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CHAPTER 14

Models of feed utilization and growth for monogastric animals

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1. Introduction

A model is an “abstraction of reality” used to understand a phenomenon and as such is an integral part of the scientific method. Models are commonly developed and applied to explore and understand the behaviour of a (physical, biological, chemical, or even sociological, philosophical or conceptual) system, and to predict output(s), consequent upon the behaviour of the underlying mechanisms, from a number of inputs. Through modelling, we can obtain predictions for the future and they can aid in decision-making. When building a model, the most relevant structural and functional elements of a system are described by mathematical (or logical) algorithms. The most challenging issue in modelling is to choose these elements in relation to the intended purpose of the model.

Different models have been developed to predict the growth of animals. A typical S-shaped curve can be used to describe the change in live weight as a function of age (Figure 1A). For a mathematical representation of the relationship between live weight and age, growth functions such as the Gompertz, Lopez, Schumacher, or Weibull functions can be used (Schulin-Zeuthen *et al.*, 2008; Strathe *et al.*, 2010). Such functions have proven their value, either for descriptive purposes or for the expression of an animal’s genetic potential (Doeschl-Wilson *et al.*, 2007). Using time or age as the sole driving force for growth is a somewhat frustrating approach for nutritionists. Alternatively, live weight can be described as a function of cumulative feed intake (Figure 1B) changing the concept from “animals grow because they get older” into “animals grow because they eat”. As animals approach maturity, they cease to grow but continue to eat for maintenance. Figure 1B can also provide information about instantaneous and cumulative feed efficiencies, both of which change during life.

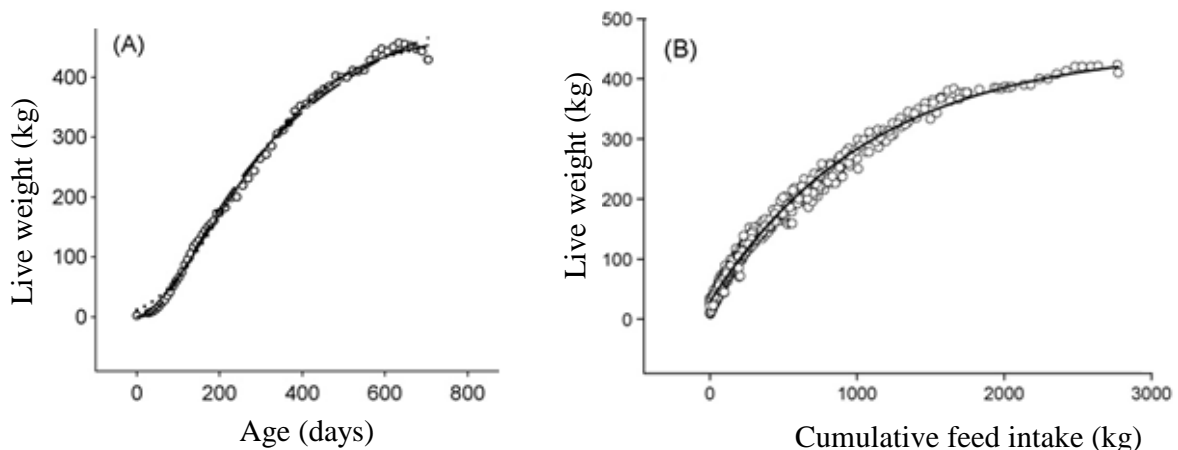


Figure 1

Empirical relationship describing animal live weight as a function of age or cumulative feed intake (Schulin-Zeuthen *et al.*, 2008).

From a nutritional perspective, the concept used in Figure 1B is an improvement over that used in Figure 1A. However, it ignores the proposition that dietary composition is a major determinant of growth and of the chemical and physical composition of body weight gain. Nutritional models comprise a set of equations describing nutrient flows and they can be used to simulate animal responses to different nutritional regimens. They have been developed for different purposes. The very first models were developed to establish nutrient requirements of animals (ARC, 1967; Blaxter, 1962; FAO, 1957), whereas later ones simulated nutrient digestion and, or nutrient partitioning (Table 1), or the performance of the herd or flock (Pomar *et al.*, 1991b; Aerts *et al.*, 2003; Stacey *et al.*, 2004; Ezcurra-Ciauriz and Plà-Aragonès, 2009).

In this chapter, we describe and discuss different types of nutritional models that have been developed for monogastric animals and particularly for pigs. The main concepts underlying these models and their application are highlighted, including the benefits of using them in livestock farm practice.

Table 1
Examples of models predicting nutrient digestion and or partitioning in growing pigs and broiler chickens

Authors	Type of model	Species	Model classification	Inputs	Outputs	Purpose of the model as stated by the authors
Usry <i>et al.</i> , 1991	Digestion	Growing pig	Mechanistic, deterministic dynamic	Feed intake within the day (by minute)	Digesta flow, absorption rate kinetics	Predict digesta flow in response to feeding
Bastianelli <i>et al.</i> , 1996	Digestion and absorption	Growing pig	Mechanistic, deterministic dynamic	Feed and nutrient intake patterns	Kinetics of nutrient digestion, digestion coefficients	Study the extent and kinetics of digestion and absorption of nutrients
Rivest <i>et al.</i> , 2000	Protein digestion	Mature pig	Mechanistic, deterministic, dynamic	Protein intake, feed intake (<i>ad libitum</i> or meal fed)	Protein digestion kinetics, kinetics of absorption	Integrate physiological processes involved in protein digestion and absorption in the small intestine; differential digestion of endogenous and dietary proteins
Strathe <i>et al.</i> , 2008	Digestion and absorption	Growing pig	Mechanistic, deterministic dynamic	Feed and nutrient intake patterns	Kinetics of nutrient absorption, digestion coefficients	Study the extent and kinetics of digestion and absorption of nutrients
Muñoz-Tamayo <i>et al.</i> , 2010	Digestion (carbohydrate fermentation in large intestine)	Human	Mechanistic, deterministic dynamic	Nutrient input into the large intestine	Fermentation patterns in the large intestine	Integrate the physiology of the large intestine to predict and understand kinetics of fermentation of carbohydrates, mass transfer between intestinal lumen and mucus
Létourneau-Montminy <i>et al.</i> , 2011	Digestion of phosphorus	Growing pig	Mechanistic, deterministic dynamic	Dietary phytate P and non-phytate P of animal, plant and mineral origin; Ca	Phosphorus digestibility	Simulate the fate of the dietary form of P in the stomach and small intestine with emphasis on the effects of Ca and exogenous phytase
Taghipoor <i>et al.</i> , 2012	Digestion	Multi-species (non-ruminants)	Mechanistic deterministic dynamic	Meal patterns	Kinetics of digesta transport and absorption	Model digestion in the small intestine by representing transport of the bolus along the intestine, enzymatic degradation, physical conditions, and nutrient absorption

Le Feunteun <i>et al.</i> , 2014	Protein digestion	Mini pig	Mechanistic, deterministic, dynamic	Intake of milk protein	Kinetics of protein digestion and absorption	Understand the kinetics of absorption of amino acids from dairy products by considering behaviour of the matrices in the stomach
Whittemore and Fawcett, 1976	Nutrient partitioning	Growing pig	Dynamic, mechanistic	Feed intake, nutrient input, Gompertz parameters for protein and lipid deposition, temperature	Body weight, body composition, feed intake, feed conversion ratio	A simple mathematical expression to calculate the direction and the magnitude of the responses of growing pigs to feed inputs
Moughan, 1984	Protein digestion and metabolism	Growing pig	Mechanistic, deterministic, static model	Feed intake, dietary energy and amino acid content, apparent ileal digestibility of amino acids, sex and live weight	Body weight gain, protein and fat deposition, urinary and faecal nitrogen excretion	Assess protein quality
Talpaz <i>et al.</i> , 1986	Digestion and metabolism	Broiler	Dynamic model including least-cost optimization	Parameters of the Gompertz function	Requirements of total protein, amino acids, and energy	Optimize feed rationing throughout the production period for any given growth path, while calculating the nutritional requirements
Emmans, 1987	Feed intake, digestion and metabolism	Broiler	Mechanistic, deterministic, dynamic	Parameters of the Gompertz function, dietary nutrient content, temperature	Body weight, body composition, energy and protein requirement, feed intake, feed conversion ratio	Growth, food intake, food conversion, efficiency and body composition. The problem of predicting feed intake is inextricably linked with the idea of potential growth rate, inherent fatness, maintenance and feed balance

Pomar <i>et al.</i> , 1991a	Nutrient partitioning	Growing pig	Mechanistic, deterministic, dynamic model	Initial body weight, maximum protein mass at maturity, diet composition	Body weight, protein fat, water, ash in the body; daily feed intake, feed conversion ratio, backfat thickness	Develop a growth model incorporating fundamental biological processes regulating the accretion of body protein, energy and protein metabolism with consideration of genotypic and nutritional effects and their interactions with growth and body composition
Danfær, 1991	Protein retention	Multi-species, adopted for pigs	Mechanistic, deterministic, dynamic	Constants of saturable kinetics	Protein synthesis, degradation, and retention	Test if a sigmoid growth curve could be simulated by mechanistic rate equations describing protein synthesis and degradation and without any definition of mature size
Danfær, 1991	Nutrient partitioning	Multi-species, adopted for pigs	Mechanistic, deterministic, dynamic	Feed intake, nutrient inputs represents a mixture of amino acids, fatty acids and glucose	Deposition and mobilization of body nutrient stores, nutrient oxidation, total nutrient flux rate	Simulate metabolic control of substrate partition between synthetic and oxidative transactions using a principle of allosteric enzyme regulation
Werkgroep TMV, 1991	Nutrient partitioning	Growing pig	Mechanistic deterministic static	Dietary energy and protein intake, digestibility /metabolizability, genotype parameters for protein and lipid deposition	Protein and lipid deposition rates, body weight	Predict the effect of feed composition, feed intake and genotype on growth rate and body composition of growing pigs
Bridges <i>et al.</i> , 1992	Nutrient partitioning	Growing pig	Mechanistic, deterministic, dynamic	Parameters of the Gompertz function, nutrient intake, ambient temperature	Feed intake, protein, fat, water, ash in the body, body weight, heat production	Simulate the interaction of feed intake and various metabolic processes

Birkett and De Lange, 2001	Nutrient partitioning	Monogastric animals, calibrated for growing pigs	Mechanistic, deterministic, dynamic model	Ileal digestible nutrients (glucose, glycerol, fatty acids, non-specific fat, amino acids, non-specific N, volatile fatty acids)	Body protein and fat, urea N, heat production	Represent energy utilization for body protein and lipid accretion
King, 2001	Nutrient partitioning	Broiler	Mechanistic, deterministic, dynamic	Age, initial body weight, dietary nutrients and energy; feed intake might be an input	Body weight, weight and chemical body composition of carcass, feed intake, limiting amino acids, heat loss	Simulate daily growth and optionally the daily feed intake of meat chickens with different growth intensities
Lovatto and Sauvant, 2003	Metabolism	Pig	Mechanistic, deterministic, dynamic	Feed intake, amino acid composition, fatty acids, glucose	Body weight, protein anabolism and catabolism, protein and fat accretion	Apply a systemic approach acknowledging the major driving forces of nutrient fluxes with the minimum of information necessary to simulate growth and influences of diet
Halas <i>et al.</i> , 2004	Nutrient partitioning	Growing pig	Mechanistic, deterministic, dynamic	Digestible nutrient intake (Lys and ideal protein; starch, fat, fibre)	Body weight, chemical composition of the body and body compartments (muscle, viscera, bone, hide and backfat)	Predict growth rate and both the chemical and anatomical body compositions of gilts of 20-105 kg live weight from digestible nutrient intake
Ferguson, 2006	Feed intake	Growing pig	Mechanistic, deterministic, dynamic	Potential growth, desired fatness, gut capacity, dietary factors	Feed intake	Predict the amount of feed daily that satisfies the requirement of both energy and protein
EFG (Emmans, Fisher and Gous) model	Nutrient partitioning	Broiler	Mechanistic, deterministic, dynamic	generic parameters, diet composition, feeding program, temperature,	Body weight, growth rate, body composition, feed	Scientific and management tool for poultry nutritionists, geneticists and managers - in short, anyone concerned with technical

				stocking density	conversion + economic calculation	developments in broiler production.
van Milgen <i>et al.</i> , 2008	Nutrient partitioning	Growing pig	Mechanistic, dynamic model	Nutrient content, potential protein deposition, feed intake	Body weight, body composition, feed conversion ratio, backfat thickness, nutrient utilization and nutrient requirements	Analyse nutrient utilisation for characterised pig types and to evaluate different nutritional strategies in terms of nutrient utilisation, performance and carcass characteristics in growing pig (15–150 kg BW)
NRC, 2012	Nutrient partitioning	Growing pig, gestating and lactating sow	Mechanistic, deterministic, static model	Nutrient content, body weight, sex, genotype	Daily weight gain, protein and lipid gain, feed conversion ratio, nutrient requirement, N, P, and C loss	Estimate nutrient requirements of swine
Strathe <i>et al.</i> , 2015	Nutrient partitioning	Growing pig	Dynamic, semi-mechanistic model	Feed intake, nutrient input, water-to-feed ratio, initial age, Gompertz parameters for protein and lipid deposition, temperature	Body weight, body composition, heat and methane production, water excretion, manure production	Describe and evaluate a mathematical model of nutrient partitioning and predict manure excretion and composition on a daily basis

2. Types of models

Mathematical models can be either static or dynamic, deterministic or stochastic, and empirical or mechanistic. For an extensive classification of model types, the reader is referred to France and Thornley (2007). Briefly, a static model does not explicitly include a time element (changes over time) and, therefore, describes the state of a system, rather than describing the change of a system over time. The first nutritional models were static, predicting nutrient requirements of farm animals at a given state (e.g. FAO, 1957; Blaxter, 1962; ARC, 1967). By nature, growth models are dynamic. Deterministic models provide predictions that describe the response over time of an individual animal or the mean of the population. In contrast, stochastic models include random elements so that for a given set of inputs, different outcomes can be obtained. Stochastic models can predict not only the mean but also the variance of model outcomes. Empirical models describe the relationships without an explicit representation of causality, while mechanistic models include some of the underlying biological mechanisms. As such, mechanistic models are usually more complicated but can provide sensible predictions over a wider range of conditions and provide biological explanations for the predicted response. The distinction between empirical and mechanistic models is somewhat arbitrary because mechanistic models contain empirical elements, but at a lower level of aggregation. Mechanistic models are generally aimed more at the understanding of a system.

3. Modelling the feed-use mechanisms

3.1. Modelling voluntary feed intake

Short-term regulation of feed intake

Feed intake is regulated by central nervous- and neuro-hormonal systems but also by cognitive-hedonic factors. Initiation of a meal is the response to hunger, while termination of a meal is the response to satiation. Modelling feed intake patterns within the day in domestic animals has been limited mainly to the fitting of mathematical equations to measured patterns of feed intake (e.g. Tolkamp *et al.*, 2011). This allows defining feeding bouts or meals, and enables the analysis of the duration and frequency of feed intake. These traits can be connected to satiating mechanisms (e.g. da Silva *et al.*, 2013), but linking the short-term regulation of feed intake to the long-term regulation, requires a thorough conceptual homeostatic and homeorhetic modelling framework (Sauvant, 1994). In a feed intake and growth model for pigs, Boumans *et al.* (2015) hypothesized that feeding patterns emerge from metabolic processes and motivational cues (Figure 2). In a “motivational decision-making” module, the pig assesses four motivation states: feeding, resting, drinking, and exploring. The chosen behaviour affects the energy use and feed intake, which subsequently change the nutrient balance and growth, represented in a separate growth module. The feedback between the two modules ensures that the outcome of the growth module is used as an input for the feed intake module.

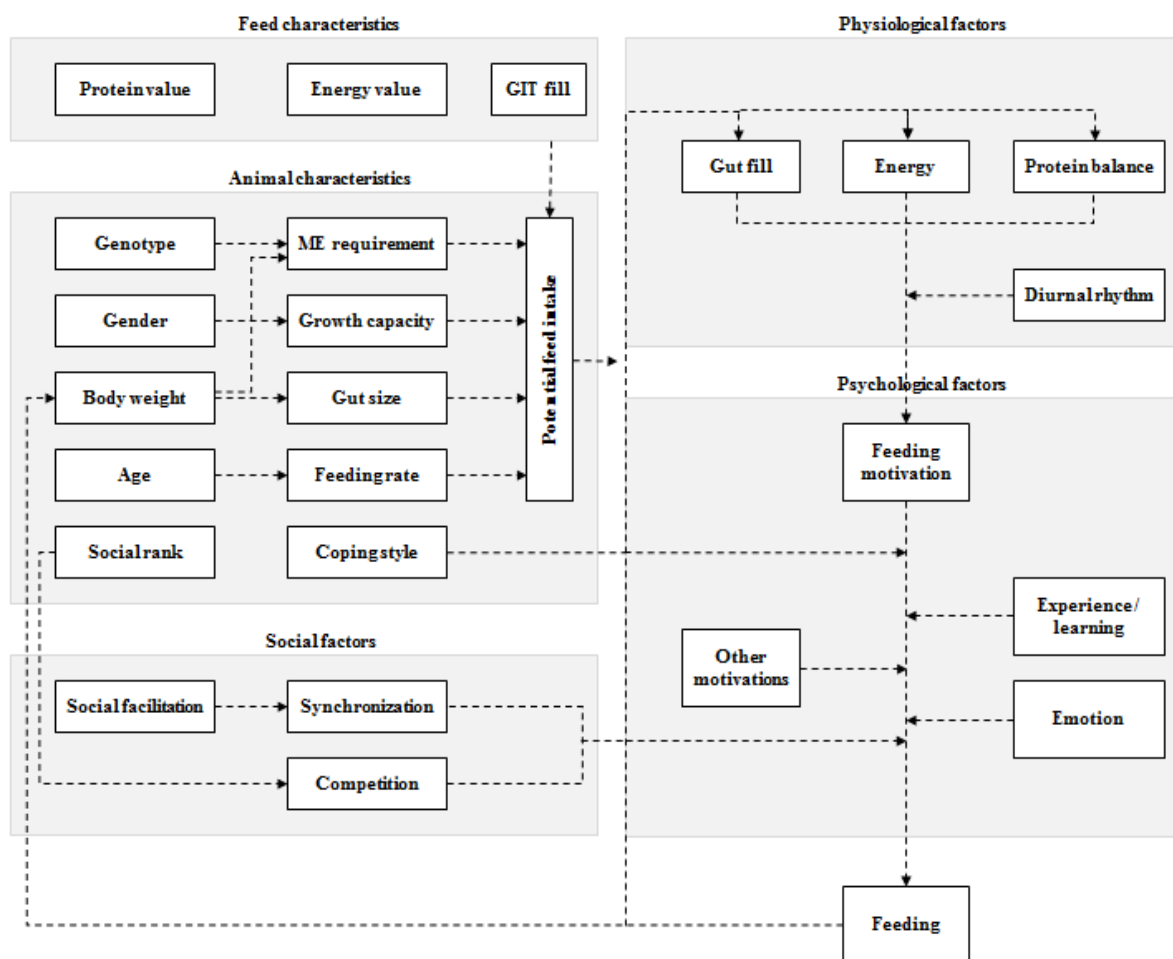


Figure 2
Schematic overview of feeding behaviour in a model: the formation of feeding motivation and factors affecting meal decision-making of animals (Boumans *et al.*, 2015)

Long-term regulation of feed intake

The long-term regulation of feed intake is complex but, at the same time, energy intake is normally well regulated in relation to energy expenditure (see chapter 9). However, variation in feed intake is one of the main sources of variation in animal performance. The question as to whether “animals grow because they eat” or “animals eat because they have a desire to grow” has been an issue of discussion among modellers. In many nutritional growth models, feed intake is a model input driving nutrient partitioning. In these “push” models, feed intake is defined by the user or calculated based on the (metabolic) body weight or rate of body weight gain (Table 2). As shown later, if there is no specific control in the model over feed intake, the push approach may lead to erroneous predictions of body composition, especially of body fatness. Feed intake regulation has been considered on an as-fed or on an energy basis. The choice of the type of regulation has an impact on how feed intake (and thus nutrient supply) responds to differences in diet composition. For example, consider two diets with either a high fibre (low energy) or a high fat (high energy) content. Using a feed intake equation on an as-fed or dry matter basis results in a very different nutrient supply compared with equations based on metabolisable (ME) or net energy (NE). Other factors that may affect feed or energy intake include ambient temperature, body composition or composition of body

weight gain (i.e. protein and lipid), and water holding capacity or bulk density of the feed (see e.g. Nyachoti *et al.*, 2004). Also factors such as palatability of the feed, social environment, and animal health are known to affect voluntary feed intake, but the quantification of these factors is difficult and these factors have not been considered in any of the equations listed in Table 2.

Table 2

Prediction equations for daily energy and feed consumption in pigs and poultry

Reference	Species	Driving force	Equation	Unit
NRC, 1987	Pig	BW	$DEI = 575 BW^{0.675}$	Kcal/d
			$DEI = 13.162 (1 - e^{-0.0176BW})$	Kcal/d
Close, 1996	Pig	BW	$DEI = 3.44 BW^{0.54}$	MJ/d
NRC, 1998	Pig	BW	$DEI = 1250 + 188 BW - 1.4 BW^2 + 0.0044 BW^3$	Kcal/d
van Milgen <i>et al.</i> , 2008	Pig	BW	$NE \text{ intake} = (a (b BW \exp(-b BW)) + 1) 0.75 BW^{0.60}$	MJ/d
Quiniou <i>et al.</i> , 2000	Pig	BW and T	$FI = -1264 + 73.6 BW - 0.26 BW^2 + 117 T - 2.4 T^2 - 0.95 T BW$	g/d
Nienaber <i>et al.</i> , 1987	Pig	BW and T	$FI = 0.11 + 0.31 \times 10^{-3}T - 0.53 \times 10^{-4}T^2 - 0.95 BW \times T$	g/kg ^{0.75} /d
Kyriazakis and Emmans, 1999	Pig	Body composition	$DEI = 0.44 W^{0.75} + 52 dP / dt + 53 dL / dt$	MJ/d
			$dF/dt = (1/FEC)(MH + k_1 dP / dt + k_2 dL / dt)$	g/d
Ferguson, 2006	Pig	Body composition	$cFI = (-26.78 + 173.34 Pt - 2.3316 Pt^2) / BD$ where $BD = 0.36 + (0.857 + form) IOM$	g/d
Sakomura, 2004	Broiler	Production and T	$ME = BW^{0.75} (307.87 - 15.63T + 0.31T^2) + a WG$	kcal/d
			$ME = BW^{0.75} (307.87 - 15.63T + 0.3105T^2) + 3.52 FG + 12.59 PG$	kcal/d
Sakomura, 2004	Layer	Production and T	$ME = BW^{0.75} (165.74 - 2.37 T) + 6.68 WG + 2.40 EM$	kcal/d
Black <i>et al.</i> , 1986	Pig	BW	$F_{phys} = 0.111 BW^{0.803}$	g/d
Kyriazakis and Whittemore, 2006	Pig	BW	$F_{phys} = 0.013 BW / (1 - dig)$	g/d
Kyriazakis and Emmans, 1995	Pig	Dietary WHC	$SFI = 1.74 + 167.7 / WHC$	g/kg/d
			$SFI = 174.1 / WHC$	
			$SDMI = 153 / WHC$	
Ndou <i>et al.</i> , 2013	Pig	Dietary NDF	$SFI = 82.0 - 0.18 NDF + 0.0002 NDF^2$	g/kg/d
		Dietary crude fiber	$SFI = 63.4 - 0.16 CF + 0.0003 CF^2$	
		Dietary WHC	$SFI = 77.3 - 7.43 WHC$	

DEI = DE intake, BW = body weight (kg), T = ambient temperature ($^{\circ}\text{C}$), dF / dt = feed intake per unit time, dP/dt and dL/dt = estimation of potential rate of protein and lipid accretion, respectively; FEC = energy content of the feed (kJ/kg), MH = maintenance heat production (kJ/d), k_1 and k_2 = energy constants; a = a factor depending on sex and age (female from 1 to 3 wks a=3.98; 4 to 6 wks a=3.93; 7 to 8 wks a=4.07 male from 1 to 3 wks a = 3.72; 4 to 6 wks a = 4.21; 7 to 8 wks a = 4.51); WG = daily weight gain (g/d); FG = fat weight gain (g/d); and PG = protein weight gain (g/d); EM = egg mass (g/d); F_{phys} = physiological feed intake capacity (kg/d); dig = digestibility of the feed; SFI = scaled feed intake (g/BW kg); WHC = water holding capacity of the feed (g/g); SDMI = scaled dry matter intake (g/kg BW); cFI = feed intake capacity (g/d); Pt = protein weight (kg); BD = bulk density of the feed; form is the form of the feed: for pellets form = 0, for crumbles form = 0.01, for mash form = 0.02; IOM = indigested organic matter; DM = dry matter.

In the “pull approach”, the animal eats to obtain the nutrients and, or energy it requires. In some pig and in most poultry models, animals are assumed to eat to meet their energy requirement for maintenance and a target rate of protein and fat deposition (Tess *et al.*, 1983; Black *et al.*, 1986; Kyriazakis and Emmans, 1999; Sakomura, 2004; Gous, 2014). When pigs and broilers are given a choice of different quality feeds, the animals are able to select a diet for which they do not deposit excessive amounts of fat, illustrating the capacity of animals to maintain a desired body fatness (Gous *et al.*, 1990; Kyriazakis and Emmans, 1991). Even in a pull approach, feed intake may not be determined only by the nutrient or energy requirement (Pomar *et al.*, 1991a). For example, gut capacity may restrict feed intake, especially in young animals and for diets with a low energy density (Table 2). Gut capacity has been described by an allometric function of empty body weight (Black *et al.*, 1986; NRC, 2012), and the water holding capacity of the feed has also been used as a potentially limiting factor for feed intake (Table 2). The water holding capacity depends mainly on the dietary fibre content and fibre type. Especially soluble dietary fibres increase the water holding capacity of the diet and thus reduce the actual feed intake of pigs, however, there is little information on the effect of the water holding capacity on feed intake in poultry (Gous, 2014).

In pigs and poultry, voluntary feed intake increases for diets moderately low in protein content (Cheng *et al.*, 1997; Ferguson and Gous, 1997). In contrast, deficiencies in certain amino acids such as the branched-chain amino acids (i.e. Leu, Ile, and Val) and Trp have been shown to reduce feed intake (Black *et al.*, 2009; Gloaguen *et al.*, 2011; Soumeh *et al.*, 2014; 2015a; b). These amino acids share the same transporter in the brain. Not only the level but also the ratio of these amino acids can have an impact on feed intake. Including mechanisms representing such effects can be considered a challenge for future models for monogastric animals. The pull approach combined with other potentially limiting factors is used in the broiler model of Emmans (1987) and the pig model of Ferguson (2006). The “desired feed intake” is driven by the growth potential of the animal but the desired intake may not be attained if, for example, a specific nutrient, gut capacity, or physical or social environment conditions limits the actual feed intake. Once the limitation is overcome, the model animal attempts to regain its desired feed intake (compensatory growth).

3.2. Modelling digestion kinetics

Traditionally, emphasis in research related to nutrient digestion in growing livestock species has focussed on determining the extent of digestion, typically at the end of the digestive tract or at the end of the ileum. This focus has been highly valuable, as the total yield, rather than release kinetics of monomeric compounds absorbed, determines the value of feed ingredients. Decreasing the rate of protein digestion, for example, does not affect the quantity of amino acids absorbed as long as the protein is digested to its full potential prior to the terminal ileum.

To date, world-wide, diets for livestock species have been formulated based on feeding table values (e.g. CVB, 2016; NRC, 2012; Sauvante *et al.*, 2004). In these tables, feeding values (nutrients) are assigned to single feed ingredients, and coupled to nutrient requirements using least-cost optimization techniques. Extensive tables with best estimates of the extent of ileal or faecal digestion of nutrients for many feed ingredients are the basis for such feed evaluation systems. These have served their purpose well, as most of the variation in feeding value among feed ingredients originates from digestibility.

For many reasons, attention is now shifting towards the measurement of digestion kinetics of macronutrients. For starch, a main macronutrient in diets for growing livestock, it has long been recognized that digestion kinetics can influence postprandial glucose and insulin profiles, influence meal patterns, postprandial lipogenesis, and fermentation. For proteins, digestion kinetics are clearly very different among sources (e.g. fast whey versus slow casein

digestion). Apart from effects on nutrient synchrony, e.g. (a)synchronous absorption of amino acids and glucose (van den Borne *et al.*, 2007), the impact of variation in protein digestion kinetics are less well researched. There are reasons to believe (though the conjecture remains unproven) that colonic fermentation of proteins that escape small intestinal digestion can have deleterious effects on gut health (Heo *et al.*, 2015), and understanding digestion kinetics is vital for the prediction of “escape proteins” that are fermented further down the intestinal tract. For dietary fibres, the effects of digestion kinetics have long been recognized as, microbial degradation kinetics relate well to the extent of degradation. For both soluble and insoluble fibres, degradation kinetics directly affect the changes in rheological properties when digesta moves along the intestinal tract. It is believed that in many species, fibrous components have a regulatory role on the kinetics of digesta passage. The impact of variation in digestion kinetics is at the level of interactions among nutrients and between nutrition and health rather than on the extent of nutrient digestion *per se*.

Models of digestion

In early models of nutrient digestion, the focus was mainly on describing the flow of dry matter and liquid through the stomach and small and large intestine (e.g. Usry *et al.*, 1991), but also on predicting the absorption of food dry matter. Later models have focused on improving the representation of digesta transport (Rivest *et al.*, 2000; Taghipoor *et al.*, 2012) or on a more complete representation of hydrolysis and the absorption of nutrients (Bastianelli *et al.*, 1996; Strathe *et al.*, 2008). Representation of the physico-chemical environment inside anatomical compartments of the gastro-intestinal tract is included to a variable extent in a limited number of models (Le Feunteun *et al.*, 2014; Taghipoor *et al.*, 2012; Taghipoor *et al.*, 2014).

Digesta transport

Most digestion models consider digesta transport between anatomical compartments as a function of digesta mass or volume (Bastianelli *et al.*, 1996; Belward *et al.*, 2013; Strathe *et al.*, 2008). Based on approaches commonly used in ruminants, these models use fixed fractional outflow rates, based on determined mean retention times in experiments. While connecting well to experimentally derived values, the obvious disadvantage of this approach is that its description is not based on the biology of digesta transport. For example, immediately upon ingestion, nutrients are predicted to appear in the small intestine. This problem can be alleviated by the introduction of a delay function (Belward *et al.*, 2013), or by regarding the stomach as comprising two compartments (Le Feunteun *et al.*, 2014).

The model by Usry *et al.* (1991) focuses on transport of digesta through the gastro-intestinal tract of the pig, representing stomach emptying by first-order kinetics and, making the fractional outflow rates dependent on time after a meal (~40-50%/h for the first hour after the meal and ~10%/h for the remaining part of the day). Digesta transport through the small intestine is modelled by dividing the length of the small intestine into 6 cm sections and assuming a fixed transport rate during a contraction of 2 cm/s in the first half, and 1 cm/s for the second half of the small intestine. In time cycles of 3 s in the first half and 6 s in the second half, each section is subjected to a chance of a contraction occurring, modelled by a third-order Markov type model, assuming that the probability of a contraction taking place decreases depending on contractions occurring in the three previous time cycles. In the model of Rivest *et al.* (2000), stomach emptying is modelled assuming a fixed fractional outflow rate. Subsequently, the 18-m small intestine of pigs is split into 50 segments of variable lengths, but with equal retention times, allowing a near continuous flow of digesta throughout the small intestine. The speed of digesta in m/min decreases with an increasing distance from the stomach (m), obtaining a total retention time of around 250 min. In the approach taken by

Taghipoor *et al.* (2012), a bolus of digesta is followed throughout the 18 m porcine digestive tract. The bolus, treated as a homogenous cylinder of fixed length but variable radius, moves through the intestinal tract by peristaltic waves of 7.2 m/h following so called spikes that occur once every 10 s. The efficiency of peristaltic waves increases with the size of the bolus, but decreases with an increasing distance from the pylorus. Subsequently, friction effects on the bolus are modelled to represent effects of digesta viscosity, and lubrication effects by varying the water content of the bolus. In a further refinement of this model, Taghipoor and colleagues (Taghipoor *et al.*, 2014) included the effects of the physico-chemical environment on the transport of the bolus and on degradation rates, by modelling the effect of soluble and insoluble dietary fibres on water holding capacity, dry matter content and viscosity of the bolus.

The colon is explicitly represented as a single anatomical compartment in some pig digestion models (Bastianelli *et al.*, 1996; Strathe *et al.*, 2008) assuming fixed fractional outflow rates. Applying a bioreactor approach, Muñoz-Tamayo *et al.* (2010) modelled carbohydrate fermentation in the colon, distinguishing three anatomical compartments (proximal, transverse, and distal colon). Within each compartment, a mucus layer and a lumen is represented, with digesta transfer between luminal compartments modelled using mass-action equations. To prevent wash-out of microbiota species responsible for degrading the substrate, the residence time of micro-organisms is higher than that of digesta.

Hydrolysis and absorption

Apart from transit, nutrients disappear from intestinal pools following hydrolysis and absorption. In the model of Usry *et al.* (1991), this is represented in its simplest possible form (i.e. feed-dependent fractional disappearance rates for each small intestinal segment) disregarding differences among nutrients. In the models of Bastianelli *et al.* (1996) and Strathe *et al.* (2008), various nutrients are represented in the anatomical compartments, applying either first- or higher-order kinetics, or using a saturable enzyme kinetics approach, allowing the incorporation of various affinity constants as well as substrate concentrations, or inhibition by end products. This allows the modelling of interactions between fibre and protein digestion by for example changing the affinity constants of proteases in the presence of fibre. In the approach taken by Taghipoor *et al.* (2012; 2014), hydrolysis of macronutrients within a digesta bolus occurs in two steps; firstly, the enzymatic degradation of substrates in the bolus, and secondly further degradation at the surface of the bolus by brush border enzymes, which is strongly dependent on solubilisation of the nutrients. In both steps, hydrolysis is driven by substrate concentration, following a mass-action law. By including the effect of soluble and insoluble fibres on hydration properties and viscosity of the digesta bolus, effects of dietary fibres on nutrient hydrolysis are modelled (Taghipoor *et al.*, 2014).

3.3. Simple models of nutrient partitioning

One of the first nutritional model for growing pigs was developed by Whittemore and Fawcett (1974). The purpose of this model was to “*represent a simple mathematical expression which enables the calculation of the direction and the magnitude of the responses of growing pigs to feed inputs*”. The model was based on the accumulation of body protein and body lipid. Body weight gain is calculated directly from protein deposition (PD) and lipid deposition (LD) and, through its association with body water, PD is assumed to contribute four times more to body weight gain than LD. The PD is assumed constant between 20 and 100 kg BW (in case of a sufficient protein supply) or determined by the dietary protein intake and the gross efficiency of protein utilization. The latter was described by an exponentially declining function of BW so that for a given BW, young pigs use a limited protein supply more efficiently than finishing pigs. The maintenance energy requirement was assumed to be a function of metabolic body

weight, while lipid deposition was the result of energy intake not used for protein deposition or for maintenance. Whittemore and Fawcett (1976) further refined this model by reconsidering the representation of PD, protein quality, and the energy costs of metabolic processes. The modellers acknowledged that energy could be diverted from growth to thermogenesis at low ambient temperatures. The available protein supply, calculated from the digestible protein supply and the biological value of the protein, was partitioned into endogenous protein maintenance losses, PD, and excess protein. The inclusion of the biological value of protein in the model is a means to account for differences in protein quality and amino acid composition. The concept of a gross efficiency of protein utilization used by Whittemore and Fawcett (1974) was replaced by explicitly representing protein turnover. The ratio between PD and protein synthesis was described by a logistic function resulting in PD becoming zero when the animal approaches maturity. Whittemore and Fawcett (1976) also assumed that there was an upper limit to PD (referred to as PDmax), which was assumed to be constant between 20 and 120 kg BW. Another change compared with the initial model of Whittemore and Fawcett (1974) was the assumption of the existence of a minimum ratio between LD and PD. This, combined with the existence of an upper limit to PD, implied that the relationship between PD and energy intake would be described by a so-called linear-plateau model (Figure 3). The predicted PD is, therefore, determined by the supply of available protein, the minimum LD:PD ratio, and PDmax.

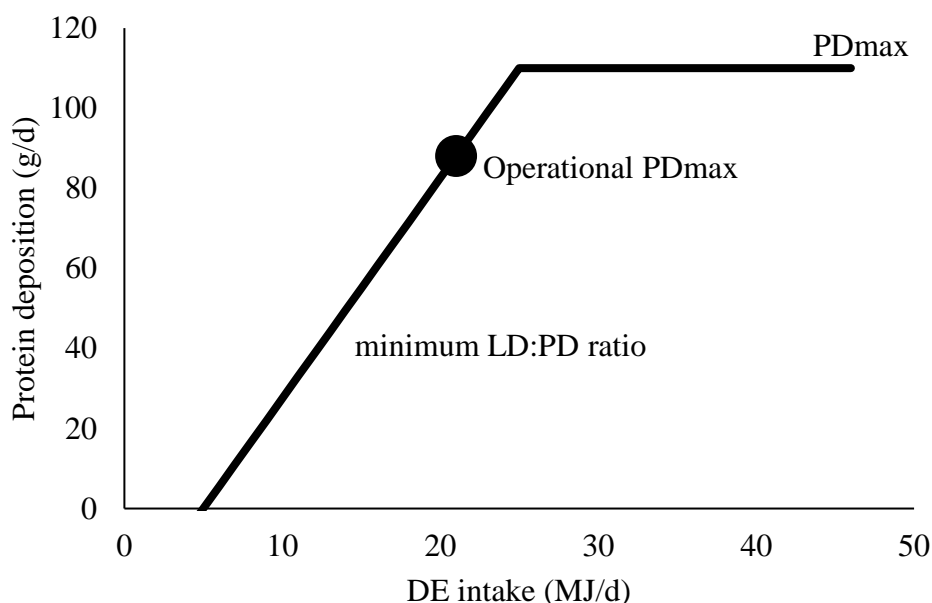


Figure 3
Linear-plateau relationship between protein deposition and DE intake (as used by Whittemore and Fawcett, 1976)

The research group at Massey University in New Zealand further expanded on the concepts developed by Whittemore and Fawcett (1974) and introduced “an operational PDmax”, a practical, on-farm limit to protein deposition, lower than the biological maximum recorded in breeding centres. Moughan (1995) indicated that it may be difficult to determine PDmax (the plateau representing the upper limit to PD), because in practice pigs may not have the feed intake capacity (particularly for lean genotypes), health or environment status to attain PDmax. The operational PDmax can be lower than PDmax and can be influenced by factors such as management and sub-clinical disease (Moughan, 1995). Rather than using faecal

digestible crude protein (Whittemore and Fawcett, 1974, 1976), Moughan (1984) and Moughan and Smith (1984) used the supply of ileal digestible amino acids as model inputs. They also refined the representation of amino acid utilization by using an empirically-derived ideal amino acid balance and used linear programming, allowing transamination of essential to non-essential amino acids, to calculate available balanced protein. Moughan (1984) acknowledged that the representation of PD as the difference between protein synthesis and degradation used by Whittemore and Fawcett (1976) was biologically more appropriate, but underlined the difficulty in obtaining relevant and accurate information to quantify these processes. Consequently, he preferred a constant value for PD_{max}, which could vary with sex or phenotype. However, the efficiency of protein turnover was represented implicitly. The model assumed In the model, it was assumed that the limiting essential amino acid or protein cannot be used with a post-absorptive efficiency greater than 85%, such as in the model of de Lange (1995; see later). Moughan (1995) refers to the complement of this as “inevitable amino acid catabolism”, meaning that at least 15% of the absorbed amount of an amino acid would be catabolized, even if the supply of the amino acid was a limiting factor for PD. There is surprisingly little information in the literature about the magnitude of inevitable amino acid catabolism and values for amino acids seem to range from almost 0 to 40% (Moughan, 1995). Moughan and Smith (1984) also assumed that the maintenance energy expenditure was a function of BW but in a later version of the model, this was made a function of the whole body protein mass (Moughan *et al.*, 1987). The partitioning of energy between LD and PD was assumed to be a function of a minimum ratio between lipid mass and protein mass in the body (Moughan *et al.*, 1987), rather than a minimum LD:PD ratio, thus allowing the use of lipid reserves for energy supply.

To facilitate the understanding and use of models in practical situations, de Lange (1995) developed a simple “reference” model, based largely on the concepts of the New Zealand model. In two companion book chapters, the reference model was challenged to indicate areas for further development, such as factors affecting feed intake and energy utilization (Black, 1995) and protein and amino acid utilization (Moughan, 1995). The reference model of de Lange (1995) also uses a linear-plateau relationship to describe the relationship between PD and energy intake. The slope of this relation is determined by the LD:PD ratio, which was assumed to be constant. However, experimental data suggest that the slope depends on BW, with a higher slope for younger pigs (Figure 4; Black *et al.*, 1986; de Lange, 1995). The reference model assumes that both PD and LD are zero when energy retention is zero (i.e. at the maintenance energy intake). This does not agree with observations that pigs can sustain PD while mobilizing lipid at very low feed intake levels (Black, 1995). However, although such a situation can occur for a short period of time, it appears to be incompatible with the concept of maintenance (van Milgen and Noblet, 1999; van Milgen *et al.*, 2000).

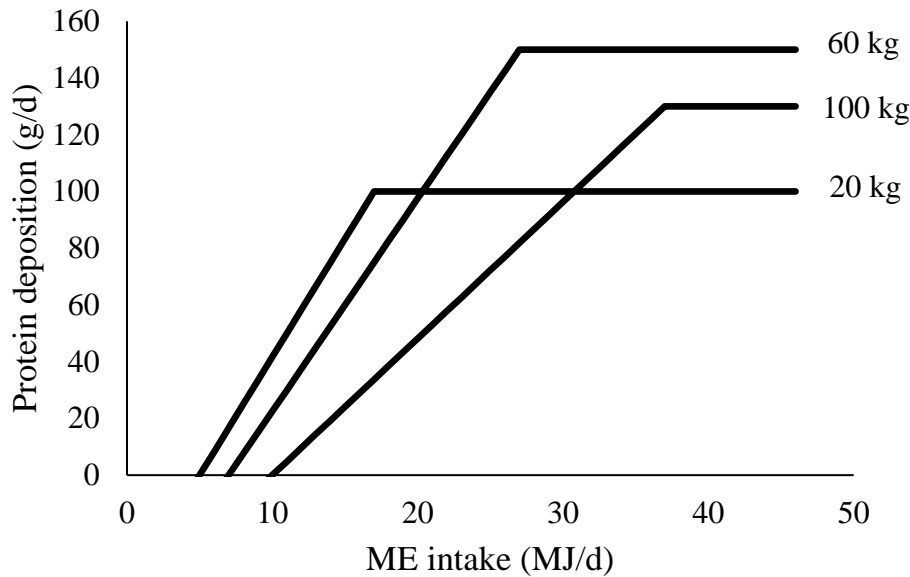


Figure 4

The effect of body weight on the relationship between protein deposition and energy intake (Black *et al.*, 1986)

The models developed by Whittemore and Fawcett, and Moughan, and de Lange are all “push” models, where feed intake is an input driving nutrient partitioning. Because PD is modelled as an independent phenomenon, all energy not used for PD or for maintenance will accumulate in body lipids. Consequently, LD is an “energy sink”. The representation of lipid as an energy sink has important consequences because it means that there is no direct control of LD and inaccuracies in feed intake, and in model concepts and parameters, will accumulate as an error in predicted lipid. The CSIRO group in Australia led by John Black reversed the concept of push and pull. Rather than feed intake driving downstream phenomena related to BW gain, Black *et al.* (1986) explicitly represented the potential PD and energy retention (i.e. energy retained as protein and lipid), resulting in the desire of the pig to grow “pulling” feed intake. Feed intake, therefore, becomes a model outcome. Using a pull approach is conceptually appealing, but it may be difficult to model parameters that describe the observed phenotypic variation. As indicated above, the “desire to eat” does not necessarily mean that animals can eat as they desire. Actual feed intake in the model of Black *et al.* (1986) was determined by the desire to eat, and also by the environmental temperature and gut capacity. In the model of Black *et al.* (1986), similar functions were used to describe potential PD and energy retention:

$$dX/dt = k BW^a ((X_m - X) / X_m),$$

where dX/dt is the potential PD or energy retention, BW is the body weight, X_m is the protein or energy content at maturity, while k and a are parameters specific for each phenotype. This equation resembles the logistic function with an additional term (BW^a). With the logistic function, PD and energy retention tend to approach zero when the animal approaches maturity. Black *et al.* (1986) assumed that the maintenance energy requirement is not only a function of protein mass (like in the model of Moughan *et al.*, 1987), but also of the growth rate. The model also included a mechanistic representation of heat exchange between the animal and its environment.

The InraPorc model (van Milgen *et al.*, 2008) also uses a push approach for feed or energy intake. This, in combination with an explicit description of PD, makes LD an energy sink. As indicated earlier, this approach may be prone to error, because without an explicit control of energy intake, errors accumulate in predicted LD. Through its association with body water, errors in body protein can be verified (more or less easily and accurately) by measuring BW. However, errors in body lipid are more difficult to detect. Although backfat thickness is frequently used as an indicator for lipid mass, lipids in backfat represent only approximately 18% of total body lipids (Kloareg *et al.*, 2006). Because of the potential difficulty of an “uncontrolled” LD (and without reliable ways to verify it), the InraPorc model includes a feed intake equation with specific control over energy intake. A Gamma function was proposed in which the *ad libitum* feed intake is expressed relative to the maintenance energy requirement. During growth, pigs eat above maintenance, but, as they mature, *ad libitum* feed intake will approach the maintenance energy requirement and the animal will thus stop growing. The phenotypic potential to deposit protein (or operational PD_{max} in the terminology of Moughan, 1995) is described by a Gompertz function. The maximum efficiency of amino acid utilization for all essential amino acids was determined from the ideal amino acid profile and the efficiency of lysine utilisation (72%). Another change in the InraPorc model relative to the approach of Whittemore and Fawcett (1976) is the use of a curvilinear-plateau relationship between energy intake (expressed as multiples of the maintenance energy requirement) and PD. It is assumed that pigs can eat to attain PD_{max} at 70 kg of BW, but this value can be changed by the model user.

The model developed by Birkett and de Lange (2001) and the NRC (2012) model also use a push approach based on concepts proposed earlier. Feed intake and operational PD_{max} are described by empirical equations based on BW. Birkett and de Lange (2001) used nutrient partitioning rules based around Moughan *et al.* (1987), however, they considered the stoichiometry of nutrient transactions, and represented the energy yielding and consuming processes on the basis of ATP. The NRC (2012) model takes into account that different management and housing conditions (e.g. ambient temperature, stocking density, ractopamine feeding, immunocastration) can change feed intake and, or PD. The issue of the maximum efficiency of amino acid utilization has been developed further in this model. Based on experimental data, the maximum efficiency of amino acid utilization is assumed to decline with increasing BW (e.g. for lysine, the efficiency declined from 68% at 20 kg BW to 57% at 120 kg BW).

The nutrient partitioning models described above are all based on concepts proposed more than 40 years ago. As such, they are variations on a theme that have been challenged and for which improvements have been suggested (e.g. de Greef and Verstegen, 1993; Emmans and Kyriazakis, 1997; Moughan, 1989). However, “*the calculation of the direction and the magnitude of the responses of growing pigs to feed inputs*” (Whittemore and Fawcett, 1974) requires that published models be transformed into software tools. The more simple models such as the reference model of de Lange (1995) can easily be programmed in a spreadsheet. For the more complex models, dedicated software tools have been developed such as Auspig (Black *et al.*, 1986), the Dutch TMV model (Werkgroep TMV, 1991), InraPorc (van Milgen *et al.*, 2008), and the NRC (2012) model. The early dynamic pig growth model of Moughan *et al.* (1987) which included a stochastic element, formed the basis of the Workgroup TMV Model (Werkgroep TMV, 1991) and an interactive software interface (ModPig, later called Leantec™). Further model development by the International Modelling Group led by Dr Kees de Lange of the University of Guelph, led to the OptiPork™ version of this model. An important challenge in the development of these tools is model simplification, so that a maximum of variation can be accounted for by a minimum number of inputs to be provided in an understandable way by the user.

3.4. More mechanistic approaches towards modelling nutrient partitioning

The above-mentioned models are based on relatively simple nutritional concepts of energy and amino acid partitioning. A different approach and model structure was suggested by Schulz (1978) who proposed a biochemical basis for nutrient partitioning and metabolism in monogastric animals, replacing the concepts of protein and energy by an explicit representation of intermediary metabolism. This approach has been adopted to develop models for young sheep (Gill *et al.*, 1984), beef cattle (France *et al.*, 1987) and lactating cows (Baldwin and Gill, 1987). For monogastric animals, this approach was first used by Pettigrew *et al.* (1992) for the performance of reproductive sows, and later by Gerrits *et al.* (1997) for pre-ruminant calves and Halas *et al.* (2004) for growing pigs and Coles *et al.* (2013) for humans. These models are “push models” using feed intake as a model input driving metabolism.

The rate:state formalism used in these models assumes that the rate of change of a state variable (or pools) is expressed as a function of a state variable. For example, the rate of glucose utilisation would be described as a function of the glucose concentration, resulting in a differential equation for each state variable (i.e. $dX/dt = f(X)$, where X is the state variable such as the glucose concentration). When there are several interacting state variables, an analytical solution of the system of differential equations may not exist and the differential equations have to be solved numerically. Models based on the rate:state formalism use pools of intermediary metabolites and body storage pools. The partitioning of nutrients between different pathways is usually expressed by assuming first-order or saturable enzyme kinetics. In this way, priorities for nutrient partitioning are set by the relative values of maximum velocity parameters and affinity or inhibition constants. Because not all biochemical pathways can be represented, simplifications are needed focussing on the most relevant nutrient pathways, referred to as “pivots” by van Milgen (2002). The equations determining nutrient fluxes (i.e. rates) are based on the assumption that i) certain transactions can be aggregated (e.g. protein synthesis from amino acids, *de novo* fatty acid synthesis from acetyl-CoA), ii) mass action kinetics follow an average standard stoichiometry, and iii) separate but closely related metabolites might be represented by common pathways (e.g. using ATP or acetyl-CoA as an “energy currency”) thus simplifying the biology without compromising the reliability of model predictions.

A disadvantage of models using enzyme kinetics is that there are more parameters than in simple nutrient partitioning models and it is difficult to obtain relevant data for these parameters. Moreover, these parameters have to be estimated indirectly because several metabolic reactions are often aggregated in a single reaction. An advantage of the approach is the flexibility of the model since the rates of nutrient transactions are regulated by the requirement and availability of metabolites. In addition, the time-scale can be changed from days (as in nutrient partitioning models) to within-day kinetics of nutrient metabolism, thereby providing a more in-depth representation of the biology of nutrient utilization without changing the conceptual approach.

Danfaer (1991) proposed a mechanistic rate:state model of nutrient utilization, which was able to predict a sigmoidal growth curve for growing pigs without an explicit empirical term for mature size of the animal. Protein metabolism and protein turnover were represented as protein synthesis from free amino acids and degradation of body protein to free amino acids. It was assumed that the fractional rates of protein synthesis and degradation decrease exponentially with age and with protein pool size. The model is parameterized in a way that ensures identical rates of daily protein synthesis and degradation at mature weight. The dynamics of body fat are represented in a similar way. Nutrient oxidation is regulated by the

energy requirement, resulting in a higher priority for maintenance compared to using nutrients for growth.

Lovatto and Sauvant (2003) have further refined the regulatory mechanisms of nutrient metabolism by explicitly representing homeostatic and homeorhetic control mechanisms. The homeostatic regulation (tactical purpose) acts as a dynamic buffer between the inflow of nutrients and the demand for nutrients driven by the homeorhetic control (strategic purpose). Nutrient utilization is described by a combination of anabolism and catabolism. In case of a large nutrient supply, anabolism increases more than catabolism whereas in the case of a nutrient undersupply anabolism will likely decrease relative to the reference situation. The homeorhetic control defined the difference between anabolism and catabolism for the reference situation. For a growing animal in the reference situation, anabolism is greater than catabolism but the difference becomes smaller as animals grow towards maturity.

In biochemical models of growth such as the model of Lovatto and Sauvant (2003), nutrients are present in different body compartments or pools, which can be represented as transition pools (such as plasma lysine, glucose, and fatty acids) or as storage pools (such as body protein and body lipid). The size of the transition pools must be kept within reasonable limits to maintain homeostasis, while the storage pools increase in size reflecting body weight gain.

Prediction of anatomical body composition

Whole body protein and lipid mass provide limited direct information on carcass quality. The distribution of body protein and lipid among tissues (e.g. muscle and fat) and the prediction of weight and composition of different body parts is, of course, of practical interest. Therefore, some growth models not only estimate the chemical body components but also their allocation among tissues and organs. For example, the growing pig model developed by Halas *et al.* (2004) predicts muscle, bone, viscera, and hide mass, the latter including subcutaneous fat. The protein and fat deposition is simulated in these four compartments allowing the prediction of the chemical composition in different anatomical body parts (Figure 5). Muscle protein synthesis is driven by lysine and acetyl-CoA concentrations following saturable enzyme kinetics, and the maximum rate of protein synthesis depends on the potential of a genotype. Furthermore, muscle protein synthesis is assumed to drive the rates of protein synthesis in other compartments, while fixed fractional rates of protein degradation are assumed for each tissue. The energy cost of protein and fat turnover, substrate cycles, and transport transactions across membranes are considered explicitly. The partitioning of protein, lipid, water, and ash in muscle, organs, hide, and bone fractions is described by allometric equations, based on rates of muscle protein and body lipid deposition.

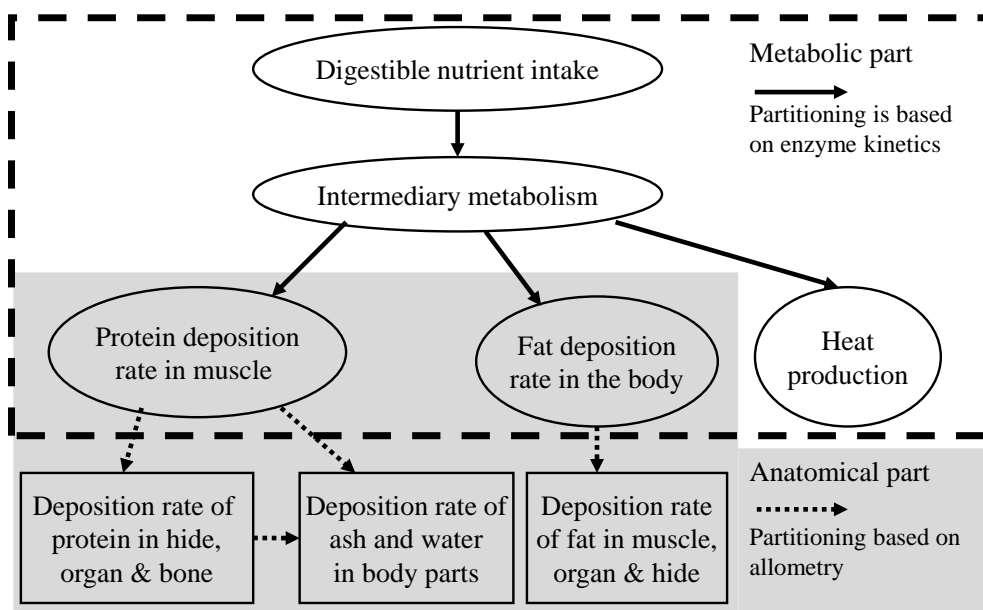


Figure 5
Schematic representation of the partitioning of dietary digestible nutrients in a pig model predicting body protein and fat distribution (Halas *et al.*, 2004)

Lizardo *et al.* (2002) developed a model in which dietary and *de novo* synthesized fatty acids were partitioned using an allometric approach among different tissues (intra- and inter-muscular fat, subcutaneous fat [and backfat], and perinephric fat). However, uncertainties about the fate of dietary fatty acids (i.e. between oxidation and deposition) and the allometric approach for the partitioning of fatty acids resulted in a somewhat unsatisfactory outcome. Kloareg *et al.* (2007) have proposed alternative approaches in which the partitioning of the *de novo* synthesized fatty acids and the uptake of dietary fatty acids by a tissue can be modelled either as a locally-driven or centralized phenomenon, allowing for a greater flexibility to explain differences in fatty acid composition among tissues.

Addressing mechanistic aspects of lipid and fatty acid metabolism has been a weak point in most nutritional models because lipid deposition is very well controlled. As illustrated in chapter 9, even in obese adults, the difference in daily energy intake and energy expenditure is very small, implying that lipid cannot be considered as a simple energy sink. This means that changes in energy intake should not automatically result in downstream changes in lipid deposition, because changes in energy intake can also affect energy expenditure, for example through uncoupling proteins that affect the efficiency of ATP synthesis (Busiello *et al.*, 2015).

Modelling nutrient partitioning within the day

Whereas all nutrient partitioning models described in this section simulate changes in the rate of protein or lipid deposition, the time scale used almost exclusively reflects changes over days and not changes within a day. One of the reasons to avoid smaller time steps is to avoid computational problems. In addition, most growth models assume a net anabolic state, and are not intended to represent mechanisms of mobilizing body reserves. This is a simplification of biological reality, because feed intake occurs as meals and there are, therefore, distinct periods where the nutrient supply largely exceeds the “average” net anabolic state and periods

where the animals are in a net catabolic state, particularly in the morning before feeding. To date, no animal growth models have been developed representing within-day variation in nutrient metabolism, and which aim to predict longer-term changes in body protein and lipid mass. For representing the impact of feed intake patterns or of meal feeding, representing within-day kinetics of nutrient metabolism, is essential. Not all approaches discussed in this chapter can be adapted to represent within-day kinetics in nutrient metabolism. For example, the classical nutrient partitioning models based on the concept of Whittmore and Fawcett (1974) are based on concepts that do not apply within the day and cannot be adapted. The more biochemical approaches can be adapted but they require structural modifications, and probably also functional modifications in parameter values. For example, the model of Lovatto and Sauvant (2003) uses a step size of 0.001 d (1.44 min), which may be too long to properly represent meal patterns. Structural modifications would require inclusion of pools of temporary nutrient storage such as glycogen to regulate post-prandial glucose metabolism (Taghipoor *et al.*, 2016). The glucose stored temporarily as glycogen could be used and, or released to produce ATP (e.g. in the muscle or liver) or be used for fatty acid synthesis (in the liver or adipose tissue). Likewise, mobilization of body lipid and body protein should be represented explicitly to allow the model to function in a catabolic state (i.e. just before the next meal). Functional changes may be required by adjusting model parameters because the metabolic load of, for example, a feed intake of 2 kg will be completely different if it is used as a continuous model input over 24 h or if it is consumed in 4 meals of 500 g each. In addition, the concept of a single dietary amino acid potentially limiting the rate of protein deposition originates from a simple approach of net anabolism. A more mechanistic and within-day approach of amino acid metabolism would require conceptual and thus structural model changes.

4. Application and prospects

4.1. Feed evaluation systems

Feed evaluation systems have been developed to express the value of a feed ingredient and the nutrient requirement of the animal on a common scale, thereby allowing formulation of diets for a desired rate of production. Classical energy systems, such as DE, ME, and NE systems, estimate the energy yielding potential of the feed in relation to the requirement of the animal and they are all based on the premise that energy values are additive. Because the energy value and the energy requirement have to be expressed on the same scale, choices have to be made if a trait is to be attributed to the feed or to the animal. For example, in an ME system, the efficiency of energy use is part of the requirement (typically expressed as the energy efficiency of protein and lipid deposition), whereas in an NE system, the energy efficiency is attributed to the feed. The same holds for protein and amino acid systems. If the value of an amino acid is expressed on an apparent ileal digestible basis, basal endogenous losses are part of the feed value, whereas on a standardized ileal digestible basis, it is part of the animal's requirement.

The development and use of energy and nutrient systems has been an enormous asset in putting science into practice. However, the fact that these systems have to be based on a compromise (between the value of a feed and the requirement of the animal) implies that it has been difficult to account for interactions. Numerous studies have shown that feeds are used with different efficiencies in different genotypes and if the animals are kept in different environments. For example, the INRA feed tables attribute different energy values to an ingredient depending on when it is used for growing pigs or for sows (Sauvant *et al.*, 2004). Static feed evaluation systems, therefore, provide a relative value for feed ingredients (and perhaps for the type of animal), which is easy to understand but is less appropriate to account for interactions.

By nature, modelling is a useful method to account for interactions between the animal, its feed, and the environment (Moughan, 1995), but also for interactions between feed ingredients in the gastro-intestinal tract. Therefore, mechanistic models of animal nutrition undoubtedly provide a more solid theoretical basis for feed evaluation. However, they still explain only a part of the variation in efficiency with which nutrients are used for different productive purposes (Van Milgen, 2006). Mechanistic models integrating the digestive and metabolic utilization of nutrients, phenotypic animal aspects, and environmental conditions can help us to understand and to quantify interactions. These dynamic feed evaluation models should take into account i) feed composition including physico-chemical properties, ii) age, physiological stage, and health status of the animal, and iii) environmental conditions. There are currently no complete dynamic feed evaluation models available, but some coordinated research efforts are engaged to progress this area, such as the Dutch Feed4Foodure program and the European Horizon 2020 Feed-a-Gene project. However, replacing classical feeding systems by a modelling approach for practical feed evaluation will take time. Classical systems are transparent and robust, have proven their value, and are an established reference basis in practical animal nutrition. A modelling approach needs to prove an important benefit over classical systems before major change can be anticipated.

4.2. Prediction of animal performance

A properly calibrated growth model predicts the performance of an individual animal or a group of animals (i.e. mean and variation) by simulating the changes in daily gain, feed conversion ratio, and the chemical composition of the body over time. These models can also predict derived traits such as backfat thickness and muscle thickness. Growth models can, therefore, be used effectively to identify an appropriate strategy for grower–finisher pig or broiler farms by evaluating different management and feeding strategies and comparing the predicted outcomes (de Lange and Schreurs, 1995). The optimal feeding strategy may depend on local market conditions (e.g. target live weight or carcass weight, carcass quality), farm rotation system, and feed and labour costs. Slaughterhouses commonly use payment grids and apply penalties for outlier pigs (i.e. for pigs that are too light or too heavy, low lean meat percentage) or rewards for premium quality carcasses (high lean meat percentage, better conformation). Although the relationship between carcass quality and price premiums or discounts by slaughterhouses is not always transparent, quality is an important issue in the search for an optimal delivery weight (Leen *et al.*, 2017). Based on input and output data and costs, economic analyses of alternative feeding strategies can be assessed, which are important in decision-making (Whittemore, 1987). An on-farm protocol for model application to derive economically-optimal diets for the growing pig has been described by Moughan *et al.* (1995) and de Lange *et al.* (2001) for pigs and for broilers by Gous (2001).

From a practical point of view, models for use in commercial animal production should be reasonably accurate and easy to use, relying on a few parameters from which easily measurable traits such as body weight and backfat thickness can be predicted (de Lange *et al.*, 2001). Many growth models contain a large number of parameters that may be difficult to provide by the model user. Therefore, software tools usually simplify model inputs to capture a large part of the variation (among animals resulting from different management strategies) in a limited number of user-modifiable model parameters. However, development of software tools is time consuming and involves identification of the most relevant and accessible inputs to run the model under a variety of conditions. Also, model outputs should allow the user to analyse and understand the responses predicted by the model (van Milgen and Dourmad, 2015).

4.3. Using dynamic models to determine nutrient requirements

As nutrient requirements change during growth, dynamic models may be used to predict responses of important traits (e.g. daily gain) to changes in nutrient supply. The advantages of using the response output of a dynamic model rather than static table values are obvious. As indicated by Morris (2006), the response of an animal to nutrient supply can be curvilinear and feeding the animals to the requirement may not be the optimum economical solution. Knowledge of how the animal responds to a limiting nutrient supply is, therefore, as important as knowledge of the requirement itself. Dynamic models can also account for phenotypic differences in growth rate over time, while nutrient recommendation tables contain only a limited number of genotypes defined by their growth rate or rate of lean gain for a certain body weight range (e.g. NRC, 1998; 2012). Performing simulations with InraPorc, van Milgen *et al.* (2008) demonstrated that two animals can have the same average daily feed intake and average daily gain between 30 and 115 kg body weight, but very different lysine requirements during growth as shown in Figure 6. The difference in the lysine requirement is due to different dynamics of feed intake on the one hand and the potential for protein deposition on the other hand. If, during the first part of the growing period, a high potential for deposited protein is associated with a low feed intake capacity, the lysine requirement (in g/kg diet) will be relatively high. Amino acid requirements are essentially determined by the ratio between the potential to deposit protein and feed intake (van Milgen and Dourmad, 2015). Knowledge of how these two traits evolve during growth is, therefore, essential in determining nutrient requirements.

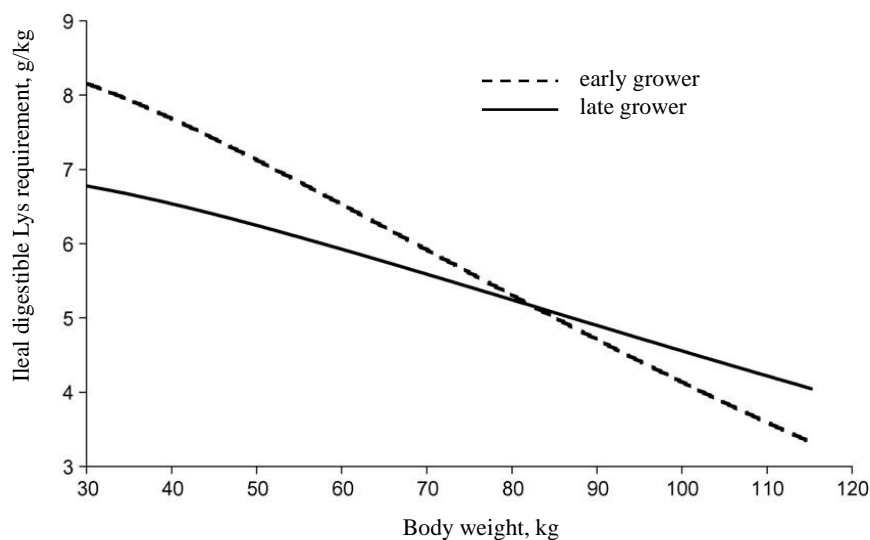


Figure 6

Simulated digestible lysine requirements for two pigs having the same average daily gain and feed intake, but different shapes of the growth curves (precocity is 0.010 vs. 0.014/d; van Milgen *et al.*, 2008)

In the case of using dynamic growth models, the number and duration of feeding phases can be defined. The benefit of using multiphase feeding rather than one- or two-phase-feeding is that excesses of dietary nutrients can be reduced (Pomar and Pomar, 2012). It is even possible to formulate diets with day-by-day adjustments to the actual requirements, but this requires specific feeding systems. By blending two premixes in variable ratios, pigs can be offered a diet according to their requirement throughout the growing period (Pomar *et al.*, 2009). There

is an increasing number of studies exploring the potential impact of daily tailored feeding systems (i.e. precision livestock feeding) on feed cost and environmental impact relative to multiphase feeding systems. In an *in silico* study, Pomar *et al.* (2011) simulated the lysine requirement and the growth response of individual pigs and of the population of pigs using a slightly modified version of the growing pig module of InraPorc. The results indicated that by adjusting the diet on a daily basis, nitrogen intake and excretion could be reduced considerably. Due to the lower protein content of the diet, feed cost was 10% lower compared to a 3-phase-feeding system (Pomar *et al.*, 2011). However, the diets in the simulation did not include safety margins as normally used in commercial feeds. In an actual growth trial, Andretta *et al.* (2014) reported that tailored feeding allows a reduction of the standardized ileal digestible lysine supply by more than 20%, and the excretion of nitrogen and phosphorus by 22 and 27%, respectively, compared to 3-phase-feeding, without affecting growth performance and carcass quality.

4.4. Models as a research and education tool

Conceptual models aim to improve our understanding of complex phenomena such as growth or reproduction by representing the underlying biological principles. Therefore, they are used particularly in setting research priorities. However, a good conceptual model is not necessarily useful as an advisory tool in commercial animal production. Models are capable of answering “what-if” type questions and, therefore, help to formulate research goals and demonstrate principles of feed and nutrient utilization in education (Gerrits *et al.*, 2008). Application of modelling techniques shifts the teacher-student relationship from the one-way knowledge transfer to a skills-oriented problem-solving approach. Experimental learning either by developing simple nutritional models or using existing ones is far more effective in honing the students’ cognitive skills than simply listening in a classroom setting (Gous, 2014). Development of a model creates insight into the system, and stimulates the development of skills for analysis, systematization and construction, and critical evaluation. Simulation techniques allow design of *in silico* experiments, and students can be actively involved in real-world problem solving (Gous, 2014).

4.5. Future directions in modelling

It seems that the further evolution of nutritional models includes adapting new approaches and statistical methods as well as integrating multidisciplinary results to improve understanding of interactions and causality of phenomena.

Agent-based modelling is a relatively new approach to simulate the dynamics of complex systems and complex adaptive systems (Macal and North, 2010). The approach has been used in different disciplines, in animal nutrition, firstly by Boumans *et al.* (2015) and Boumans (2017). To simulate the feeding behaviour and motivational states of pigs, Boumans (2017) combined the agent-based modelling approach with a model of nutrient metabolism based on the approach by de Lange (1995). The model increases understanding of the interactions between internal physiological factors and external social factors, and shows the effect of behavioural strategies of pigs to food-related competitive situations in various feeding and social interaction patterns. The model of Boumans (2017) provides a good example of how results from different disciplines, like animal nutrition and ethology, can be integrated.

To date, static digestion models have focused on prediction of the feeding value of individual ingredients. In contrast, dynamic digestion models have addressed interactions among nutrients in the digestive tract (Strathe *et al.*, 2008; Taghipoor *et al.*, 2014). Prediction of the availability of nutrients from (various mixes of) feed ingredients requires an understanding of the complex interactions among feed ingredients, mediated through variation in physical and

chemical properties of digesta, passage kinetics, and digestion rates of nutrients. The intestinal conditions (e.g. pH, rheological properties, hydration properties) and digesta transit rates determine the extent to which nutrients are potentially available to the animal. An additional challenge will be quantifying intestinal metabolism in relation to metabolism oriented towards growth in muscle and adipose tissue. Splanchnic tissues are metabolically very active and are responsible for the changes between nutrients disappearing from the gastrointestinal tract and nutrients being available for growth.

Although a number of predictive models have been developed, considerable work remains to be done for the robust prediction of animal growth, body composition, nutrient requirements, outputs of waste products from the animal, and production costs (Thornton, 2010). There is great potential for growth models for use in precision livestock farming and nutrition, being a central part of the controlling module. The enormous progress made in high frequency (and real time) data acquisition opens new opportunities for the use of actual measurements as model inputs (e.g. feed intake) and to verify model outputs. Likewise, information on behaviour and activity of animals can now be obtained (e.g. through video analysis or sensor technology), which can be used to modulate the maintenance energy requirement. However, it remains a challenge to handle these non-parametric (or indirect) data as model inputs.

With classical growth models, the effect of interactions between the animal, the feed, and the environment can be simulated. However, in practical situations unexpected and, or unknown events may decrease the feed intake or animal performance. Metabolic flexibility is a key element for a better understanding of the individual adaptation to environmental challenges. There are attempts to estimate the robustness of farm animals in evaluating and predicting the animal response to unknown perturbations (Taghipoor *et al.*, 2016). However, it is clear that there might be large differences in phenotypic traits according to the individual variance of the population. Most of the growth models predict the response of an individual animal, representing the effect of feed intake on the performance of the mean animal. In practical conditions, variation among animals is one of the main uncertainties of the projected production potential. There are only a few models dealing with variation of individual animals, although this kind of information could help the farmer in production management (e.g. to optimise the slaughter strategy). Integration of variation among individuals to obtain population responses is rarely addressed and only a few stochastic models have been developed so far (Brossard *et al.*, 2009; Pomar *et al.*, 2003; Wellock *et al.*, 2004). It is expected that mathematical models will be improved to represent variation in nutrient metabolism and thus the probability distribution of future production.

In the last few years, nutritional research has made considerable progress using techniques such as genomics, transcriptomics, proteomics, and metabolomics. The effect of nutrient supply on gene expression, including regulatory mechanisms of nutrient metabolism and transformation, can provide insight into the mechanisms controlling protein and lipid accretion. Mechanistic models can play an important role in translating findings from such “omics” studies to practice, but can also be of critical importance in the process of designing, refining and interpreting such studies, as these are rarely quantitative in nature, and are used to address open questions. Mechanistic models typically allow incorporation of new concepts and data emerging from research at lower levels of aggregation (Dumas *et al.*, 2008).

Concluding remarks

Models of feed utilization and growth have been developed and used for decades. This chapter provides an extensive overview of published models and their objectives. In addition, historical developments in growth modelling are summarized, particularly in pigs. It addresses empirical ways to model feed intake, and more mechanistic or conceptual approaches to the

modelling of digestion and post absorptive metabolism. The purposes for developing mathematical models in animal nutrition differ; a number of them have been applied in practice to support farm management and decision making to achieve desirable and cost-effective animal production, while others have been developed to provide a better understanding of the underlying mechanism of nutrient digestion and partitioning in metabolism. Mathematical models play an important role in testing concepts, as well as translating research findings to practice, and evaluating different scenarios in animal production such as feeding strategies or phenotypic traits. Such information is useful for nutritionists and geneticists, and for on-farm practice.

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