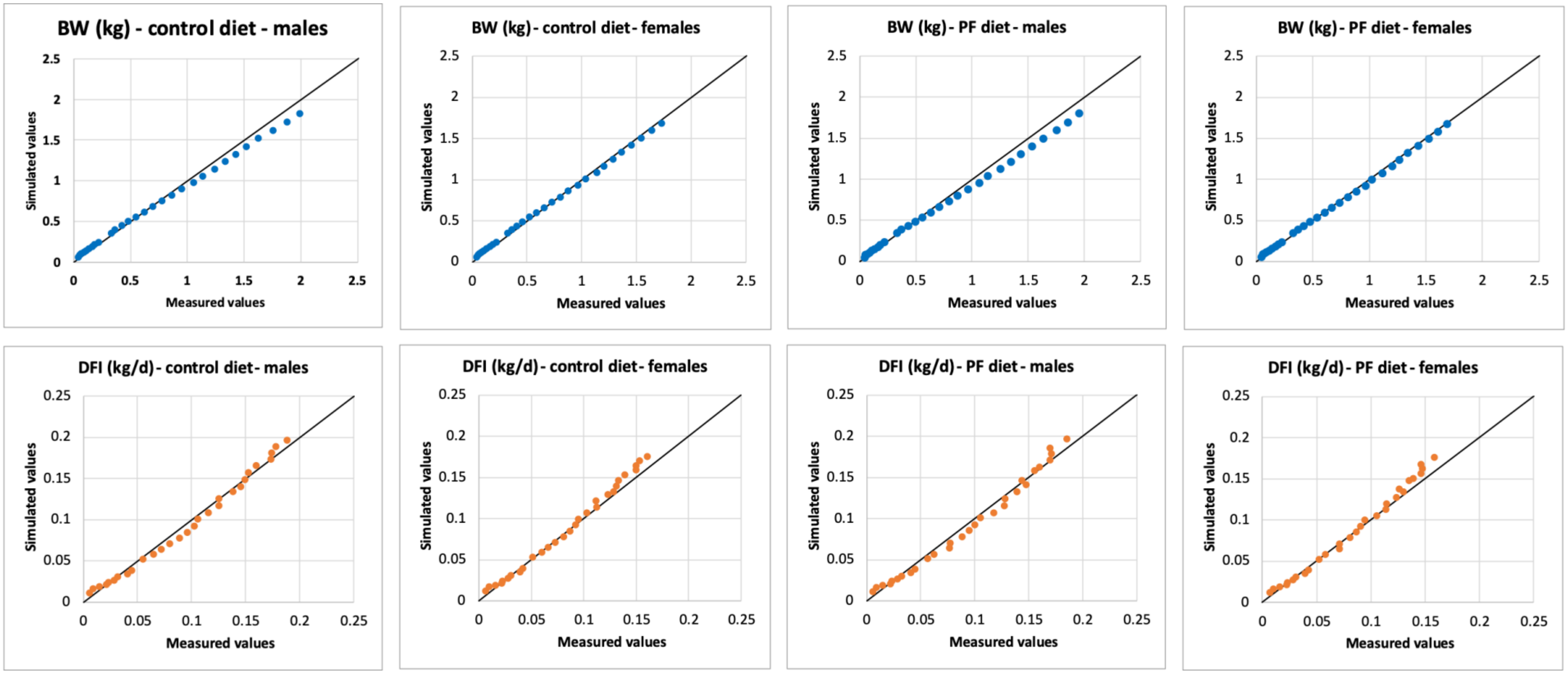


Figure 15. Comparison of simulated performance versus observed: body weight (upper graphs in blue, BW, kg) and daily feed intake (in orange, DFI, kg/d) for Ross 308 males and females fed control (C) and precision feeding (PF) diets over 30 days of age

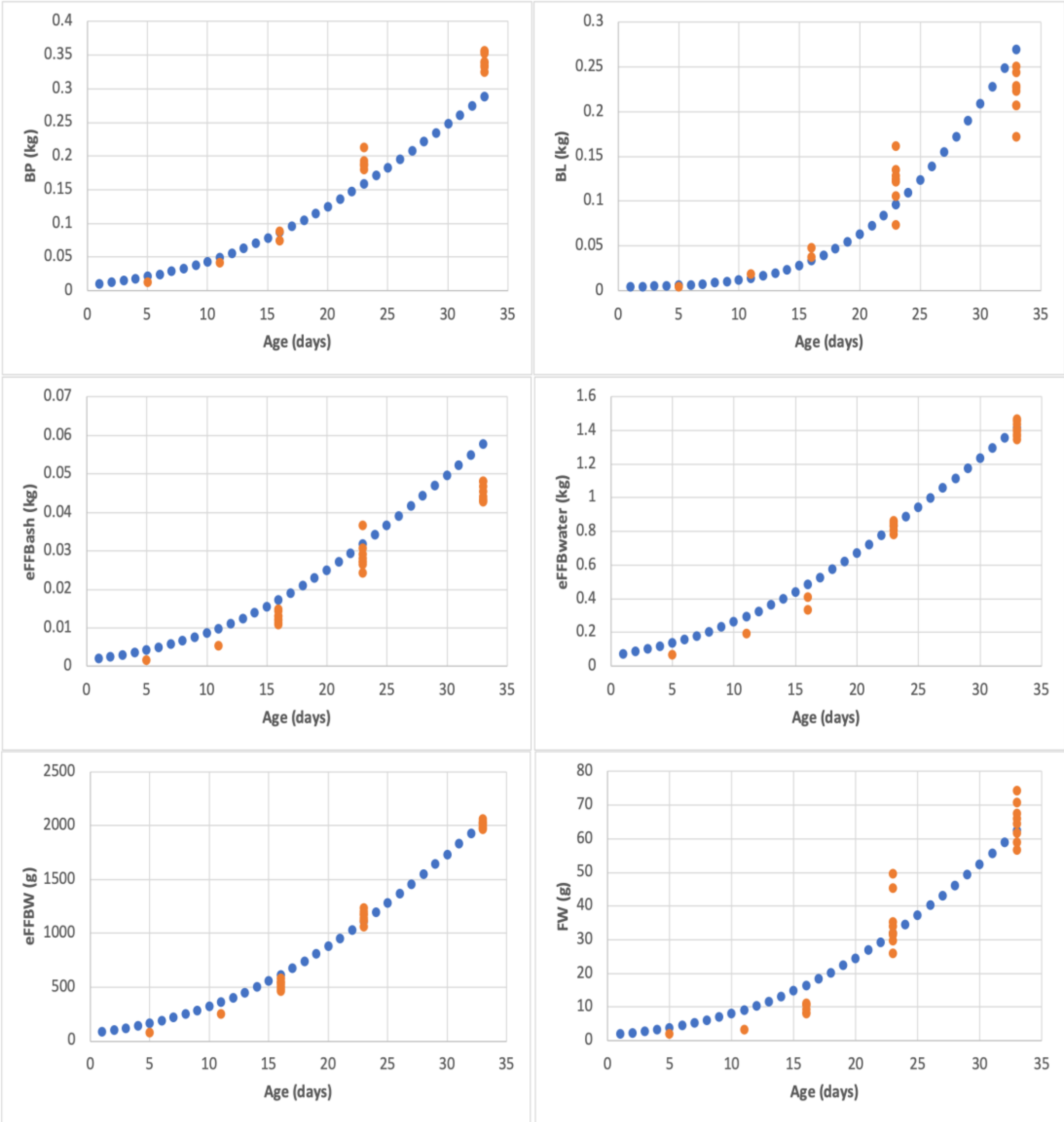


Figure 16*a*. Comparison of measured values (5th, 11th, 16th, 23rd and 33rd days of age) versus simulated performance (over 33 days of age) for Ross 308 males fed control diet: empty feather-free body protein (eBP, kg), empty feather-free body lipid (eBL, kg), empty feather-free body ash (eFFBash, kg), empty feather-free body water (eFFBwater, kg), empty feather-free body weight (eFFBW, g), and feather weight (FW, g)

It can be seen from the graphs in Figure 16a, that the model simulation for males fed control diet slightly overpredicts the BP during the first 3 weeks of age, and underpredicts it later age. Also, the eFFBash is overpredicted for the first three time points, and it is in range within observed values for 23rd day, whereas it overpredicts the measured values for the day 33. The eFFBwater, eFFBW and FW are following a similar tendency with overprediction the first three points of time, while for the days 23 and 33 it is in range for the estimated values.

BL, however, seems to be in range within observed values, with a little overprediction over the 33rd day.

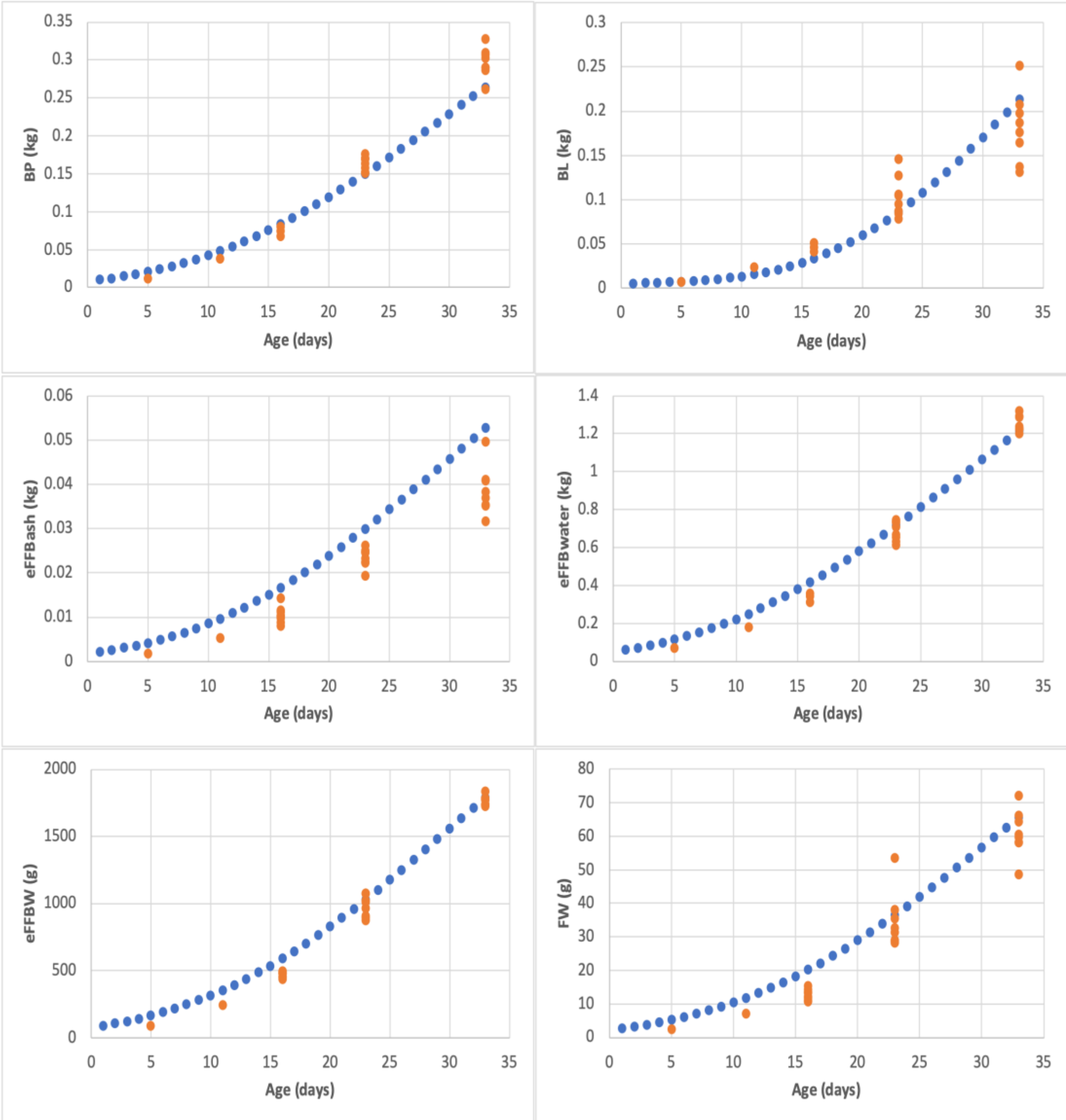


Figure 16*b*. Comparison of measured values (5th, 11th, 16th, 23rd and 33rd days of age) versus simulated performance (over 33 days of age) for Ross 308 females fed control diet: empty feather-free body protein (eBP, kg), empty feather-free body lipid (eBL, kg), empty feather-free body ash (eFFBash, kg), empty feather-free body water (eFFBwater, kg), empty feather-free body weight (eFFBW, g), and feather weight (FW, g)

For the females fed control diet, the BP prediction seems to be in line with observed values, whereas the blue dots touch the lower part of the measured values diapason at 23rd and 33rd days. The eFFBash is overpredicted, while the BL is in range within the estimated values, and in contrary to BP at the day 33 blue dots touch the highest value of the septimated diapason.

The simulations for eFFBwater, eFFBW and FP are overestimating the measured values at days 5, 11 and 16, however, it is in range of measured data for the last two measured datapoint on day 23 and 33.

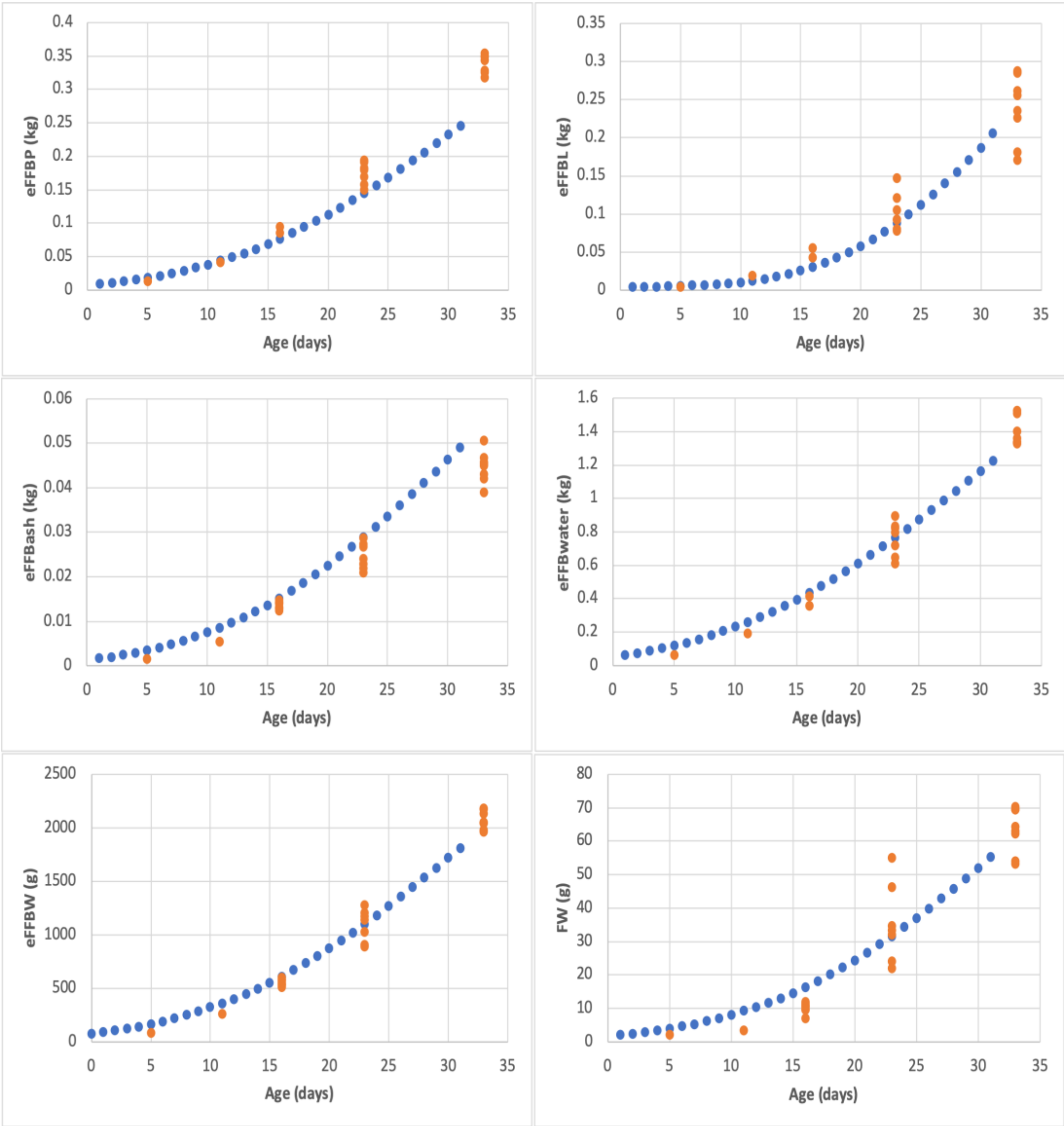


Figure 16*c*. Comparison of measured values (5th, 11th, 16th, 23rd and 33rd days of age) versus simulated performance (over 30 days of age) for Ross 308 males fed precision feeding diet: empty feather-free body protein (eBP, kg), empty feather-free body lipid (eBL, kg), empty feather-free body ash (eFFBash, kg), empty feather-free body water (eFFBwater, kg), empty feather-free body weight (eFFBW, g), and feather weight (FW, g)

For the male broilers in precision feeding group, the BP prediction seems to follow the same tendency as for the male broilers fed the control diet, however, the measured values on the day 16 are being lower (0.15 kg vs 0.17 kg). Thus, the prediction is more precise with relMSPE 2.7% vs 7.7%, respectively (Table 12). It can be seen from the graph on Figure 16c, the BL prediction is closer to the measure values, which is confirmed by a lower relMSPE: 4.9% vs 14.7%, for precision feeding and control feeding, respectively. The simulation for eFFBash is falling in range with observed data only in the two dots at 16 and 23 days of age, and otherwise it has an overprediction tendency up to the last day of simulation. The eFFBwater, eFFBW and FW simulations tendencies are like those in Figure 16a.

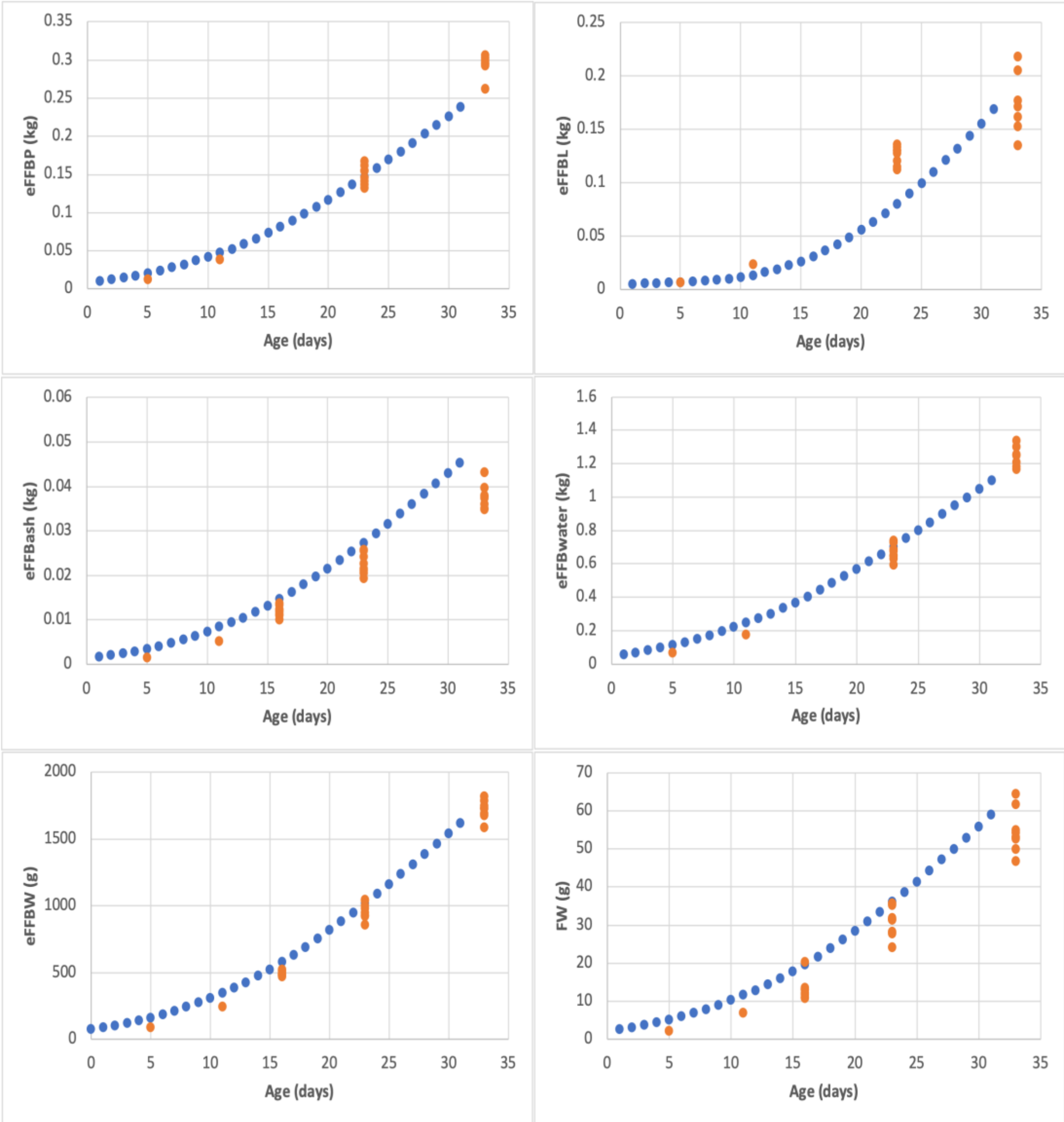


Figure 16*d*. Comparison of measured values (5th, 11th, 16th, 23rd and 33rd days of age) versus simulated performance (over 30 days of age) for Ross 308 females fed precision feeding diet: empty feather-free body protein (eBP, kg), empty feather-free body lipid (eBL, kg), empty feather-free body ash (eFFBash, kg), empty feather-free body water (eFFBwater, kg), empty feather-free body weight (eFFBW, g), and feather weight (FW, g)

For females in precision feeding group, the BP prediction is the most precise, with the lowest relMSPE being 1.4% (Table 12). There are BL and eFFBwater data missing for day 16. Nevertheless, the eFFBwater, eFFBW, and FW simulations are overpredicting the measured data on 5th and, 11th days, whereas the blue dots are in measured data range starting from the second week of age. The simulation for eFFBash is likewise over the observed orange data points except in the middle part of prediction where it touches the upper values in the range on days 16th and 23.

Table 12. Root mean square prediction error (rootMSPE) and relative MSPE (relMSPE, %) for the simulations run with experimental diets with dynamic dataset from the *in vivo* Ross study

	rootMSPE	relMSPE %	B%	R%	E%
C-m BP	0.0102	7.6735	1.0507	4.0007	94.9485
C-m BL	0.0120	14.6972	0.0100	1.5447	98.4453
C-m eFFBwater	0.0131	2.2909	0.7667	0.1928	99.0405
C-m eFFBash	0.0038	20.1522	0.2133	2.1429	97.6438
C-m eFFBW	0.0088	1.0943	0.4617	0.1424	99.3959
C-m FW	0.0011	4.6917	0.0188	1.6353	98.3459
C-f BP	0.0042	3.5981	0.1392	2.4536	97.4072
C-f BL	0.0252	35.0425	1.3433	5.4947	93.1620
C-f eFFBwater	0.0164	3.2510	1.6234	0.5379	97.8388
C-f eFFBash	0.0060	37.6963	0.4340	0.9011	98.6649
C-f eFFBW	0.0131	1.8453	1.0193	0.4599	98.5208
C-f FW	0.0014	5.7641	0.2342	0.7227	99.0432
PF-m BP	0.0021	2.7019	0.0686	2.9209	97.0105
PF-m BL	0.0000	4.9267	1.0956	0.1680	98.7364
PF-m eFFBwater	0.0193	5.5280	4.0616	2.3964	93.5420
PF-m eFFBash	0.0021	18.7568	0.3676	0.6426	98.9898
PF-m eFFBW	0.0137	2.7850	1.4119	0.4648	98.1233
PF-m FW	0.0020	16.1459	0.1351	0.4403	99.4246
PF-f BP	0.0009	1.4065	0.8244	0.5762	98.5993
PF-f BL	0.0053	10.3060	2.5602	0.0061	97.4338
PF-f eFFBwater	0.0247	8.0573	5.0953	2.9698	91.9348
PF-f eFFBash	0.0028	26.5380	0.6396	0.0384	99.3221
PF-f eFFBW	0.0183	4.0658	2.8423	1.5334	95.6243
PF-f FW	0.0024	17.5409	0.8656	0.0115	99.1229

where: C-m – males fed control diet, C-f – females fed control diet, PF-m – males fed precision feeding diet, PF-f – females fed precision feeding diet, BP – empty feather-free body protein, BL – empty feather-free body lipid, eFFBwater – empty feather-free body water, eFFBash – empty feather-free body ash, eFFBW – empty feather-free body weight, FW – feather weight, rootMSPE – root mean square prediction error, measure in the same units as the output and is also expressed as a percentage of the observed mean as a relative MSPE – relMSPE, B% – represent the proportion of MSPE due to bias, R% – represents the proportion of MSPE due to regression slope, E% – represents the proportion of MSPE due to non-defined error.

To conclude, the calibrated model with 5 initial parameters for an average Ross broiler was run with diets from the experiment and the model output was compared with experimental dataset. The DFI was simulated by the model and not adjusted to the observed values. The deviation from the estimated BP values was the highest for males, following females on control diet, and lower for males following females for precision feeding diet. The variability of derived data, such as eFFBash and eFFBwater is based on the prediction precision of BP values, as it is a core of the model. The data comparison is also showing a general agreement of the simulated vs. measured data with normal individual variance originating from the variety between the guideline and birds in the experiment.

7.1.5.2. Dynamic Cobb dataset from the in vivo study

The particularity of this dataset is that each DFI and BW were measured in real time from individual bird, which allows more accurate model testing. Therefore, the model was run with and without the real-time DFI inputs for both, classic and alternative diets. Table 13 demonstrates the absolute benefit of real-time data application. The rootMSPE as well as relMSPE are considerably decreasing when the actual DFI was applied as an input too. For the BW prediction for birds fed by classic diet rootMSPE reduced from 0.005 to 0.001 and relMSPE from 0.5% to 0. 5%. Whereas for birds fed alternative diet the error decreased from 0.170 to 0.002, and from 19.1% to 0.2% for rootMSPE and relMSPE, respectively.

Moreover, this dataset displays the model's weak point – model "diet" part: the DFI simulation based on multiples of energy intake and not inclusion of mechanisms influencing the FI of the animal related to the diet characteristics. Nevertheless, with correct nutrient content of the diet and real-time data on feed consumption, the model "animal" part is able to predict adequately the BW performance output.

Table 13. Root mean square prediction error (rootMSPE) and relative MSPE (relMSPE, %) for the simulations run with experimental diets with dynamic dataset from the *in vivo* Cobb study

	rootMSPE	relMSPE %	B%	R%	E%
BW classic	0.0047	0.4963	0.1067	0.3253	99.5680
DFI classic	0.0033	2.9363	0.6770	0.1794	99.1436
BW+ classic	0.0005	0.0536	0.0588	0.0174	99.9237
BW alternative	0.1687	18.1017	8.9249	7.2742	83.8008
DFI alternative	0.0111	9.5115	15.4616	2.3185	82.2199
BW+ alternative	0.0021	0.2235	0.1623	0.0949	99.7428

where: BW – body weight (kg) , DFI – daily feed intake (kg/d), BW+ – body weight with actual DFI application (kg); rootMSPE – root mean square prediction error, measure in the same units as the output and is also expressed as a percentage of the observed mean as a relative MSPE – relMSPE, B% – represent the proportion of MSPE due to bias, R% – represents the proportion of MSPE due to regression slope, E% – represents the proportion of MSPE due to non-defined error.

Figure 17 displays the character of model behaviour when "feeding" the average Cobb male broilers with classic or alternative diets. Each coloured dot is representing the individual bird randomly chosen from the experimental flock. It is clearly shown that model is underpredicting the BW of the broilers fed alternative diet and that the situation is considerably changes as real-time DFI is applied instead of simulated one.

Also, the uniformity of model output in the beginning of the fattening period and the stochasticity of the flock further over age. For instance, for BW+ graphs, the model is overpredicting the performance for C128 (yellow dots), when underpredicting the BW for C114 (green dots) or C162 (grey dots) for classic diet fed birds. Whereas, for A073 (green dots) the simulation is in line with observed values and underprediction is visible and the last days for all five individual animals.

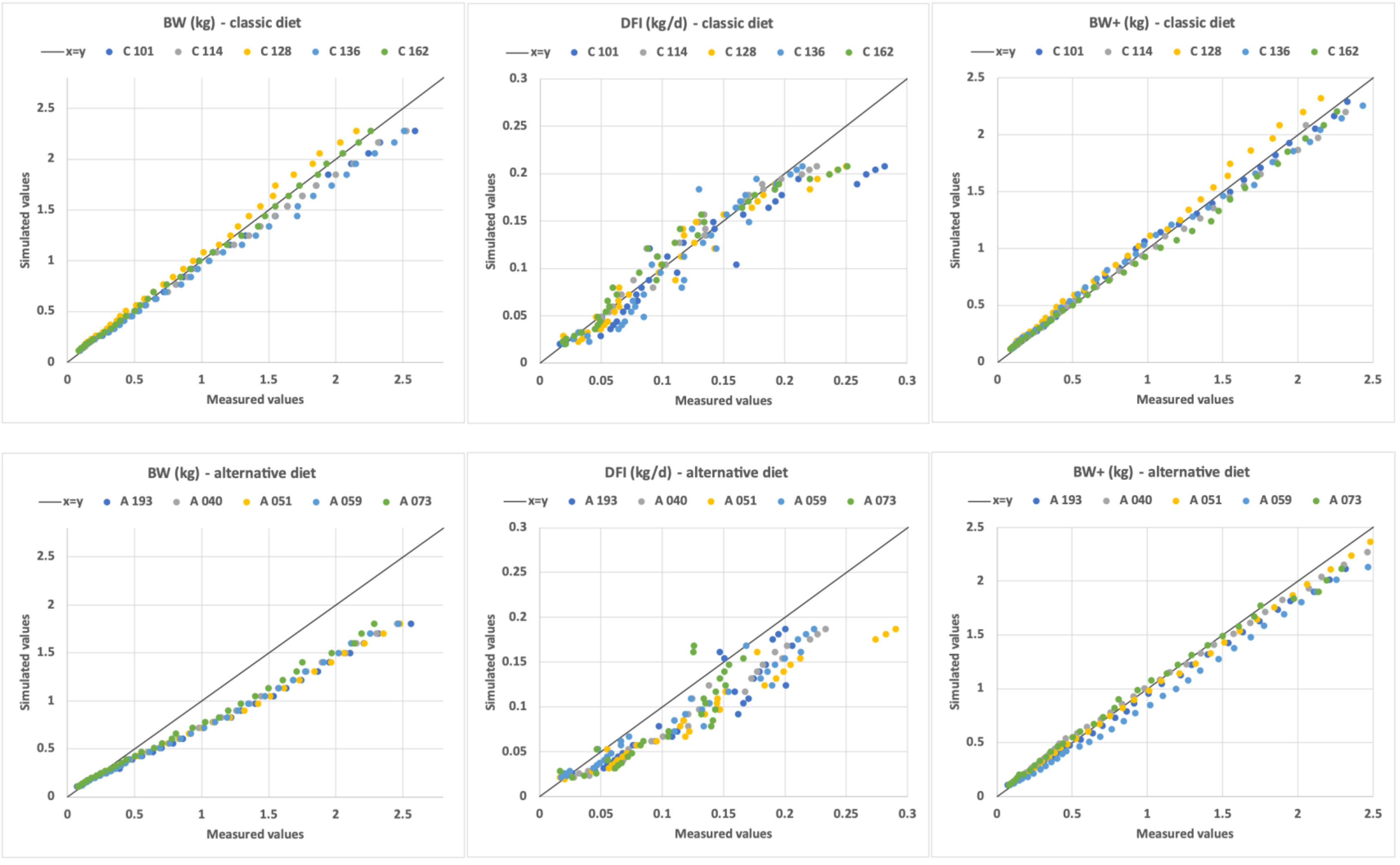


Figure 17. Comparison of simulated versus observed performance of Cobb broilers on body weight (BW), daily feed intake (DFI) and body weight with actual DFI (BW+): classic (C) diet (upper graphs) and alternative diet (A) from 4 to 36 days of age

7.1.5.3. *Independent literature data*

In this section evaluation of the broiler model in terms of body weight response to different energy and protein levels as well as dietary AAs is presented. The model was challenged by comparing the animal vs. the model response to different dietary treatments in specific time intervals as reported in the relevant studies. The root of mean square prediction error (root MSPE) and relative MSPE (relMSPE, %) for the simulations of BW (kg) and FI (kg/d) run with experimental diets from the literature data are presented in the Table 14.

From the Table 14 it can be seen that the relMSPE is the highest in case of Li (2017) for BW datasets (together for three treatments), following by Liu *et al.* (2017*b*), Najafi et al (2017), Zhai *et al.* (2016), Sigolo *et al.* (2019), Liu *et al.* (2017*a*), and Lee *et al.* (2018) studies for both BW and FI data. However, the partitioning between bias, regression and undefined errors is different. Further the graphical representations of simulated versus observed values are shown (Figures 18-24).

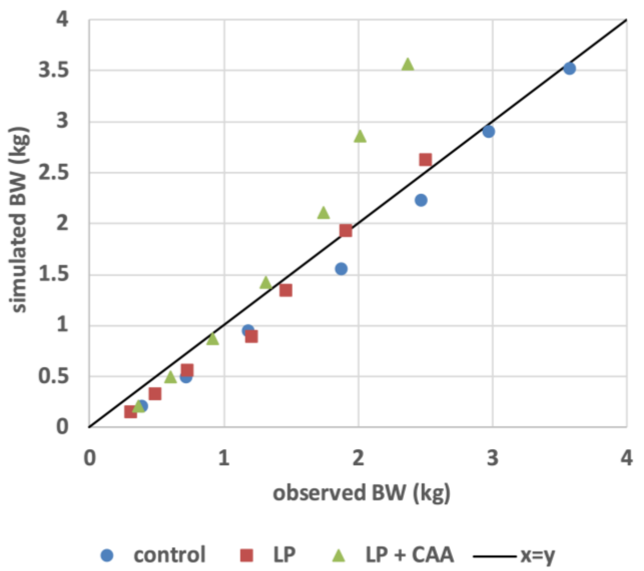


Figure 18. Simulation of the broiler performance based on the dataset of Li (2017), where: BW – body weight, control – control diet, LP – low protein diet, LP + CAA – low protein diet supplemented with crystalline AAs

Figure 18 displays simulation on the research of Li (2017) with an objective to compare the growth performance of broilers fed control, low protein (LP) and low protein supplemented with crystalline AAs diets (CAA). The results showed that dietary protein restriction had a retarding influence on the growth and development. In the study the supplementation of CAA helped to compensate the negative effect of low protein diet in terms of body weight. The simulation demonstrated in the Figure 18 following the tendency from the original study with reducing growth when fed LP diet, however the response in case of CAA diet is over predicted.

Table 14. Root mean square prediction error (root MSPE) and relative MSPE (relMSPE, %) for the body weight simulations run with experimental diets from the literature data

	root MSPE	relMSPE %	B%	R%	E%
Feed intake (kg/d) without adjustment					
Li, 2017	no feed intake data				
Lee *et al.*, 2018	0.002	10.532	0.000	48.419	51.581
Sigolo *et al.*, 2019	0.022	24.439	83.175	16.384	0.441
Zhai *et al.*, 2016	0.004	0.109	98.374	0.033	1.619
Najafi *et al.*, 2017	0.097	39.837	76.739	12.938	10.323
Liu *et al.*, 2017*a*	0.107	5.585	13.560	53.877	32.563
Liu *et al.*, 2017*b*	0.195	26.722	0.051	99.919	0.030
Body weight (kg) without feed intake adjustment					
Li, 2017	0.243	16.46	0.17	38.98	60.85
Lee *et al.*, 2018	0.003	20.472	0.000	74.017	25.983
Sigolo *et al.*, 2019	0.017	33.208	89.909	1.903	8.188
Zhai *et al.*, 2016	0.037	1.288	95.238	4.656	0.107
Najafi et al., 2017	0.106	59.352	59.533	28.568	11.899
Liu *et al.*, 2017*a*	0.047	3.310	22.719	2.493	74.788
Liu *et al.*, 2017*b*	0.215	47.913	25.723	71.389	2.887
Feed intake (kg/d) with adjustment					
Li, 2017	no feed intake data				
Lee *et al.*, 2018	0.000	0.003	0.000	38.057	61.943
Sigolo *et al.*, 2019	0.000	0.204	28.104	2.547	69.350
Zhai *et al.*, 2016	0.000	0.0001	45.759	8.889	45.353
Najafi *et al.*, 2017	0.015	6.174	12.459	7.297	80.244
Liu *et al.*, 2017*a*	0.012	0.001	14.080	16.724	69.196
Liu *et al.*, 2017*b*	0.000	0.001	0.000	100.00	0.000
Body weight (kg) with feed intake adjustment					
Li, 2017	0.243	16.46	0.17	38.98	60.85
Lee *et al.*, 2018	0.000	1.650	0.000	14.608	85.392
Sigolo *et al.*, 2019	0.003	5.754	77.991	1.089	20.920
Zhai *et al.*, 2016	0.028	0.958	93.091	4.377	2.532
Najafi *et al.*, 2017	0.026	14.673	9.799	31.535	58.666
Liu *et al.*, 2017*a*	0.016	1.129	4.600	80.673	14.727
Liu *et al.*, 2017*b*	0.060	13.385	0.299	87.500	12.200

where: rootMSPE – root mean square prediction error, measure in the same units as the output and is also expressed as a percentage of the observed mean as a relative MSPE – relMSPE, B% – represent the proportion of MSPE due to a consistent over- or underestimation of the experimental observations by the model predictions, R% – represents the proportion of MSPE due to inadequate simulation of differences among experimental observations, E% – represents the proportion of MSPE related to the undefined errors of model prediction.

The main reason could be related to the fact that birds change FI when the AA concentration in the diets are changing, which was not applied in the model and, thus, the additional studies on FI should be conducted.

Alternatively, to evaluate the model response in terms of predictive ability from digestible nutrient input the original DFI values should be used for this kind of simulation. However, the actual and dynamic feed intake data are rarely available in the publications. Another possible reason while the model overpredicts the study data is that something else than the AA supply was probably limiting for growth in the study. It might be the case, since the reliability of estimation of the control birds' BW seems to be relatively high.

Further graphs in Figures 19-24, represent the original model outputs – shown on the upper part of the figure, and model outputs when model was repeatedly run with adjusted feed intake – on the lower part. The adjustment was processed by applying multiplication coefficient as described in Material and Methods (see page 50).

Figure 19 represents the results of simulations for the study of Lee *et al.* (2018), where broilers were fed 6 experimental diets with different Lys levels up to 11 days old. Sigolo *et al.* (2019), Figure 20, studied the response of broilers between 1-14, 15-28, and 29-42 days of age to three different dietary Lys levels.

The conclusion is that the main variation factor in the model is DFI, and the model output is becoming closer to the observed values if the adjustment is applied. It has been repeatedly shown that the feed intake is a multivariate trait depending not only on the genetic potential of the animal but vary importantly by environmental factors such as dietary composition, ambient temperature, and number of stress factors (Classen, 2017). In the present model the DFI is a phenotypic trait represented by two values (*FI_1* and *FI_2*) and it is based on the premise that birds eat according to a consume desired amount of energy described by multiples of maintenance. Thus, in the model nothing else but dietary energy content and the BW determine the DFI which is likely an oversimplification of the phenomena. However, the more precise model outputs in case of adjusted FI in most tests confirm the reliability of the nutrient partitioning model. The inaccuracy of FI prediction is likely not critical, since real-time on-farm systems are being developed to measure actual FI, thus those data might be used as inputs in a nutrient partitioning model when adopted to farm situation (Guettier *et al., 2022*). In case of the two studies dealing with different dietary Lys level (Lee *et al.*, 2018 and Sigolo *et al.*, 2019) the model shows goodness of fit to the measured data (Figures 19 and 20).

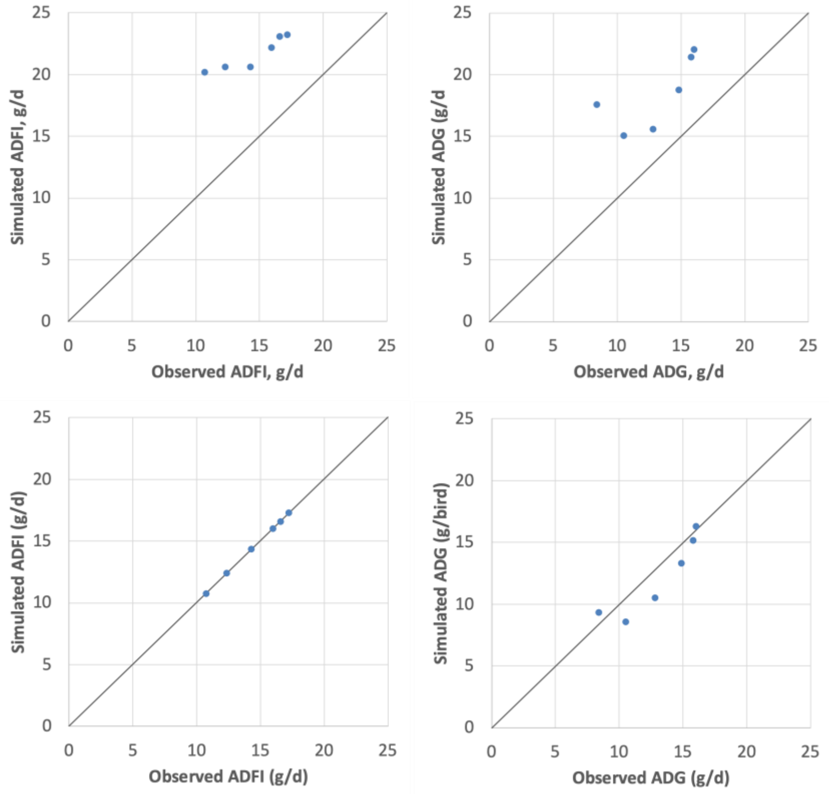


Figure 19. Simulation of the broiler performance based on the dataset of Lee *et al.* (2018). Upper graphs show the model simulation as run with the published nutrient content and simulated FI, while lower graphs present the model outputs after adjusting the FI according to the actual FI obtained in the study

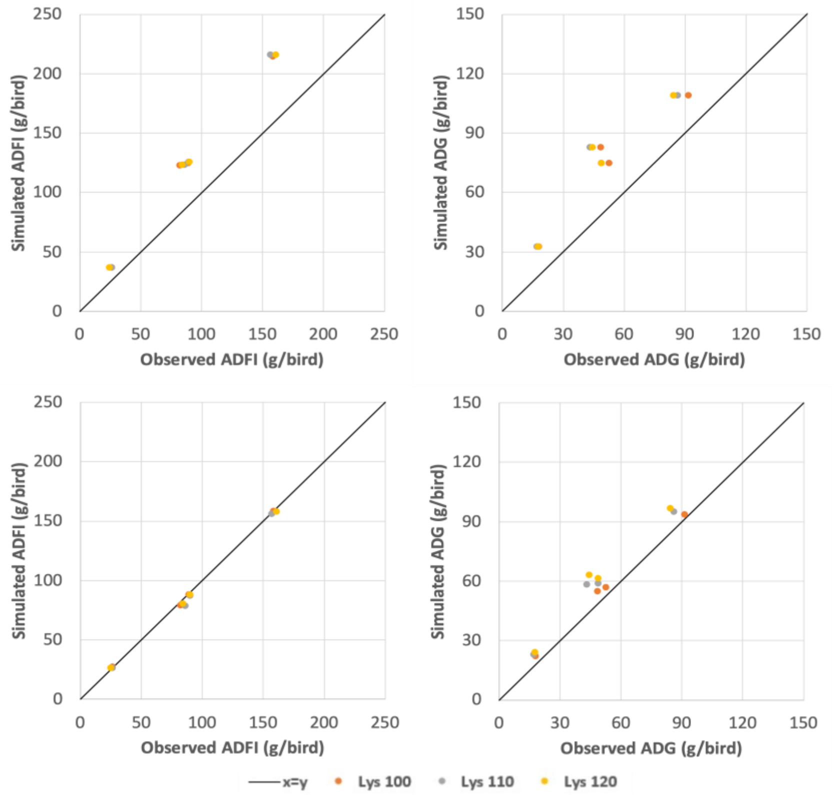


Figure 20. Simulation of the broiler performance based on the dataset of Sigolo *et al.* (2019). Upper graphs show the model simulation as run with the published nutrient content and simulated FI, while lower graphs present the model outputs after adjusting the FI according to the actual FI obtained in the study

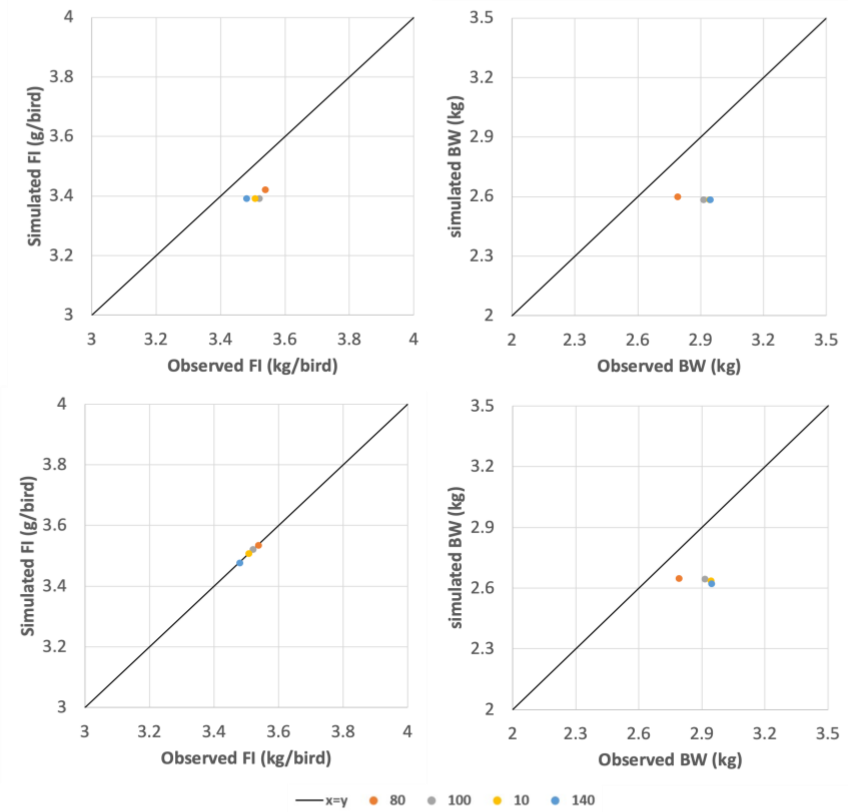


Figure 21. Simulation of the broiler performance based on the dataset of Zhai *et al.* (2016). Upper graphs show the model simulation as run with the published nutrient content and simulated FI, while lower graphs present the model outputs after adjusting the FI according to the actual FI obtained in the study

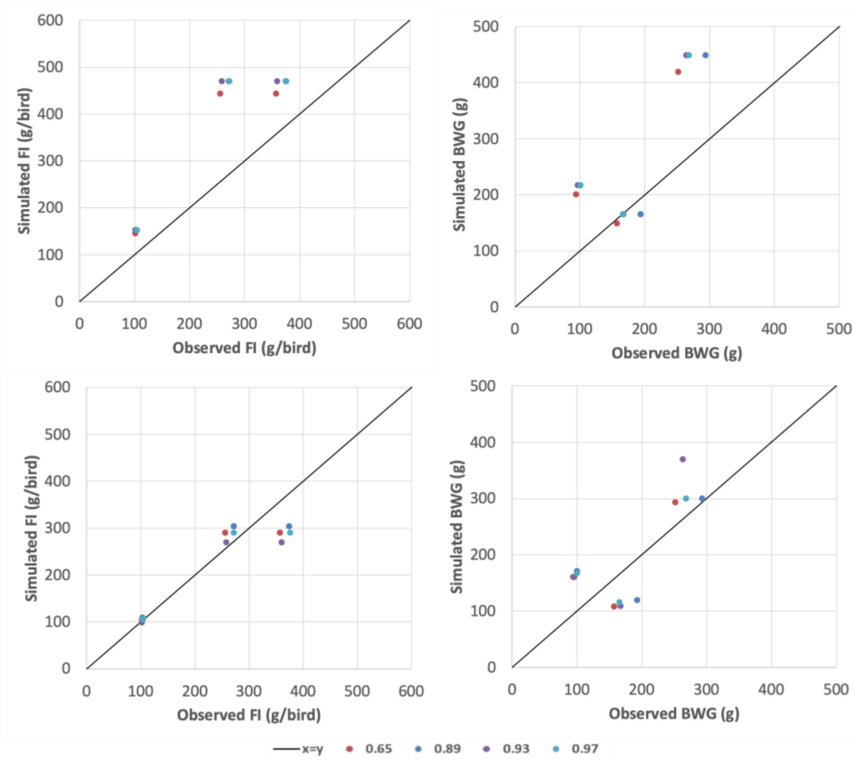


Figure 22. Simulation of the broiler performance based on the dataset of Najafi *et al.* (2017). Upper graphs show the model simulation as run with the published nutrient content and simulated FI, while lower graphs present the model outputs after adjusting the FI according to the actual FI obtained in the study

Figure 21 shows the simulation output run with four different levels of Met in the diets fed from 21 to 42 d of age, according to the trial of Zhai *et al.* (2016). The FI prediction error attributed to regression is minor and the main source of deviation is due to undefined error or the bias. The similar errors distribution is observed for BW prediction.

Four different levels of Thr in the diets fed over 14 days of age and BW were measured as average values between 1-7, 7-14, and 1-14 days, according to Najafi *et al.* (2017), Figure 22). The trial examined the effect of dietary Thr on the BW gain. Comparison of the simulations and observations for FI shows a large relative error of the model (almost 40% overprediction), yet the major source of the error is attributed to the bias. Consequently, the BW prediction error distribution is the highest (39%) among other literature datasets. Deviation from the bias could be a result that only three data points on the coordinates were compared, and those were delivered as average values (as mentioned above).

The simulations for the experiments of Liu *et al.* (2017*a* and 2017*b*) are presented on Figures 23 and 24, respectively. Figure 23 represents 10 simulations run for experimental diets with protein concentrations ranging from 154 to 400 g/kg and two lipid levels (46 and 85 g/kg) with identical energy densities offered to broilers from 7 to 28 d post-hatch. Figure 24 illustrates the simulation output for 14 experimental diets with different concentrations of starch, protein and lipid is shown. The broiler chickens were from 10 to 23 d after hatching and the growth performance and nutrients utilization was studied.

The prediction is generally considered sufficient if the model error attributed to regression slope is low. The model was able to simulate the results on BW performance of Liu *et al.* (2017*a*) study with a relative high accuracy (Figure 23), the relative MSPE was only 3.3%, where the main source of deviation of the model was due to the undefined error. Unexpectedly the other study of Liu *et al.* (2017*b*), shown on the Figure 24, with similar experimental design was used and quite the same dietary treatments, the prediction showed 48% relative model error and even the FI adjustment (however, with 100% attributed to the regression error) could not compensate for the deviation, reducing the relMSPE from 48 to 13.4%. This suggests that some further model improvement and development may be necessary, in terms of "animal" part when nutrient composition of the diet is manipulated (the energy is coming from starch or from fat), should have place.

To conclude, the prediction appears to be much more precise for each case study if FI data are adjusted, and it is shown on the graphs 18-24 and in Table 14.

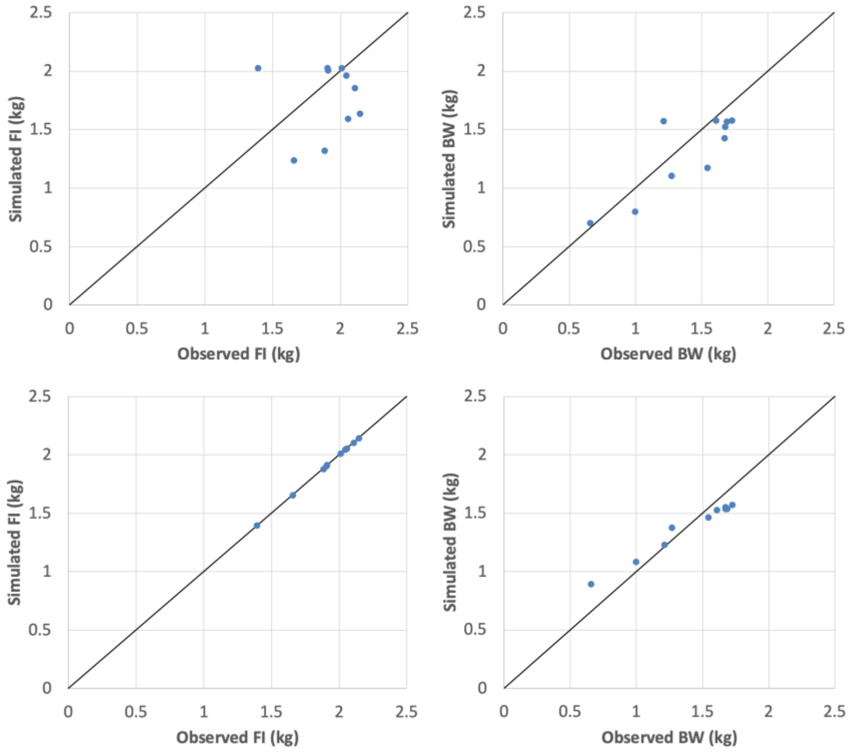


Figure 23. Simulation of the broiler performance based on the dataset of Liu *et al.* (2017a). Upper graphs show the model simulation as run with the published nutrient content and simulated FI, while lower graphs present the model outputs after adjusting the FI according to the actual FI obtained in the study

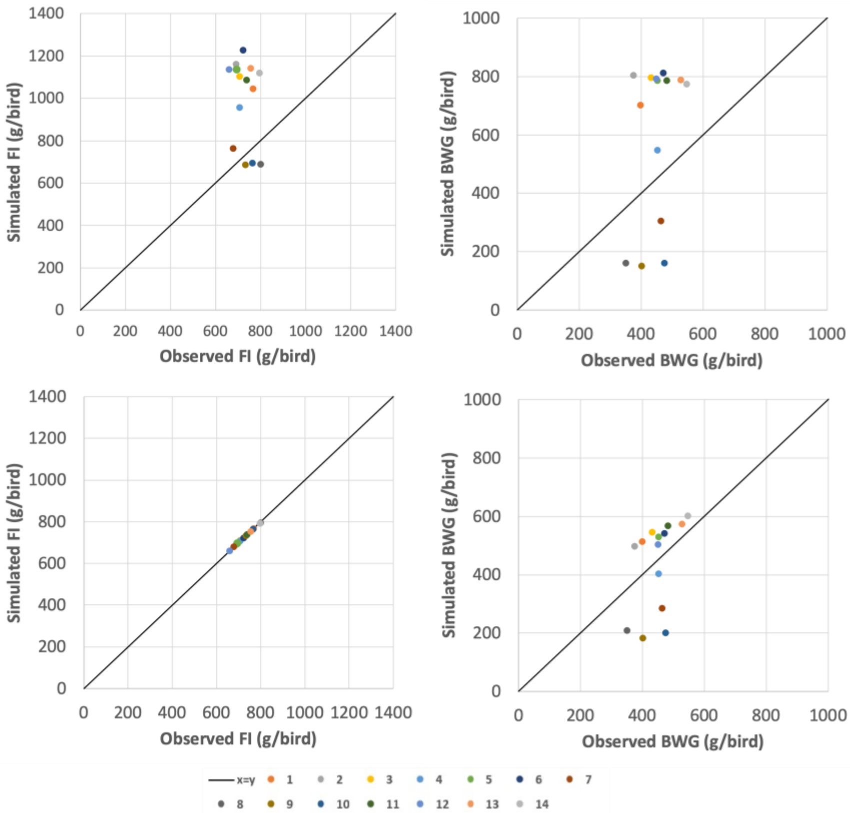


Figure 24. Simulation of the broiler performance based on the dataset of and Liu *et al.* (2017b). Upper graphs show the model simulation as run with the published nutrient content and simulated FI, while lower graphs present the model outputs after adjusting the FI according to the actual FI obtained in the study

7.2. Phosphorus partitioning

The model extended with the P partitioning module was developed to estimate the digestible P requirement that is crucial from both ecological and economic points of view. An example of the model simulation for Ross male and female broilers is shown in Figure 25. Females, due to their lower potential to deposit protein from approximately 15 days of age, need less digestible P compared to males.

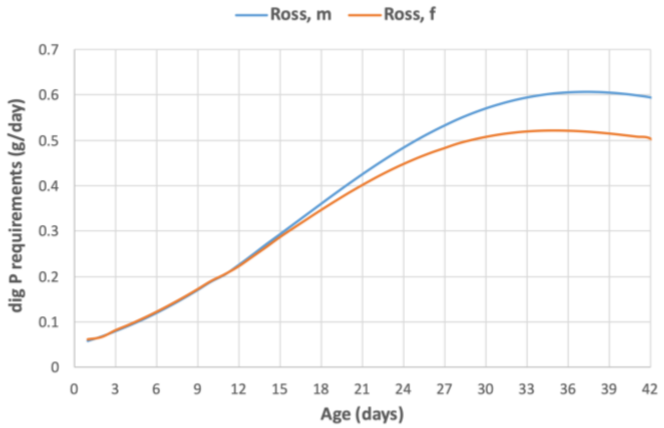


Figure 25. Simulation of the digestible phosphorus (P) requirement of Ross broilers for males (blue line) and females (orange line) in grams per day

Insufficient P supply reduces the P-retention that is often examined in parallel with bone mineralization studies, in which a reference bone's chemical and physical characteristics are evaluated. According to the literature, changes of P content in bone tissue are not directly proportional to lean growth. Thus, in the present model soft and bone tissue P pools are considered separately and the bone P is considered 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 often reported that a P-deficient diet reduces feed intake (Digger and Adeola, 2006; Imari *et al*., 2020), 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 as a reservoir may be deplenished. If 50% of the bone Ca is sacrificed it might become critical and below that threshold level, soft tissue is no longer given a priority. The simulation on the shifts between soft and bone tissue in response to the dietary P deficiency as well as P partitioning to obligatory losses for maintenance needs including feather loss (P maint), retention in feather (ret P feather), retention in soft tissue (ret P soft), and retention in bone tissue (P bone), is represented in grams per day (left axis) as well as BPD and BLD in grams per day (right axis) as a function of age in Figure 26.

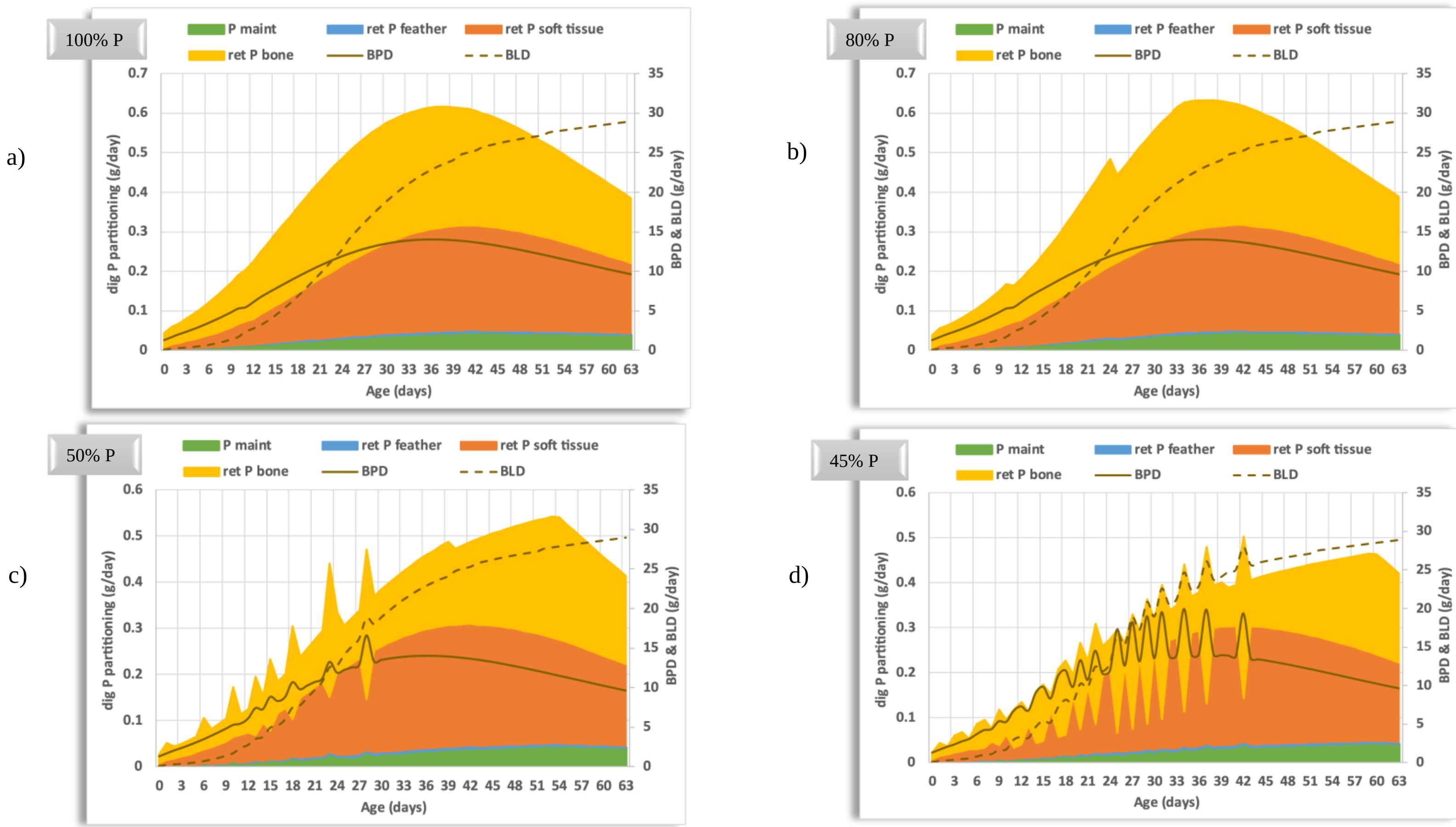


Figure 26. Simulation of the digestible phosphorus (P) partitioning, empty feather-free body protein deposition (BPD), and empty feather-free body lipid deposition (BLD) in grams per day (g/d) for average broiler fed digestible P according to the Ross 308 recommendation ranging 4.80 – 3.75 g/kg (a), 80% of the requirement ranging 3.84 – 3.00 g/kg (b), 50% of the 2.64 – 2.06 g/kg (c), 2.16 – 1.69 (d) g/kg during 9 weeks. Partitioning of dietary P is shown in the figure as follows: P used in obligatory losses for maintenance needs including feather loss (P maint), retained P in feather (ret P feather), retained P in soft tissue (ret P soft), retained P in bone tissue (ret P bone)

Our *in silico* results seem realistic if compared to the literature data. In study of Konieczka *et al*. (2020) the Ross 308 birds received adequate standard diet, the value for the final BW at 35^{th} day of the experiment was 2.34 kg, CFI was 3.15 kg, total P retention was 37.78% and total N retention was 52.21%. Whereas the model output for BW at 35^{th} day is 2.345 kg, 3.758 kg for CFI, and 36.2 % and 51.58 % of P retention and N retention, respectively. In the mentioned study reduced nutrient content feeds were also applied with or without phytase supplementation. Crude protein, total P, and Ca was reduced by 3.8%, 21.5%, and 22.3% respectively in grower-type diet and by 2.5%, 19.0%, and 18.7% in finisher-type diet, respectively.

The measured values on day 35 of the experiment were: 2.35 kg of BW, CFI 3.65 kg, total P retention 38.70 % and total N retention 47.11%. The model's output for the reduces nutrients content feeds was: 2.333 kg of BW, CFI 3.695 kg, and 41.81% and 49.39% of P retention and N retention, respectively. When the phytase was added to the reduced nutrient content diets, the experimental values were: 2.31 kg of BW, CFI 3.14, total P retention 48.32% and total N retention 61.48%. Phytase increases the digestibility of dietary P, thus increase of P digestibility by 5% was assumed in the model and the output values were the followings: the BW, CFI and N retention did not change, however the total P retentions increased from 41.81% to 46.46%.

The comparison of results shows that model is following the tendency for decreasing N and P retention when feed is low in crude protein, total P, and Ca. The model displays similar tendency with the data from study of Imari *et al.* (2020). In this study broilers were fed with control or 10, 20, and 30% lower available P compared to the control. The efficiency of P retention gradually increased as 45.71, 51.44, 52.99 and 56.83 % in different treatments and the model output was 34.09, 37.37, 40.53 and 42.11% in simulations with control feed, or feed containing 10, 20 and 30 % lower available P, respectively.

Authors also mentioned that retarded growth of birds in starter period was compensated in post-starter phase. This compensation is feasible in the model as well. The P level in blood serum was not affected by reduced P, but the total P retention (%) on day 42, was significantly higher in birds fed 30% P reduced diet diets than 10 and 20% P reduced diets groups. The main effect of 30% reduction in dietary P was decreased tibia ash compared with 10% lower dietary P group. This conclusion agrees with model logic: 9.142, 9.079, 8.535, 7.156 g P retained in bone tissue, respectively for 0, 10, 20 and 30% of available P dietary reduction. In the experimental data the tibia P content was decreased too: from 17.86 to 17.08, 15.42, and 15.20%, respectively when available P was reduced by 10, 20 and 30%.

The study of Imari *et al.* (2020) demonstrates the reduction in FI and BW, when dietary available P reduced by 30% commencing from early age in starter period. The simulated FI does not respond to P supply directly, since there was lack of quantitative data to see a consequent relationship between P supply and feed consumption in broilers. By theory there may be some reduction in simulated FI if dietary P supply is limiting. If the available P entering the metabolism is insufficient and the bone cannot be used as a P reserve, the soft tissue deposition becomes limited by the P supply and that reduces the gain and thus the further BW. In the simulation of Imari's data, however, the P supply was not low enough to result in a lower BW. It seems that in Imari's study the appetite of the birds was also influenced. As mentioned, in the model the energy consumption is the driving force for the daily FI and no other mechanism is involved in FI regulation.

To conclude, the model gives a reliable simulation and follows the main trends about P retention reported in the literature. However, further improvements may be needed, in particular more detailed datasets would be useful to evaluate the P retention and P partitioning in dynamic datasets in order for the prediction to be in accordance with metabolic model part.

7.3. Environmental issues of Nitrogen and Phosphorus excretion

In a view that BW and the chemical body composition can be predicted with goodness of fit it has been concluded that the model is valid for estimating the performance of an average broiler chicken at various nutrient supply. Since based on nutrient partitioning the amino acid and the P requirement can be estimated it has been presumed that the model output on the nutrient, particularly N and P excretion is reliable too. Although, in modern animal nutrition, feeds are not directly formulated on dietary crude protein (CP) basis, is should be kept in mind that the excess protein will be excreted and result in high environmental pressure. It is also known that N excreted by the urine is more harmful from environmental point of view since urinary N is easily volatilized (Konkol, *et al.*, 2022), and that protein intake above the requirement burdens the animal's metabolism. This leads to a decrease in the energetic efficiency of protein deposition, maybe resulting in deterioration of production parameters (*e.g.*, ADG, FCR). Dietary CP and P above the digestible CP and P requirement will be excreted via urine. Since CP is one of the most, or probably the most expensive nutrient in compound feeds, overfeeding of dietary CP increases the feeding cost with extra load on ammonia emission. Therefore, protein intake in excess causes not only environmental pollution problems, but also worsens the efficiency of production. Any tool that helps to mitigate the overfeeding of digestible CP is useful for animal nutritionists and the poultry sector.

The model is able to simulate the dynamics of faecal and urinary excretion of N and P in daily steps. Faecal excretion is easy to calculate since the digestibility of CP (and AAs) or P is a given value, and if in the simulation it is presumed that the digestibility is constant. Urinary excretion is partitioned into obligatory losses that depends on homeostasis maintaining requirements, and excess which will be utilized neither for organism's support, or for growth. The aim with the following case study is to show the quantitative impact of N and P levels in different feeding strategies and to stress how useful the models are also in that strategic issue.

Two scenarios are presented on Table 6 (subchapter 6.4.2): scenario 1 (Sc1) is the 4 phases feeding strategy as recommended by the breeder (Aviagen, 2017) and scenario 2 (Sc2) is 8 phases feeding program adjusted according to the breeders' guideline based calibrated model output. The dietary digestible CP and P contents fed in the feeding programs Sc1 and Sc2 and the simulated "actually" required levels of digestible CP and digestible P are graphically represented on Figures 27 and 28, respectively. It is shown that feeding strategy in Sc2 with multiple phases leaves smaller differences between dietary and required levels of N and P comparing to recommended Sc1. Considering the difference of nutrient supply by Sc1 strategy with the simulated requirement (the space on the graph under orange line and above the blue or green surfaces, for CP and digestible P, respectively), it can be stated that particularly from the second phase (from 11th day) both the CP and the P are oversupplied.

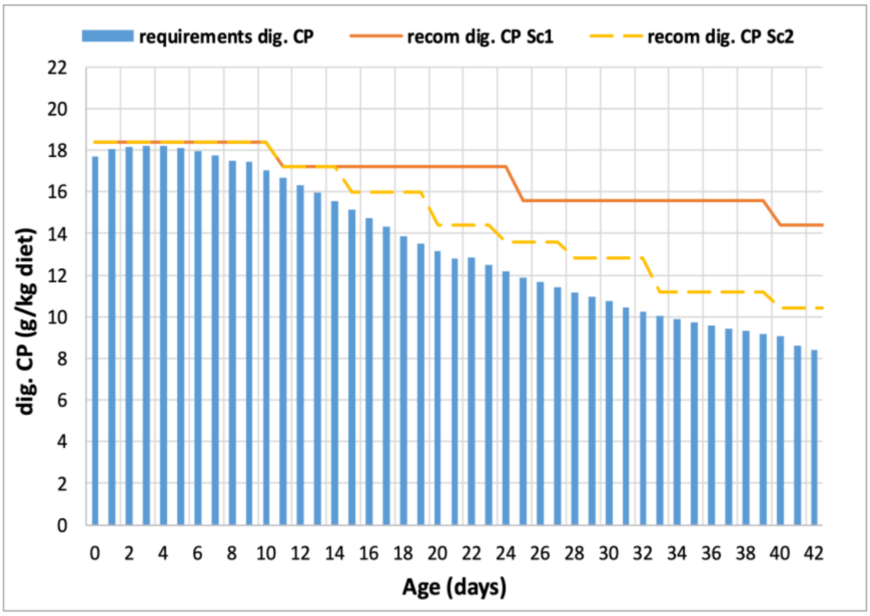


Figure 27. Estimation of actual digestible crude protein (CP) requirement for Ross 308 hybrid (requirements dig. CP, g/kg diet), and digestible CP content recommended by the breeder (Sc1 – Ross recommendations) and that in the feeding strategy developed based on the model (Sc2 – multiple phases feeding)

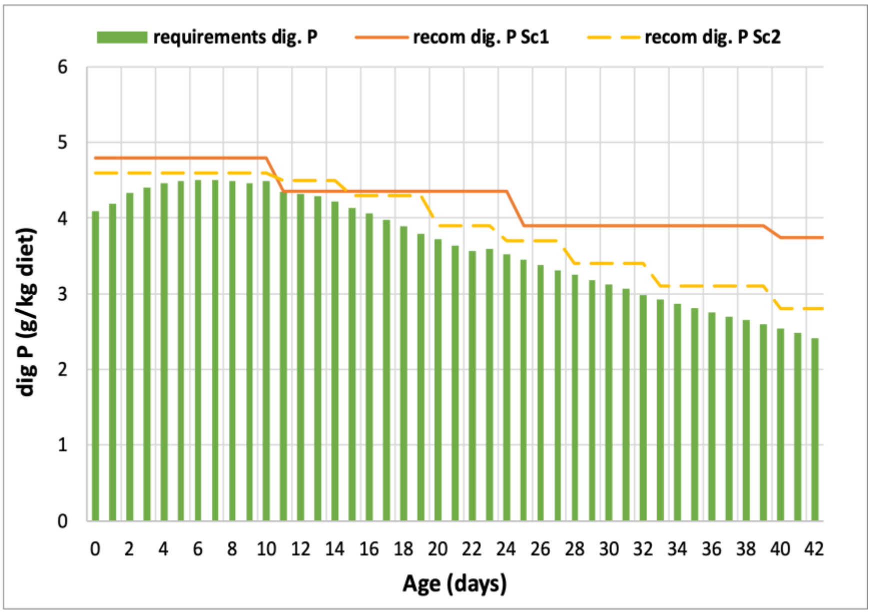


Figure 28. Estimation of actual digestible phosphorus (P) requirement for Ross 308 hybrid (requirements dig. P g/kg diet), and digestible P content recommended by the breeder (Sc1 – Ross recommendations) and that in the feeding strategy developed based on the model (Sc2 – multiple phases feeding)

The Sc2 values are very closely approach the model estimated requirements. This is reasonable, because the most accurate way to cover an area under the curve (in this case, the nutrient requirements) is to use multi-phase feeding.

Though, it is a common practice for the guidelines recommendations to keep the meat producer on a "safe side" and to suggest some higher CP or P, such a strategy, however, is not sustainable. Moreover, since modern broilers are highly productive, and continuously tending to be more and more efficient, the oversupply of nutrients, particularly CP and P, leads to unnecessary high nutrient excretion.

Considering that N excretion is an energy demanding process, in case of more phases the dietary energy level ought to be changed with more cautious. In the simulation, diets used for both strategies were isoenergetic. Thus, the protein-to-energy ratio changed in Sc2, which promoted more energy retention as fat, since the protein content of the diet in relation to the total energy is the main factor determining the amount of fat deposited in the body. The lower the protein-to-energy ratio, the greater the fat content of the bird. Lower CP level in the Sc2 diet resulted in 3.4 % more body fat of simulated performance, compared to one in Sc1. This agrees with literature data when an excess dietary CP results in a leaner bird but reduces feed efficiency, whereas a less-than-optimal protein content increases feed intake but also consumed an excessive amount of energy in this process (Buyse *et al.*, 1992; Buyse and Decuypere, 2015).

Some bias in simulated requirements for the first days of age can be seen on the figures. The trend for the recommendations increases in the first few days suggesting that the birds need an increasing energy and nutrient density of feed from hatch to 4-5 days of age. In fact, explaining that tendency with the yolk sac nutrient supply wouldn't be reliable, since the increase in simulated nutrient requirement (expressed in g/kg) takes almost a week. It is well known that in addition to a 24-hour-long hatching window the birds are often fasting due to the long transport too, and they have access to feed and water with time delay. Under practical conditions feed is often available only 48 hours or more post-hatch (Noy and Sklan, 2001), and that nutrient gap is covered certainly by the yolk sac. The nutrient requirements of the first week of life for broilers are influenced by many factors which have become increasingly important for nutritional and managerial consideration lately (Birk, 2016), but it is unlikely that dietary protein and digestible P should be increased up to 4-5 days of age. Nevertheless, the source of bias in the initial period is present due to the fact that very early metabolic transactions might be different in some extent from what would happen in later age. For instance, it has been confirmed that the digestibility of nutrients is increasing with age, thus, a lower digestibility in the first week that is not considered in the model should be compensated with a higher nutrient content feed. Thus, all in all, it is recommended to use a higher CP and digP content feed during the first days post-hatch than recommended by the model, but later when the digestibility data are reliable the model recommendation can be applied.

The simulation for distribution of digestible N and digestible P intakes (solid for Sc1 and dashed for Sc2 pink curves) between retention in the body and excretions are shown on Figure 29 and 30, respectively for N and P. The blue line describes the level of simulated N (Figure 29) or simulated P retention (Figure 30). The reduced CP and digestible P levels in Sc2 during the rearing did not compromise the production of the bird while decreased the N and P excess (the area above green line and under orange curves, solid or dashed for Sc1 and Sc2, respectively).

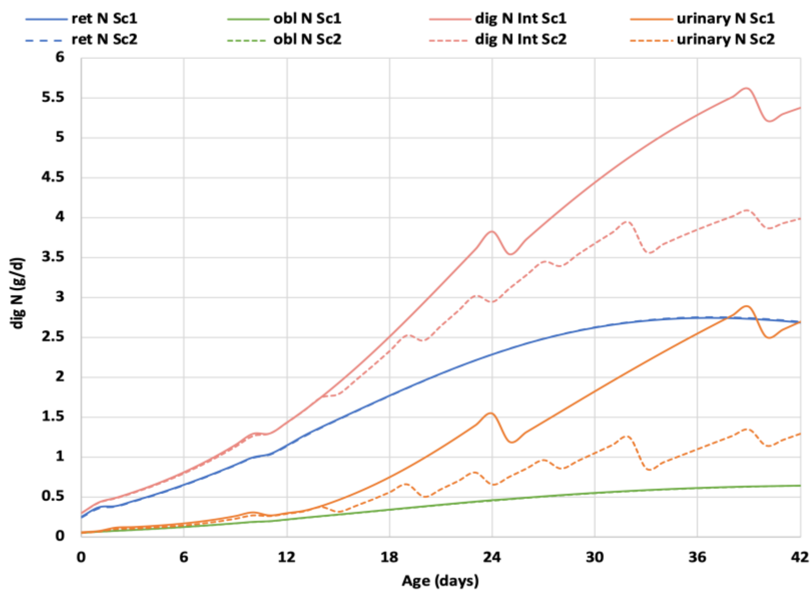


Figure 29. Distribution of N excretion in two feeding strategies, where: Sc1 – Ross recommendations; Sc2 – multiple phases feeding; dig N Int – digestible nitrogen intake; ret N – retained nitrogen into body and feather; dig N excr – urinary excretion of digestible N; obl N– obligatory urinary nitrogen loss

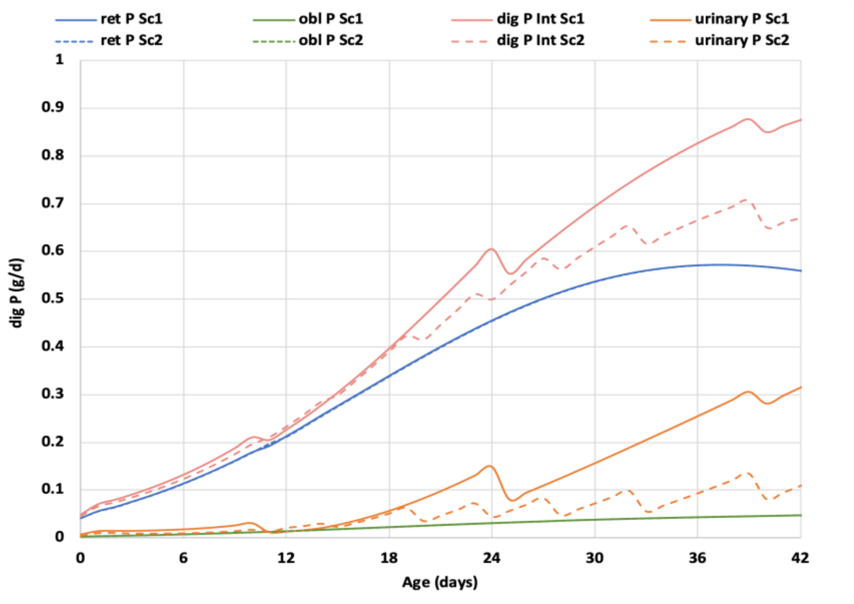


Figure 30. Distribution of P excretions in two feeding strategies, where: Sc1 – Ross recommendations; Sc2 – multiple phases feeding; dig P Int – digestible phosphorus intake; ret P – retained phosphorus into body soft tissues, bones and feathers; dig P excr – available phosphorus urinary excretion; obl P – obligatory urinary phosphorus loss

The cumulative intakes over the fattening period of 42 days were: 161.44 vs. 131.9 g of N and 45.3 vs. 39.5 g of P, respectively for Sc1 vs. Sc2. The N retention in both scenarios was 78 g, and the P retention was 15.5 g. The N excretion from undigestible protein was 32.3 vs. 26.4 g, and P excretion from undigestible P was 24.9 vs. 21.7 g, respectively Sc1 vs. Sc2. The total N excretion was 83.47 vs. 54.03 g, whereas the total urinary N surplus was 35.1 vs. 11.5 g, for simulations run for Sc1 vs. Sc2, respectively. The total P excretion was 4.9 vs. 2.2 g, whereas the total urinary P surplus (excess) was 3.7 vs. 1.1 g, respectively for simulations run in case of Sc1 vs. Sc2. Thus, according to the model output, adopting Sc2 resulted in 67.1% less surplus N, and in 70.3% less surplus P excreted.

There is a strong need for mitigation of the pollutants, it is likely realized by manipulating the AA profile of the lower CP diets and further improving broiler performance (Malomo *et al.*, 2013). *In silico* method gives a cheap tool to evaluate different concepts and to experiment with scenarios. For instance, if to assume that enzyme supplementation of Sc1 and Sc2 diets increases protein digestibility one can experience the shift in N partitioning. Expecting that N intake will not change, due to the better digestibility the fecal N excretion will decrease and the urinary N excretion (surplus), consequently, increase as shown on the Figure 31.

This figure demonstrates the major issue in case of bad practice of enzyme supplementation in broiler feeds without reducing dietary CP level. This situation and the consequence of it can be studied by using the model. In our case study it was assumed that enzyme supplementation was applied in Sc1 diets thus increased protein digestibility by 5%.

The Figure 31 demonstrates the output of the simulation carried out for comparison of model simulation results for the reference vs. higher digestibility value for dietary protein. The N retention is quite the same in the simulations (blue curves). Comparison of simulation outputs shows that the improvement in protein digestibility did not change the total N excretion. Since the AA requirement of the genetic potential was fulfilled in the default simulation, no extra N retention was expected. The N cannot be retained at a higher amount (in terms of g/day) that is allowed by the genotype (potBPD), thus, the higher digestible protein and AA supply (Figure 31) resulted in higher N entering the metabolism. However, the amount of N (in form of AA) that cannot be utilized as body protein in the metabolism must be excreted. Therefore, higher protein digestibility shifted the form of excreted N, *i.e.*, reduced the faecal to urinary N ratio from 0.63 to 0.41. An increase in protein digestibility without adjusting the feed CP to the digestible AA requirements increased the N excess by more than 18%, from default 35.08 to 43.07 g. The lower faecal N to urinary N ratio results in higher total ammonia N (TAN) in both absolute and relative term (51.19 vs. 59.17 g, and 0.61 vs. 0.71, respectively). It can be concluded that using feed supplements or specific feed processing technology to improve protein digestibility is beneficial only if the diet is formulated on digestible protein and AA basis (Dukhta and Halas, 2023).

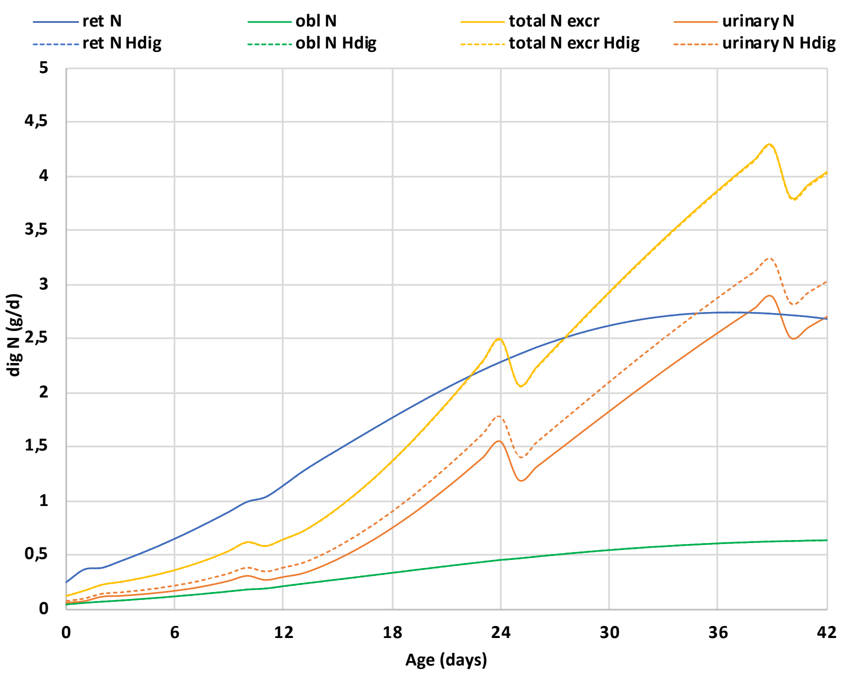


Figure 31. Effect of higher (85% vs 80%) dietary crude protein digestibility (Hdig) on N-excretion and its partitioning: ret N – retained nitrogen (g/d); obl N – obligatory urinary nitrogen loss (g/d); total N excr– sum of fecal and urinary N excretions (g/d); urinary N – urinary nitrogen excretion, (g/d)

Figure 32 represents the comparison of the model simulations for the reference vs. lower digestibility protein feeds. In case of an over-formulation or heat overtreat, the digestibility of the dietary protein is lower than the expected value. As shown in Figure 32, the 5% reduction in protein digestibility led to the same N retention in the simulations. There is no difference in total N excretion (blue curves) and obligatory urinary N loss (green curves). However, based on model calculation, the total N excretion increased slightly (83.47 to 83.61 g) when the protein digestibility was lower. The total urinary N excretion was lower when the dietary protein had lower digestibility compared to the default situation (Figure 32). There is approximately 15% difference in TAN and 22% in excess N, and the low digestibility protein feed resulted in lower values, 51.19 vs. 43.21 g of TAN, and 35.08 vs. 27.09 g surplus N for the total simulation. To conclude, similar to the case with Hdig, it was also notable that if the CP has a lower than expected digestibility, it would not make any difference in protein retention and thus growth performance of broilers. However, as shown in the earlier example, the more precise diet formulation closer to the actual nutrient (AA) requirement is demanded from economic and ecological points of view.

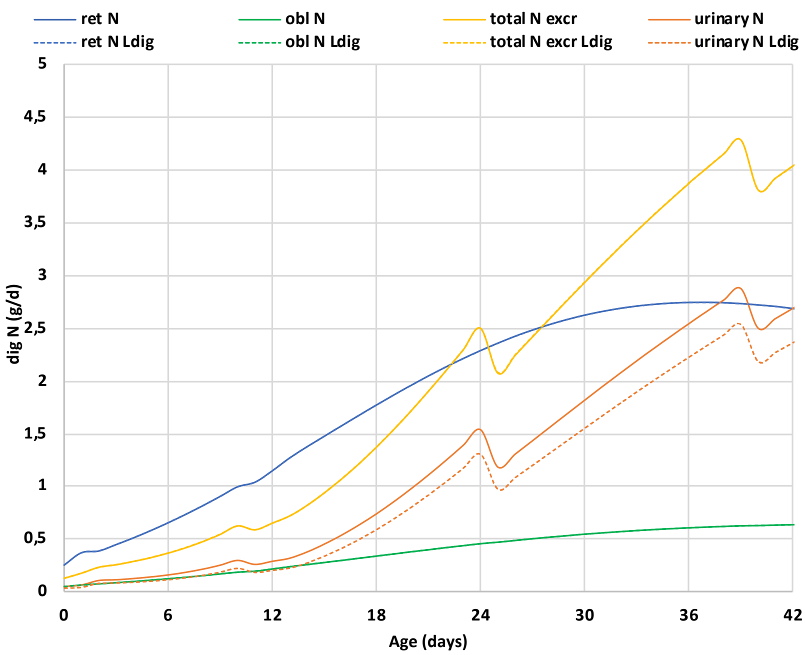


Figure 32. Effect of lower (75% vs 80%) dietary crude protein digestibility (Ldig) on N-excretion and its partitioning: ret N – retained nitrogen (g/d); obl N – obligatory urinary nitrogen loss (g/d); total N excr– sum of fecal and urinary N excretions (g/d); urinary N – urinary nitrogen excretion, (g/d)

It has been confirmed in animal studies that N footprint and particularly urinary N excretion can be reduced considerably, when formulating feeds lower than the breeders' recommended values. Despite that numerous studies of past decades are claiming that reducing dietary CP levels may lead to significantly impaired broilers' performance, the novel science and practice is dealing with AAs and their efficiency (Wu, 2014). Recent *in vivo* studies have confirmed that a reduction in dietary CP level might not compromise the protein deposition and growth rate of broilers if the AA supply is in accordance with the requirements. The experimental results of Abbasi *et al.* (2014) indicated that it is possible to reduce dietary CP level up to 10% after the starter period without any detrimental impact on growth performance, and dietary Thr supplementation up to 110% of Ross values may compensate for low CP-induced growth delay in broiler chicks. Belloir *et al.* (2015) stated that reducing of CP content of diets for broilers appears to have major benefits for the sustainability of animal production, but it has difficulty to achieve in chickens despite the knowledge available on AAs. Onwards, Belloir *et al.* (2017) demonstrated that with an adapted AA profile, it is possible to reduce dietary CP content to at least to 17% in growing-finishing male broilers, without altering animal performance and meat quality. Lemme *et al.* (2019) used a 4-phase-feeding in their performance trial and reported no significant difference in slaughter weight and feed conversion of broilers. They used a standard schedule – 22.0, 20.6, 20.0, and 19.5% CP respectively in starter (1–10 d), grower I (11–16 d), grower II (17–30 d), and finisher feed (31–40 d) – in comparison to an approximately 1.0-1.5% lower protein diet series – 21.0, 19.5, 18.7, and 18.0%, respectively. When further reduction in CP was applied (21.0, 19.0, 18.0, and 17.0% CP), the feeds slightly impaired the body weight, but not the feed conversion (Chrystal *et al*., 2020).

All these novel findings might help to convince professionals that the relatively low dietary CP level recommended by the growth models is feasible to improve the sustainability of broiler production. It is definitely an efficient way to reduce the environmental burden associated with N excretion. The present *in silico* study has confirmed too that diet formulation must be based on digestible AA requirement, using as many phases as possible otherwise the urinary N excretion is increasing. Based on the model simulation it is concluded that in the case of formulating the feeds close to the requirements, the deviation from the target values has considerable consequences. The oversupply of dietary CP – either due to the use of safety margin or underestimation of protein digestibility – will increase the total ammonia N in the manure and thus the N emission potential of poultry meat production. On the other hand, the overestimation of digestible AA supply may also impair the efficiency of N utilization, even if it has low to moderate impact on N excretion by shifting from the urinal to a faecal N excretion (Dukhta and Halas, 2023).

Modelling approach has also been used in other studies to evaluate the N footprint of farm animals. Bikker *et al. (*2011) developed a linear programming model to estimate the total tract protein digestibility as well as to optimize feed composition based on dietary crude protein, prices of the feed compounds, and season. The calculated average N digestibility of the feed is then used to calculate the TAN excretion of farm animals, including broiler chicken with consideration of total N-intake, digestibility, and N-retention. In parallel with Bikker's project Van Bruggen *et al.* (2011) and Velthof *et al.* (2012) developed a deterministic N flow model to estimate the total ammonia N based ammonia inventory (National Emission Model for Ammonia; NEMA) that has been used for calculating ammonia emission from agriculture in the Netherlands. In that model, the N excreted is calculated as the difference between the intake of N and retention of N in animal products, using standard N balance calculation methods (*e.g.*, Canh *et al.*, 1998; Valk, 1994; Wilkerson *et al.*, 1997). The fraction of TAN in the N excretion is calculated as the excretion of urinary N, which is the digested part of the N in the feed not converted into animal products, the undigested N is excreted as fecal N. The NEMA model has been adopted by the European Commission too (Velthof *et al.*, 2012). The additional value of our approach is that the N-retention is estimated more precisely than the referred methods. Therefore, we believe that the use of a N partitioning model as presented in this paper can be applied in the inventory calculation and may further refine the method of calculating the TAN produced in broiler production. Our dynamic mechanistic model predicts the retained N in broilers, as well as gives a user-friendly tool to study the rate of faecal and urinary N excretion, thus suitable to precisely estimate the TAN values and to evaluate feeding strategies from an environmental point of view when digestible dietary inputs are applied.

As concerns P requirements, Li *et al*. (2016) and Lin *et al.* (2017) reviewed and discussed the evidence in the literature, clearly demonstrating that P requirement of broilers is much lower than NRC (1994) recommendations which are currently used by the industry. It is a greatest challenge to apply a lower dietary P strategy in practice and to decide what dietary concentrations of P to use in diet formulation. All this is due to a lack of information on biologically available P values in feed ingredients for poultry and a widely agreed P evaluation system. Source of unprecise data, in many cases is attributed the so-called own phytase activity of the plant origin feedstuffs which is not considered. However, it must be stressed that the application of model output might be taken with caution due to the individual variations between the birds. Applegate *et al.* (2003) fed birds the same diet in two experiments and found that apparent hydrolysis of phytate P varied nearly two-fold between the first and second experiment. Also, caution is needed in input data of the model. Leske and Coon (2002) reported the dramatic reductions in P retention from monocalcium phosphate as dietary P concentration approached the requirement level: 98% retention at half of the P requirement to 59% retention at requirement level. With increase of P content in the diet the P intake increase as well, when P precaecal digestibility decreases along with P retention (Rodehutscord *et al.*, 2017).

Though models are very useful in education to demonstrate a certain problem and to find solutions, the digestibility value remains at a conditional level at this stage of development. More studies and observations should be run to ameliorate the algorithm. Yet, the modeling helps an understanding of the ingested nutrients partitioning, and probably might help to formulate the experiments *in vivo* to confirm or reject certain theories.

In conclusion, the baseline emission of N or P is vary depending on lots of factors such as the concentration of other nutrients in the diet and its digestibility as well as physiological, health and management factors. The current approach allows a better understanding of the concept of feed use mechanism for the decision to be taken. The model is an excellent tool to design alternative feeding strategies for animal production with a low environmental footprint. A systematic approach enables to reconsider the insights of N and P utilization, and therefore it gives a tool to reduce environmental pollution of broiler production.

CONCLUSIONS AND RECOMMENDATIONS

From the present dissertation, the following main conclusions can be drawn:

1. Although pigs and poultry (broilers) are different species, this work has confirmed that it is possible to develop a model to predict broiler production which is based on a well-elaborated pig growth model.
2. In order to develop this broiler model, new species-specific parameters and equations have been appointed, and dynamic mechanistic and deterministic model simulation has been built for chicken (*Gallus gallus domesticus*). This developed model is called: “Model Simulation for Chicken” (MsChick).
3. The MsChick model, based on the feed (Net energy) intake, simulates the post-digestive utilization of energy and amino acids, and predicts the growth performance, as well as changes in chemical body composition of the individual birds over time. The model simulation was extended for simulation of calcium (Ca) and phosphorus (P) metabolism too.
4. The growth model can be used for estimation of the protein, fat, and water deposition (g/d) in the body, as well as for determination the amount of valuable meat parts, but the fat to protein ratio as a trait of meat quality has not been evaluated.
5. Based on testing with independent data, the model simulation is reliable when different feeding schedules and nutrient supplies are estimated. The body weight and the average daily gain are well predicted in general, as well as the chemical body composition in time. The accuracy of the model is highly determined by the accuracy of feed intake estimation.
6. The model is sensitive to the parameters related to the model core – empty feather-free body protein: *meanBPD* and *precocity*, as well as to parameters related to daily feed intake: *FI_1* and *FI_2*. Besides initial parameters, it is also sensitive to *empty-feather-free body water allometry* and *c* parameters of the feed intake’s representation as multiples of energy.
7. In addition to the chemical body composition and performance of the broiler, the model is able to simulate N- and P-retention, urinary N- and P-excretion and digestible N- and P-requirement of *Gallus gallus domesticus* at different body weights and with different dietary supply.
8. The model allows testing the different multiple phases feeding in a dynamic way, as well as might serve as a great educational and/or decision support tool. Therefore, they are

useful in education for demonstrating certain problems and finding solutions, and probably could help to formulate the experiments *in vivo* to confirm or reject certain theories.

9. The model is able to determine quantitatively the environmental load of a feeding strategy. It has been shown that using multiple phases defined through the model, the N and P excretion can be significantly reduced without compromising the growth performance. The broiler growth model in the present state is a useful tool to determine the amount and partitioning of N and P excretion, and thus can support the development of feeding strategies to mitigate the environmental footprint of poultry sector.
10. It has been confirmed that an oversupply of dietary protein – either due to the use of safety margin or the underestimation of protein digestibility – will increase the total ammonia N in the manure and thus the N emission potential of poultry meat production.
11. It is necessary to continue to challenge the model with real-time dynamic datasets to improve its mechanistic approach and thus the accuracy of prediction.

NEW SCIENTIFIC RESULTS

1. A mechanistic-dynamic model for broilers has been successfully developed. It simulates the body chemical composition and production parameters of the bird with high accuracy. Therefore, it can be used for estimation of the protein, fat, and water deposition (g/d) in the body, as well as for the determination of the amount of valuable meat parts.

2. In general, the reliability of the model is sufficient, in terms of animal response in time to different feeding strategies. The model has a goodness of fit to observed data, however, its predictive power can be improved if feed intake curve is adjusted to and/or replaced by real-time on-farm data.

3. The developed dynamic mechanistic model can estimate the standardized ileal digestible amino acid requirement, and particularly the amino acid pattern of ideal protein of different strains in different point of time.

4. The developed model is able to simulate the tendency of P-retention, urinary P-excretion at different body weights upon different P supply, as well as digestible P-requirement of *Gallus gallus domesticus*.

5. Compared to use of static table values of breeder recommendation, the application of a dynamic model to define optimal level of dietary nutrients is worthwhile. The broiler growth model in the present state is a useful tool to determine the amount and partitioning of N and P excretion, thus can support the development of feeding strategies to mitigate environmental footprint of the poultry sector.

6. The model has confirmed that oversupply of dietary protein – either due to the use of safety margin or the underestimation of protein digestibility – will increase the total ammonia N in the manure and thus the N emission potential of poultry meat production.

SUMMARY

Over the past decades, the application of different selection strategies and improvements in nutrition, and management have resulted in higher yields, even faster growth rates, and tremendous feed efficiency in meat-type chickens. A constant improvement in the performance aroused the need to regularly adapt their nutritional recommendations and feeding programs to continuously maximize economical outputs while minimizing the environmental impact. Modelling of nutrient responses offers more dynamic applicability than static requirements in tabular form. Unlike many published growth models for pigs, the number of available poultry models is much less. Therefore, the aim was to develop a post-digestive metabolic dynamic mechanistic deterministic model for broilers. The basics of the broiler model is a growing and fattening pig model that has been carefully transposed.

The model parameters were re-evaluated about (1) down-scaling of a pig to a chicken (*e.g.*, *potBPD*, *precocity*), (2) to poultry-specific aspects (*i.e.*, feathers, nutrient digestibility, dietary requirement for Arg), and (3) to interspecies differences (*e.g.*, efficiency of nutrient utilization, body composition). The model is most sensitive to *meanBPD*, *precocity* in a direct way, influencing the empty feather-free body protein (BP). If BP value increases, all the traits in linear or allometric relation to BP – eFFBwater, eFFBash, BW, FW, breast meat – will increase as well. Whereas body lipid deposition (BLD) is dependent on energy intake, particularly by feed intake (FI) parameters *FI_1* and *FI_2*, which are somewhat interconnected. Those (FI) parameters are fixing the daily amount of energy to be consumed at certain BW (1 and 2 kg, respectively). Since, the daily FI is depending on net energy intake, if to decrease both *FI_1* and *FI_2*, the BL and BLD values will decrease.

The model predicts well the growth performance and the chemical body composition in case of different nutrient supply. The predictive power can be improved by adjustment (or replacement) of the daily FI curve to (by) the real-time data. The data comparison displayed a general agreement between the simulated and measured data with normal individual variance originating from the variety between the guideline and birds in the experiment.

After conducting the sensitivity analysis and the model testing with independent data, the model simulating the energy and protein metabolism was extended with a module that can simulate the phosphorus (P) partitioning and, thus, the P retention and excretion in broilers from digestible P intake. The model gives a reliable simulation and follows the main trends of P retention reported in the literature. Yet, further improvements may be needed, in particular, more mechanistic approach on P retention and P partitioning. For that purposed dynamic datasets would be in order for the prediction to be in accordance with metabolic model part. Further, the model was run to test two feeding strategies in order to study the benefit of model

application related to the environmental footprint of broiler feeding. Namely nitrogen (N) and P excretion was compared using two different feeding strategies according to nutritional recommendation vs. multiple phases feeding schedule. The model is able to simulate the dynamics of faecal and urinary excretion of N and P in daily steps. It has been confirmed that the multiphase feeding strategy with more gradual reduction of the nutrients in the diet over fattening, is beneficial for the urinary N or P excretion. Furthermore, digestibility of dietary protein was shifted by +/-5% in a separate simulation.

In summary, the model developed in the frame of the PhD programme simulates the net energy and essential amino acid (EAA), as well as the dietary P utilization for maintenance and growth with consideration of the maximum protein deposition rate during the lifetime. Thus, it enables nutrient estimation, particularly digestible EAA requirement, the ideal protein profile and digestible P requirement for an average broiler at any time point. The reliability of the model is sufficient, in terms of animal response in time to different feeding strategies the model has a goodness of fit to observed data. Though, the predictive power of the model shall be improved by adjusting the daily feed intake curve to real-time and/or on-farm data. The model can be used as a tool to evaluate feeding strategies to mitigate N and P footprint of broiler production. From the dissertation, the following main conclusions were drawn:

1. Although pigs and poultry (broilers) are different species, this work has confirmed that it is possible to develop a model to predict broiler production which is based on a well-elaborated pig growth model.
2. In order to develop this broiler model, new species-specific parameters and equations have been appointed, and dynamic mechanistic and deterministic model simulation has been built for chicken (*Gallus gallus domesticus*). This developed model is called: "Model Simulation for Chicken" (MsChick).
3. The MsChick model, based on the feed (Net energy) intake, simulates the post-digestive utilization of energy and amino acids, and predicts the growth performance, as well as changes in chemical body composition of the individual birds over time. The model simulation was extended for simulation of calcium (Ca) and phosphorus (P) metabolism too.
4. The growth model can be used for estimation of the protein, fat, and water deposition (g/d) in the body, as well as for determination the amount of valuable meat parts, but the fat to protein ratio as a trait of meat quality has not been evaluated.
5. Based on testing with independent data, the model simulation is reliable when different feeding schedules and nutrient supply are estimated. The body weight and average daily

gain is well predicted in general, as well as the chemical body composition in time. The accuracy of the model is highly determined by the accuracy of feed intake estimation.

6. The model is sensitive to the parameters related to the model core – empty feather-free body protein: *meanBPD* and *precocity*, as well as to parameters related to daily feed intake: *FI_1* and *FI_2*. Besides initial parameters, it is also sensitive to *empty-feather-free body water allometry* and *c* parameters of the feed intake's representation as multiples of energy.
7. In addition to the chemical body composition and performance of the broiler, the model is able to simulate N and P-retention, urinary N and P-excretion and digestible N and P-requirement of *Gallus gallus domesticus* at different body weights and with different dietary supply.
8. The model allows testing the different multiple phases feeding in a dynamic way, as well as might serve as a great educational and/or decision support tool. Therefore, they are useful in education for demonstrating certain problems and to find solutions, as well as probably could help to formulate the experiments *in vivo* to confirm or reject certain theories.
9. 9The model is able to determine quantitatively the environmental load of a feeding strategy. It has been shown that using multiple phases defined through the model, the N and P excretion can be significantly reduced without compromising the growth performance. The broiler growth model in the present state is a useful tool to determine the amount and partitioning of N and P excretion, and thus can support the development of feeding strategies to mitigate the environmental footprint of poultry sector.
10. It has been confirmed that an oversupply of dietary protein – either due to the use of safety margin or the underestimation of protein digestibility – will increase the total ammonia N in the manure and thus the N emission potential of poultry meat production.
11. It is necessary to continue to challenge the model with real-time dynamic datasets to improve its mechanistic approach and thus the accuracy of prediction.

ÖSSZEFOGLALÁS

DINAMIKUS SZIMULÁCIÓS MODELL FEJLESZTÉSE BROJLER CSIRKÉK TELJESÍTMÉNYÉNEK ÉS TESTÖSSZETÉTELÉNEK BECSLÉSÉRE

Az elmúlt évtizedekben a különböző szelekciós stratégiák alkalmazása, valamint a takarmányozás és tartási rendszerek fejlesztése magasabb hozamot, nagyobb növekedést és kiváló takarmányértékesítő képességet eredményezett a hústípusú csirkékben. A genetikai potenciál folyamatos növekedése miatt egyre nőtt az igényt a táplálóanyag szükségleti ajánlások és takarmányozási programok rendszeres felülvizsgálatára és módosítására annak érdekében, hogy minél gazdaságosabb és környezetkímélőbb legyen a baromfihús előállítás. Ezt az igényt a klasszikus statikus táplálóanyag szükségleti táblázatok már nem tudják maradéktalanul kielégíteni, szükséges olyan dinamikus táplálóanyag szükségleti ajánlások kialakítása, aminek segítségével az állatok igénye napra pontosan követhető. A sertésekre vonatkozóan számos növekedési modell publikálásra került, a rendelkezésre álló baromfimodellek száma azonban sokkal kevesebb. Ezért a doktori kutatás célja egy dinamikus, mechanisztikus, determinisztikus metabolikus modell kidolgozása volt brojlerek számára. A brojler modell kidolgozásához egy transzparens, sertés növekedési modellt használtunk alapnak, amelyet megfelelő körültekintéssel és szakmai megfontolások mentén adaptáltunk.

A modellparamétereket az alábbiak szerint változtattuk: (1) egyes paramétereket azért változtattunk meg, mert a két faj között jelentős méret- és léptékbeli különbségek vannak (pl. potBPD, koraérettség), (2) új paramételek, egyenletek is kerültek a modellbe, ezek elsősorban baromfi-specifikusak voltak (pl. tollképződés, táplálóanyagok emészthetősége, Arg szükséglet), és (3) a fajok közötti különbségek okán is kellett változtatni egyes paraméterek értékén (pl. a tápálóanyagok energetikai hatékonysága, testösszetétel). A modell érzékenységvizsgálata során megállapítást nyert, hogy a legfontosabb modellkimeneteket (pl. élősúly, fehérje és zsír mennyisége a testben, mellizom) jelentős mértékben befolyásolja az átlagos fehérjebeépülés mértéke (meanBPD) és a koraérettség (precocity), mivel ezek közvetlenül hatnak az úgynevezett tollmentes üres testben mért fehérje mennyiségére. Ha a testfehérje mennyisége növekszik, akkor a testfehérjéhez lineárisan és allometrikus összefüggéssel meghatározott testösszetevők – mint a tollmentes ürest testben lévő víz és hamu, valamint az élősúly, a toll tömege és a mellhús kihozatal - is növekedni fognak. A testbe épült zsír (BLD) és a testben lévő zsír (BL) az energiafelvételtől függ. A takarmányfelvételi görbe két paraméterrel kalibrálható a modellben, az FI_1 és FI_2 az 1 kg és a 2 kg élősúlyban mért nettó energia felvételre utal, amelyek egyébként némileg összefüggenek. Mivel a napi takarmány felvétel a nettó energia beviteltől függ, ha az FI_1 és/vagy a FI_2 csökken, a BL és BLD értékek is csökkennek.

A modell kielégítő pontossággal képes becsülni a növekedési teljesítményt és a kémiai testösszetételt eltérő táplálóanyagellátás esetén. A becsült teljesítmény pontossága javítható a napi takarmányfelvételi görbe valós idejű adatokra való igazításával (vagy cseréjével). A modell tesztelése során a szimulált adatok általános egyezést mutattak a mért adatokkal figyelembe véve a normál egyedi varianciát, amely a fajtát és a kísérletben részt vevő madarakat jellemezte.

Az érzékenységvizsgálat és a független adatokkal végzett tesztelés elvégzése után az energia- és fehérjeanyagcserét szimuláló modellt egy olyan modullal bővítettük, amely képes becsülni a foszfor (P) megoszlását, és ezáltal a brojlerekben az emészthető P bevitelből származó P-retenciót és kiválasztódást. A tesztelés eredménye alapján megállapítható, hogy a modell megbízható eredményeket ad, és követi a P-retenció szakirodalomban közölt főbb trendjeit. Ennek ellenére további fejlesztésekre lehet szükség a mechanikusabb megközelítéshez, különösen a P retenció és eloszlás pontosításához. Ehhez dinamikus adatkészletekre volna szükség annak érdekében, hogy a P modul összhangban legyen a modell energia és fehérje anyagcserét bemutató részével.

A modell értékelését követően két takarmányozási stratégia tesztelését végeztük el abból a célból, hogy megvizsgáljuk a modell alkalmazásának előnyeit a brojlertakarmányozás környezeti lábnyomának meghatározása kapcsán. A szimulációkban a nitrogén (N) és P kiválasztódást két különböző takarmányozási stratégia esetén értékeltük. Az egyik stratégia a brojler tenyésztő cég táplálóanyag ajánlása, míg a másik a szükségleti értékek modell szimulációja alapján meghatározott többfázisú etetési stratégia volt. A modell képes szimulálni a N és P bélsárral és vizelettel való ürülésének napi mértékét és dinamikáját. Megerősítést nyert, hogy a többfázisú takarmányozási stratégia, amely a tápanyagok mennyiségének fokozatosabb, de gyakoribb csökkentését jelenti a hizlalás során, előnyös, mert összességében kisebb N- vagy P-kiválasztást eredményez, mint a tenyésztő cég által javasolt 4 fázisú takarmányozás. További modell szimulációban a takarmány fehérje emészthetőségének +/-5%-kal való változásának hatását vizsgáltuk a N ürítés mértékére és eloszlására.

Összegezve, a PhD program keretében kidolgozott modell a takarmánnyal felvett nettó energia és az ileálisan emészthető esszenciális aminosavak (EAA), valamint a P anyagcserében való megoszlását szimulálja. Az energia és a táplálóanyagok a létfenntartáshoz és a genetikailag meghatározott növekedéshez használódnak fel. Ezzel lehetővé válik a táplálóanyag szükséglet becslése, különösen az emészthető EAA-szükséglet és az ideális fehérje összetétel, valamint az emészthető P-szükséglet meghatározása egy átlagos brojler számára egy adott időpontban. A modell megbízhatósága megfelelő, a brojlerek különböző takarmányozási kezelésekre adott, időbeni reakcióját tekintve a szimuláció jól illeszkedik a megfigyelt adatokhoz. A modell prediktív értékét azonban javítani lehet a napi takarmányfelvételi görbe valós idejű adatokkal való cseréje esetén és abban az esetben, ha historikus telepi adatokat használjuk a modellben. A modell kiváló eszközt biztosít a takarmányozási stratégiák értékelésére és a brojlerhús előállítás N és P lábnyomának csökkentésére. A disszertáció az alábbi főbb következtetéseket tartalmazza:

1. Bár a sertés és a tyúk (brojler) különböző fajok, a kutatómunka megerősítette, hogy lehetséges egy olyan modell kidolgozása a brojlertermelés előrejelzésére, amely egy kipróbált, jól működő sertés növekedési modellen alapul.
2. Ennek a brojler modellnek a kidolgozásához új, fajspecifikus paramétereket és egyenleteket határoztam meg, valamint dinamikus mechanisztikus és determinisztikus szimulációs modellt állítottam fel csirkére (Gallus gallus domesticus). Ennek a kifejlesztett modellnek a neve: „Model Simulation for Chicken" (MsChick).
3. A MsChick modell a takarmányfelvételre (Nettó energia) alapozva szimulálja az emésztést követő energia- és aminosav hasznosulást, és előrejelzi az egyes madarak növekedési teljesítményét, valamint kémiai testösszetételének időbeli változásait. A modellszimulációt kiterjesztettem a kalcium (Ca) és foszfor (P) metabolizmus szimulációjára is.
4. A növekedési modell felhasználható a szervezetbe naponta beépült fehérje-, zsír- és víz mértékének (g/d) becslésére, valamint az értékes húsrészek mennyiségének meghatározására, mindazonáltal a zsír-fehérje arány jellemzőjeként definiálható húsminőséget nem értékeltük.
5. A független adatokkal végzett tesztelés alapján a modellszimuláció megbízható, ha különböző takarmányozási kondíciókat és táplálóanyagellátás hatását becsüljük. A testtömeg és az átlagos napi gyarapodás általában megbízhatóan jósolható, csakúgy, mint a kémiai testösszetétel és ennek időbeni változása. A modell pontosságát nagymértékben meghatározza a takarmányfelvétel becslés pontossága.
6. A szimuláció eredménye érzékeny a modell alapjának tekinthető változókra – üres tollmentes testfehérje átlagos fehérje beépülésére (meanBPD) és koraérettségi együtthatójára (precocity), valamint a napi takarmányfelvétellel kapcsolatos paraméterekre: FI_1 és FI_2. Ezen alapváltozók mellett érzékeny az üres-toll-mentes test víztartalmát meghatározó allometrikus paraméterre és a takarmányfelvétel függvényének egy paraméterére, mely az energia ellátáshoz kötődő érték (c).

7. A modell a test kémiai összetétele és a növekedési teljesítmény mellett képes szimulálni a brojler csirke (Gallus gallus domesticus) N- és P-visszatartását, a vizelettel történő N- és P-kiválasztását, valamint emészthető N- és P-szükségletét különböző testtömeg és takarmányozás esetén.
8. A modell lehetővé teszi különböző takarmányozási fázisok dinamikus tesztelését, valamint kiváló oktatási és/vagy döntéstámogató eszközként szolgálhat. Ezért hasznosnak vélem az oktatásban bizonyos problémák bemutatására és megoldások keresésére, valamint valószínűleg segíthet egyes in vivo kísérletek megfogalmazásában, bizonyos elméletek megerősítésében vagy elutasításában.
9. A modell képes mennyiségi becslést adni egy takarmányozási stratégia környezeti terhelésének mértékére. Az in silico vizsgálatok igazolták, hogy a modell által meghatározott több fázis használatával a N- és P-kiválasztás jelentősen csökkenthető a növekedési teljesítmény veszélyeztetése nélkül. A brojler növekedési modell jelen állapotában hasznos eszköz a N- és P-kiválasztás mennyiségének és megoszlásának meghatározására, így támogathatja a baromfiágazat környezeti lábnyomát csökkentő takarmányozási stratégiák kidolgozását.
10. Bebizonyosodott, hogy az étrendi fehérje túlkínálata – akár a biztonsági ráhagyás alkalmazása, akár a fehérje emészthetőségének alulbecslése miatt – megnöveli a trágya összes ammónia-N-tartalmát, és ezzel a baromfihús-termelés N-kibocsátási potenciálját.
11. Folytatnunk kell a modell értékelését valós idejű dinamikus adatkészletekkel, hogy javítsuk annak mechanisztikus megközelítését és ezáltal az előrejelzés pontosságát.

ANNEX A “MSCHICK BROILER MODEL EQUATIONS AND CALCULATION ROUTINE”

The model calculation commences with defining an empty body weight (eBW, *i.e.*, body weight without digestive tract fill), calculated using allometric relation from initial body weight (*BW_init*, kg), thus, the calculations begin by defining the initial eBW from the initial live BW:

$$\mathrm{eBW}_{init} = a_{\mathrm{eBW}} * \mathrm{BW}_{init}{}^{b_{\mathrm{eBW}}} \quad [1]$$

BW_{init} can be as hatched or, with certain modification, BW at any time point from which the simulation starts. Allometry coefficients a_{eBW} and b_{eBW} are represented in Table 1 and were calculated according to data of Hancock *et al.* (1995). Author has related the amount of feed (consumed and remained in crop, proventriculus and gizzard) to the live weight of the bird via day-old, 2nd day until 7th days of age, at 14th day and from 21st day until 11th week of age.

Further, the feather weight (FW, g) and feather protein (FP, g) are calculated via allometry from initial *BW_init* and FW, respectively. BWinit can be as hatched or BW at any time point from which the simulation starts.

The rates of feather growth (FW_{dep}, g/d) and feather protein deposition (FP_{dep}, g/d) are defined difference of current day and the previous one:

$$\mathrm{FW}_{\mathrm{dep}} = \mathrm{FW}_{(\mathrm{i})} - \mathrm{FW}_{(i-1)} \quad [2]$$

$$\mathrm{FP}_{\mathrm{dep}} = \mathrm{F}_{\mathrm{P}_{(\mathrm{i})}} - \mathrm{F}_{\mathrm{P}_{(\mathrm{i}-1)}} \quad [3]$$

Empty feather-free body weight (eFFBW, kg) and empty feather-free body protein (BP, kg) were calculated as the difference between eBW and FW (Eq. 4). The initial empty feather-free body protein and lipid contents of the as-hatched chick are calculated as shown in equations 5 and 6, respectively.

$$\mathrm{eFFBW}_{(i)} = \mathrm{eBW}_{(i)} - \mathrm{FW}_{(i)}/1000 \quad [4]$$

$$\mathrm{BP}_{init} = \frac{\mathrm{Prot_{init}}}{100} * \mathrm{eBW}_{init} - \frac{FP}{1000} \quad [5]$$

$$\mathrm{BL}_{init} = 0.1 * \mathrm{EFFBW} \quad [6]$$

Net energy intake (NEI, MJ/d) at 1 and 2 kg of BW are calculated according to the fitted polynomial equation as shown on Figure 1, when NEI (MJ/d) plotted against BW (kg). In this calculation the daily feed intake data that are usually given in weight dimension should be first converted to NEI by accounting with the NE content of the feed and the daily feed intake. The generated NEI data are plotted against observed BW data and the best fitted polynomial (preferably a cubic or quadratic) function will derive *FI_1* and *FI_2* values, the FI at 1 and 2 kg BW, respectively

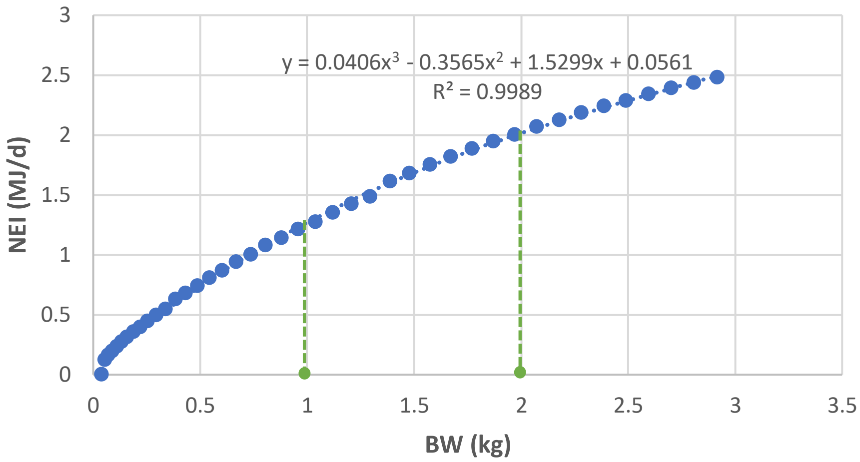


Figure 1. An example of defining parameters of net energy intake (NEI, MJ/d) at 1 and 2 kg of body weight (*FI_1* and *FI_2*, MJ/d) for an average Ross 308 male broiler based on breeder guideline values (Aviagen, 2017)

The *a* and *b* values for the FI function of multiples of maintenance *ad libitum* (page 65) are calculated according to the equations 7 and 8, respectively.

$$A = -2 * \exp(\log(2) * d) * \frac{FI1^2 - 2 * FI1 * c + c^2}{c * \left(\log\left(2 * \frac{-FI_1 + c}{-FI_2 + c * \exp(\log(2) * d)}\right) + \log(2) * d\right) * (-FI_2 + c * \exp(\log(2) * d))} \qquad [7]$$

$$b = \log\left(2 * \frac{-FI_1 + c}{-FI_2 + c * EXP(LN(2) * d)}\right) + \log(2) * d \qquad [8]$$

The maintenance requirement for each EAA is defined as a sum of basal endogenous AA losses ($AA_{endogen}$) originated from the digestive system (abrasion of the gut cells and mucin protein, non-reabsorbed enzyme proteins), the basal turnover of protein excreted via urine that is often called obligatory urinary losses ($AA_{urinary}$), and the AA loss attributed to feather protein loss in birds (AA_{f_loss}). The $AA_{endogen}$ are proportional to the dry matter intake (g/kg DMI) and AA content of endogenous loss from the gut for each EAA (Adedokun *et al.*, 2011 and Adeola *et al.*, 2016). The $AA_{urinary}$ was proportional to metabolic body weight ($BW^{0.75}$). It was assumed that the maintenance requirements of each EAA in obligatory urinary AA loss is not specie dependent, therefore the values of InraPorc were used. AA_{f_loss} was proportional to the bird's FP loss. Therefore, it was calculated as FP mass multiplied by EAA content of the FP and brought to allometry depending on sex. Difference between digestible AA intake and AA of maintenance for each EAA as well as requirements for EAA deposition into the FP defines the PD into eFFBP allowed by EAA intake for growth. The EAA presented in the smallest amount relative to the requirement serves as 1st limiting AA. Therefore, the supply of this limiting EAA determines the amount of the protein that can be deposited in eFFB on each day (*i*).

Gompertz function, which is frequently used in modelling work, particularly describes the genetic potential of protein accretion in the body that is not limited by the feed (Halas *et al.*, 2018). However, because of the difficulty to estimate one of the parameters of the equation – a potential mature protein into the eFFB mass in young animals, like in InraPorc, in MSChick the Gompertz function was parametrized to include the mean BP deposition (*meanBPD*, g/d) during the growing and finishing period (which is strongly related to the growth rate) and a *precocity* (maturity rate, d^{-1}) parameter describing the concave shape of the protein deposition curve (Eq. 13). The potential BP deposition (potBPD $_{(i)}$, g/d) is modelled using a 1st derivative of the Gompertz function (van Milgen *et al.*, 2008):

$$\mathrm{potBPD}_{(i)} = 1000 * \mathrm{precocity} * \mathrm{BP}_{(i)} * \ln\left(\frac{\mathrm{BP}_{\mathrm{maturity}}}{\mathrm{BP}_{(i)}}\right) \quad [7]$$

where BP is the current animal empty (feather-free) body protein mass (kg), precocity (d^{-1}) is the shape parameter of the Gompertz function, and $BP_{maturity}$ (kg) is the mature empty (feather-free) body protein mass considered as a technical parameter with little practical meaning.

The value of $BP_{maturity}$ (Eq. 9) is calculated based on the expected final BP (Eq. 8) weight for a certain period (which is calculated from mean protein deposition for that period) as follows:

$$\mathrm{BP}_{final} = \left(\mathrm{age}_{final} - \mathrm{age}_{init}\right) \frac{meanBPD}{1000} + \mathrm{BP}_{init} \quad [8]$$

$$\mathrm{BP}_{\mathrm{maturity}} = \mathrm{BP}_{final} \left(\frac{\mathrm{BP}_{final}}{\mathrm{BP}_{init}}\right)^{\mathrm{e}^{\left(\frac{-\mathrm{precocity} * \left(\mathrm{age}_{final} - \mathrm{age}_{init}\right)}{1 - \mathrm{e}^{\left(-\mathrm{precocity} * \left(\mathrm{age}_{final} - \mathrm{age}_{init}\right)\right)}}\right)}} \quad [9]$$

As concerns energy metabolism, the fasting heat production (FHP) when the animal had been fed *ad libitum* and heat production related to activity (HP_{act}) are shown in equations 10 and 11, respectively.

$$\mathrm{FHP}_{(i)} = \mathrm{FHP}_{\mathrm{init}} * BW_i^{0.7} \quad [10]$$

$$\mathrm{HP}_{\mathrm{act}(i)} = \mathrm{FHP}_{\mathrm{actual}(i)} * \frac{\mathrm{activity}_{\mathrm{level}}}{100} \quad [11]$$

Maintenance NE needs is assumed to be a sum of FHP, multiplied by a coefficient of energy efficiency of using body reserves (k_{BR}), and HP_{act}.

An obligatory energy flux in birds (ObligUrinELoss) related to urinary energy loss and is shown in equation 12. The broiler chicken excretes approximately 2.19 mg of endogenous uric acid per 1 kJ of FHP (eUA), while 1 mg of eUA is about 39 J of endogenous urinary energy (eUE). The eUE excreted due to excess protein (kJ/d) is calculated as amount of excess protein in grams divided per 6.25 and multiplied per 32.97 J as 1 mg of endogenous urinary N is about 32.97 J of endogenous urinary energy (VarUrineLoss, Koh *et al.*,1992). The urinary energy loss from excess protein ($\mathrm{UrineE_{loss}}$) calculation is shown in equation13. Excess protein is calculated as protein intake minus BPD, FP, and FP_loss.

$$\mathrm{ObligUrin_{E_{loss}}}_{(i)} = \mathrm{FHP}_{(i)} * \mathrm{eUA} * \frac{\mathrm{eUE}}{1000} \tag{12}$$

$$\mathrm{UrinaryE_{loss}}_{(i)} = \frac{\text{excess protein}_{(i)}}{6.25} * \mathrm{VarUrineLoss} \tag{13}$$

Metabolizable energy (ME) of excess protein is calculated as Excess protein multiplied by gross energy of protein minus UrinaryEloss. NE of excess protein is ME of excess protein multiplied by k_{prot} coefficient (Eq. 14-15).

$$\mathrm{MEexcessProt}_{(i)} = \mathrm{ExcessProt}_{(i)} * \mathrm{GEprot} - \mathrm{UrinE}_{(i)} \tag{14}$$

$$\mathrm{NEexcessProt}_{(i)} = \mathrm{k_{prot}} * \mathrm{MEexcessProt}_{(i)} \qquad [13]$$

Protein-free NE intake ($\mathrm{BPD\_freeNEI}_{(i)}$) is calculated as FI multiplied by NE of the diet minus NE of the digestible protein. BPD-free NE intake is sum of NE of excess protein and Protein-free NE.

$$\mathrm{BPD\_freeNEI}_{(i)} = \mathrm{NEexcessProt}_{(i)} + \mathrm{BPD\_freeNE}_{(i)} \tag{15}$$

BPD deposition free NE requirements to deposit BPD, is a sum of NE for maintenance plus cost for protein deposition (NEBPD, NE of 1 g of protein deposition) and shown in equation 16.

$$\mathrm{BPDfreeNEBPD}_{(i)} = \mathrm{BPD_{(i)}} * \mathrm{GEprot} + \mathrm{NEPD}_{(i)} \tag{16}$$

BPD-free NE requirement is a sum of NE for maintenance and BPDfreeNEBPD. Thus, the energy available for lipid deposition will be a difference of $\mathrm{BPD\_freeNEI}_{(i)}$ and Protein deposition free NE requirements to deposit BPD. Lipid deposition is Energy available for lipid deposition divided by GE_{lipid}.

At the end of the day (*i*) the BPD is added to BP, BLD to BL, for defining BP and BL for the day (*i+1*) respectively. The BW (*i+1*) will be a sum of empty feather free body (eFFB) and weather weight. The eFFB is a sum of BP, BL, eFFBwater and eFFBash. The last two are calculated in allometric and linear regression from BP.

Besides initial parameters, there are other parameters, presented in Table 1, which may be changed by a user. Changes might concern, for instance, the empty feather-free body water and/or empty feather-free body ash. The user can manipulate not only with values of parameters but also to change the logic of the regulating by choosing the way of regression (linear or allometric, *etc.*).

Table 1. Parameters for MsChick model

BW_init	*0.04918*	*initial body weight initial*
precocity	*0.04698*	*eFFB protein deposition rate parameter*
meanBPD	*9.83681*	*mean protein deposition rate, g/day*
FI_1	*1.23219*	*expected NE (MJ NE/day) intake at 1 kg of BW*
FI_2	*2.02846*	*expected NE (MJ NE/day) intake at 2 kg of BW*
a_eBW	0.9386	*a* coefficient in allometric function of eBW
b_eBW	0.9848	*b* coefficient in allometric function of eBW
a_FP_m	0.852	*a* coefficient in allometric function of FP, males
b_FP_m	1.0091	*b* coefficient in allometric function of FP, males
a_FP_f	0.8489	*a* coefficient in allometric function of FP, females
b_FP_f	1.0095	*b* coefficient in allometric function of FP, females
a_FW_by_eFFBW_m	0.0307	*a* coefficient in allometric function of $FW_{(i+1)}$, males
b_FW_by_eFFBW_m	1.0777	*b* coefficient in allometric function of $FW_{(i+1)}$, males
a_FW_by_eFFBW_f	0.0380	*a* coefficient in allometric function of $FW_{(i+1)}$, females
b_FW_by_eFFBW_f	1.0138	*b* coefficient in allometric function of $FW_{(i+1)}$, females
a_Bwater_m	4.287	*a* coefficient in allometric function of eFFBWater, males
b_Bwater_m	008929	*b* coefficient in allometric function of eFFBWater, males
a_Bwater_f	4.1039	*a* coefficient in allometric function of eFFBWater, females
b_Bwater_f	0.8847	*b* coefficient in allometric function of eFFBWater, females
F_loss_a_m	5E-10	*a* coefficient in allometric function of feather loss, males
F_loss_b_m	4.6698	*b* coefficient in allometric function of feather loss, males
F_loss_a_f	9E-11	*a* coefficient in allometric function of feather loss, females
F_loss_b_f	5.5421	*b* coefficient in allometric function of feather loss, females
Age_init	0	initial age at start of the simulation, days
Age_final	63	final age at the end of the simulation, days
BP_init	17	% of protein content in the eFFBP
BL_init	10	% of lipid content in the eFFBP
FHP_init	450	fasting heat production, $kJ/BW^{0.7}/day$
activity_level	33	activity level in % of FHP
GEprot	23.8	gross energy of 1 g of protein deposited into the eFFB
GElipid	39	gross energy of 1 g of lipid deposited into the eFFB
$\mathbf{k_{prot}}$	0.52	coefficient of the excess protein conversion to provide energy
$\mathbf{k_{BR}}$	0.7084	energy efficiency of using body reserves
VarUrineLoss	32.97	amount of energy in 1 g of urinary endogenous N, J
eUA	2.19	uric acid per 1 kJ of FHP, mg
eUE	39	endogenous urinary energy of 1 mg of uric acid, J
NEPD	0.484	net energy of 1 g of protein deposition, MJ
sex	1	1 for male, 0 for female
ag_ad	1.597700638	parameter "a" in FI curve (*ad libitum*)
bg_ad	0.671525317	parameter "b" in FI curve (*ad libitum*)
c	0.8	parameter "c" in FI curve (multiples of maintenance)
d	0.75	parameter "d" in FI curve (power of metabolic BW in NE system)
day of diet 2	11	beginning of the 2^{nd} phase of the diet in phase feeding, d
day of diet 3	25	beginning of the 3^{rd}phase of the diet in phase feeding, d
day of diet 4	40	beginning of the 4^{th}phase of the diet in phase feeding, d
day of diet 5	52	beginning of the 5^{th}phase of the diet in phase feeding, d

AKNOWLEDGMENTS

I am pleased to have a chance to express my sincere and eternal gratitude to the people who inspired and supported me during the PhD journey. Primarily to my supervisor and adviser, Dr. Veronika Halas, who introduced me to this PhD program, believed in me, and is my big inspiration in many aspects of life. My immense appreciation and gratitude to Dr. Jaap van Milgen, who supported me during the most challenging and crucial moments and shared his knowledge as a creator of InraPorc model. Appreciation is extended to Dr. Kövér György for his invaluable assistance with many aspects of my work and for always finding time for me. I also would like to thank Dr. Bertrand Méda for his helpful suggestions and for providing the Ross broilers dynamic dataset for the evaluation of the model, as well as Dr. Sandrine Grasteau and her PhD student Quentin Berger for the Cobb broilers dynamic dataset. My enormous gratitude goes to the Feed-a-Gene Horizon 2020 EU project. It not just partly funded my study program but also made my life rich by meeting all the great people – members of the project.

I could not fulfil my studies without the Stipendium Hungaricum Programme managed by the Tempus Public Foundation. Therefore, I appreciate the opportunity to discover, live and study in Hungary. I am expressing the thankfulness as well to the EFOP project support for the publications in Acta Debreceniensis and MDPI Agriculture journals during my studies. Lots of gratitude and warm feeling to the Animal Nutrition Department of Kaposvár University Campus of MATE, and all the dear colleagues whom I met during the way of my studies.

I am incredibly grateful to my husband and my favourite person, Julien, for his help, encouragement, and devotion during my graduate program. Also, there will never be enough words to express how much I appreciate the unstopping unconditional love and support my father, Anatoliy, gave me. He said my mom, Nataliya, could be proud if she would be still alive. I am grateful to my parents that I exist, and that today I can add some little scientific results to the grand animal science.

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CURRICULUM VITAE

Galyna Dukhta was born on November 12th in 1988, in Bila Tserkva of Kyiv region in Ukraine. She graduated from College of Technologies and Economics in Bila Tserkva with a High school Diploma, together with Junior Specialist Diploma (with honours) in Finance and Credit in 2006. In 2010 she obtained a BSc in Finance and Credit and BSc in Animal Husbandry Output Production and Processing Technology from the National University of Life and Environmental Sciences, in Kyiv, Ukraine. From the same institution, she received her graduated MSc degrees in Quality, Standardization and Certification in poultry production as well as MSc in Finance and Credit in banking.

Thanks to FAO scholarship grant she fulfilled her MSc studies in Animal Nutrition and Feed Safety at Kaposvár University and received her diploma (with honours) in 2013. She came back to Ukraine and started her career as an Intern at the Department of International Integration in the sphere of Technical Regulations, Sanitary and Phytosanitary Measures in Agriculture at the Ministry of Agricultural Policy and Food of Ukraine. And later she participated in Food Safety reform as personal assistant to the Head of the State Service for Food Safety and Consumer Protection in Kyiv.

In 2016 Galyna was employed by the University of Kaposvár as a research assistant in frames of the “Feed-a-Gene” project of the Horizon 2020 EU strategy. Also, later in 2016 she entered the Stipendium Hungaricum scholarship program as a PhD student. Currently, she is employed at the Chamber of Agriculture in France.