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Phosphorus and calcium requirements for bone mineralisation of growing pigs predicted by mechanistic modelling

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*Phosphorus (**P**) is an essential nutrient in livestock feed but can pollute waterways. In order for pig production to become less of a threat to the environment, excreta must contain as little P as possible or be efficiently used by plants. This must be achieved without decreasing the livestock performance. Phosphorus and calcium (**Ca**) deposition in the bones of growing pigs must be optimised without affecting the muscle gain. This requires precision feeding based on cutting-edge techniques of diet formulation throughout the animal growth phase. Modelling and data mining have become important tools in this quest. In this study, a mechanistic model taking into account the distribution of P between bone and soft tissues was compared to the established factorial models (INRA (Jondreville and Dourmad, 2005) and NRC (National Research Council, 2012)) that predict P (apparent total tract digestible, **ATTD-P**; or standardised total tract digestible, **STTD**-P) and Ca (total and STTD) requirements as a function of BW and protein deposition. The requirements for different bone mineralisation scenarios, namely, 100% and 85% of the genetic potential, were compared with these two models. Sobol indices were used to estimate the relative impact of growth-related parameters on mineral requirements at 30, 60 and 120 kg of BW. The INRA showed the highest value of ATTD-P requirement between 29 and 103 kg of BW (6%) and lower for lighter and higher BW. Similarly, the model for 85% bone mineralisation showed lower STTD-P requirement than NRC between 29 and 93 kg of BW (7%) and higher for lighter and higher BW. Contrary to other models, the Ca requirement of the proposed model is not fixed in relation to P. It increases from 95 kg of BW while the others decrease. The INRA showed the highest Ca requirements. The model Ca requirements for 100% bone mineralisation are higher than NRC from 20 to 38 kg of BW similar until 70 kg of BW and then higher again. For 85% objective, the model showed lower Ca requirements from 25 to 82 kg of BW and higher for lighter and higher BW. The potential Ca deposition in bones is the most sensitive parameter (84% to 100% of the variance) of both ATTD-P and Ca at 30, 60 and 120 kg. The second most sensitive parameter is the protein deposition, explaining 1% to 15% of the ATTD-P variance. Studies such as this one will help to usher in a new era of sustainable and eco-friendly livestock production.*

Keywords: model, minerals, swine, prediction, need

Implications

Using mechanistic models to assess nutrient requirements, resource utilisation by the livestock sector may be fine-tuned. If animal protein production is to become universally accessible, affordable and safe, basic research, data mining and process modelling must be applied. This article describes a mechanistic approach developed to predict dietary calcium and phosphorus requirements for bone mineralisation of growing pigs based on multiple criteria. The livestock sector must take advantage of the power of data mining in order to remain competitive, intensify and achieve sustainability.

Introduction

As a key component of DNA and all known metabolic energy systems, phosphorus (**P**) is an essential nutrient for all life forms. It is a non-renewable resource with no substitute (U.S. Geological Survey, 2019). The sustainability of animal production and of agriculture in general largely depends on its judicious use. In the bodies of vertebrates, about 60% of the P occurs in bone at a fixed ratio with calcium

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(**Ca**), while the remaining portion is found mainly in muscle (Nielsen, 1973). An adequate supply of P is therefore essential for animal growth, health and well-being; and this must be provided using efficient and sustainable means that minimise the P footprint of livestock production. This implies precise estimation of the P content of feed ingredients, which has been the subject of many publications and recent methodological standardisation (National Research Council, 2012; Bikker and Blok, 2017). This has brought to light important factors determining P availability, namely, chemical form, Ca supply and the use of phytase (Létourneau-Montminy *et al.*, 2012). Efficient utilisation of potentially absorbable P requires equally precise knowledge of actual requirements for animal growth.

The two factorial methods currently used to predict P and Ca requirements of growing pigs are proposed by Jondreville and Dourmad (2005) and National Research Council (2012). The first one predicts P retention for maximal bone mineralisation based on an allometric relationship between body P and BW, with the total Ca requirement corresponding to a fixed ratio of 2.9 for total Ca to apparent total tract digestible P (**ATTD-P**). The National Research Council (NRC) predicts the whole-body P retention based on protein deposition. The requirement is set at 85% of the maximal retention according to the proposed model, which uses a fixed ratio of 2.15 for total Ca to standardised total tract digestible P (**STTD-P**). In both models, it is assumed that changes in skeletal tissue are directly proportional to lean growth, which has been shown not to be true (Pomar *et al.*, 2006; Couture *et al.*, 2018). In addition, both predict requirements only and not responses to transient deficiency or compensatory retention that occur in practice (Gonzalo *et al.*, 2018). The right amount of P to be provided in the diet depends on interacting and sometimes conflicting production goals (e.g. profitability, animal well-being, environmental protection) and multiple response criteria (e.g. growth performance, bone mineralisation, excretion). However, multi-objective models are difficult to implement, and the single-value requirement remains the most applied approach.

To meet the challenge of optimising multiple livestock responses to dietary P and Ca (e.g. performance, health) and balancing them with the environmental impact, social acceptability and profitability of production, mechanistic models have been found effective. At least one such model of dietary P and Ca fate has been developed (Létourneau-Montminy *et al.*, 2015; Lautrou *et al.*, 2019b) from the principles of InraPorc (van Milgen *et al.*, 2008) simulating the growth of total body main chemical constituents which are total body protein, lipid, ash and water (Whittemore and Fawcett, 1976). This model integrates multiple biological processes in pigs, with protein deposition non-dependent-ash deposition predicting the impact of Ca and P deficiencies and imbalances as well as compensatory retention after periods of deficiency.

Therefore, the objective of this article is to use inversion modelling principles (Doeschl-Wilson *et al.*, 2006) of the model developed by Létourneau-Montminy *et al.* (2015) and improved by Lautrou *et al.* (2019b) to estimate digestible P and digestible and total Ca requirements for a specific bone mineralisation objectives, compare these estimates with those proposed by conventional models and identify the most influential factors modulating P and Ca utilisation. Preliminary results were already published in an abstract for the 9th Workshop on Modelling Nutrient Digestion and Utilization in Farm Animals (Lautrou *et al.*, 2019a).

Material and methods

General background

Following few modifications of the Létourneau-Montminy *et al.* (2015) model, Lautrou *et al.* (2019b) model has been validated using data of whole-body bone mineral content of pigs receiving contrasted Ca and P dietary supply generated for that purpose (Pomar *et al.*, 2006; Langlois *et al.*, 2016a and 2016b; Gonzalo *et al.*, 2018). It was showed that the predictions of total body P and Ca content had a relative mean square error of about 5% in the case of pigs fed adequate amounts of these minerals, while challenges remained in predicting the response to deficient diets. Indeed, because of a lack of knowledge for a mechanistic representation, regulations of Ca and P metabolisms and its impact on Ca and P intake, gain and efficiency are not included yet. Based on these findings, the mechanistic model was considered accurate enough to predict P and Ca requirements for bone mineralisation of growing pigs.

General structure of the model

The proposed mathematical model has two modules, namely, soft tissue and ash (Figure 1). Based on the recent

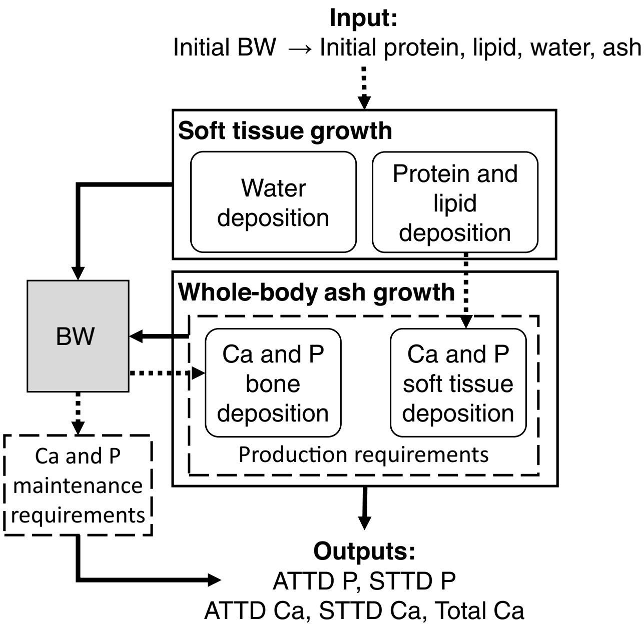

Figure 1 General layout of the proposed mechanistic model predicting total calcium (Ca) and apparent and standardised digestible phosphorus (ATTD and STTD P) requirements of growing pigs.

studies, bone mineral deposition in growing pigs no longer depends only on body protein in terms of potential and actual deposition (Couture *et al.*, 2018). The equation defining potential Ca deposition during growth clearly differs from that of protein. Concentrations of P and Ca in muscle and adipose tissues have been generated for modern genotypes at BW of 25, 75 and 125 kg (Lautrou *et al.*, unpublished). The model outputs, which are the requirements for a certain objective of bone mineralisation, are the amounts of Ca and P to be absorbed in order to reach the mineral deposition target.

Description of the model proposed for estimating calcium and phosphorus requirements for bone mineralisation

The proposed model predicts ash and soft tissue mineral compositions separately (Figure 1) using a factorial approach to predict Ca and P requirements for maintenance and growth of soft tissues. It was written with Model Maker version 3.0 (Cherwell Scientific Ltd, 2000) using Euler integration method for BW of 20 to 120 kg. Unless otherwise specified, rate variables are expressed in grams per day (g/day) and state variables in grams. The proposed mathematical model first predicts the growth of tissues that then determines Ca and P requirements.

Simulation of soft tissues growth. Using Inraporc principles (van Milgen *et al.*, 2008), based on initial BW, it calculates the chemical composition in terms of protein, lipid and water at the start of the simulation. It should be noted that other models to predict soft tissue growth (e.g. NRC, 2012) or user data can be easily incorporated. As recommended by Van Milgen *et al.*, (2008), model parameters related to feed intake and growth potential are adjusted by the model user and feed intake, and protein and lipid deposition are thereafter calculated daily. The daily feed intake is controlled by the net energy of the diet, and the net energy intake desired was calibrated with previous studies (Pomar *et al.*, 2006; Langlois *et al.*, 2016a and 2016b; Gonzalo *et al.*, 2018). Potential protein deposition is described by a Gompertz function that can be changed by user, and actual deposition is determined as the lesser among the potential and the allowable deposition based on energy and amino acid supplies. The difference between the potential and achieved depositions represents a deficit that cannot be compensated. The energy not used for protein is deposited as lipid still following Inraporc principles.

Simulation of bone growth and bone ash. In comparison to the classic pig growth models (van Milgen *et al.*, 2008; NRC, 2012), bone mineral deposition in growing pigs no longer depends only on body protein, but is dependent on BW in terms of potential and actual deposition based on recent studies (Couture *et al.*, 2018). The equation defining potential Ca deposition during growth clearly differs from that of protein (Figure 2).

The driving force of bone mineral deposition is Ca deposition, which depends on BW (equation (1), Figure 2). It was

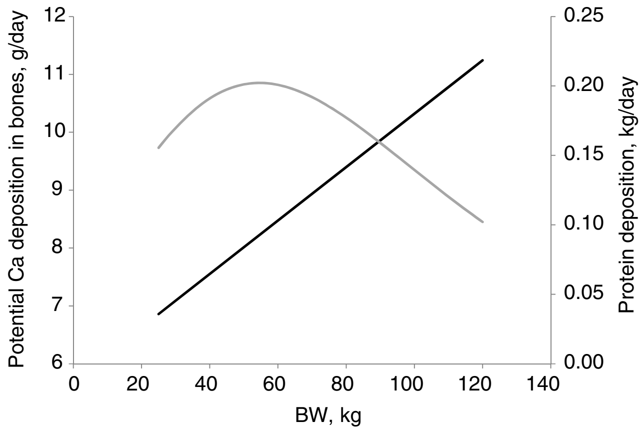

Figure 2 Potential Ca deposition in bones (g/day) and protein deposition over BW in growing pigs.

built using the data from pigs fed P and Ca in amounts exceeding NRC requirements (2012) by about 135% (Pomar *et al.*, 2006; Langlois *et al.*, 2016a and 2016b), with both terminal and hybrid F1 lines that do not differ in body bone mineral content. Therefore, this equation represents the potential Ca deposition into bone of growing pigs. Again, the user may change this curve with his or her own data. Deposition of P in bone is assumed to be on a fixed Ca : P ratio of 2.16, with other minerals representing 43% of the bone ash (Crenshaw, 2001). The potential ash depositions are calculated from BW in kg and is the sum of the following equations:

$$\text{PotentialBoneCaDeposition (g)} = 5.701 + 0.0461 \times \text{BW} \tag{1}$$

$$\text{PotentialBonePDeposition (g)} = \text{PotentialBoneCaDeposition}/2.16 \tag{2}$$

$$\text{PotentialBoneMiscDeposition (g)} = 0.43 \times ((\text{PotentialBoneCaDeposition} + \text{PotentialBonePDeposition})/0.57) \tag{3}$$

Simulation of soft tissue ash. The ash composition of soft tissue is not well-known as only Nielsen (1973) measured it. Therefore, concentrations of protein, lipid, P and Ca in different tissues have been generated for modern genotypes at BW of 25, 75 and 125 kg (Lautrou *et al.*, unpublished). Being the anatomical compartment that contains the most protein (85% to 90%), the muscle was used as the reference tissue to calculate the amount of P, Ca and other minerals deposited with protein (PD) (equations (4) to (6)). In the same way, the subcutaneous fat was used to calculate the amount of P, Ca and other minerals deposited with lipid (LD) (equations (7) to (9)). The ratio of protein, P, Ca and Misc to muscle as well as lipid to subcutaneous fat (respectively, **Protein : Musc, P : Musc, Ca : Musc, Misc : Musc** and **Lip : SubFat**) depends on BW (equations (10) to (14)). Mineral analysis of subcutaneous adipose tissue from dissections (Nielsen, 1973) suggested 0.045% P (**P : SubFat**), 0.005% Ca (**Ca : SubFat**) and 0.26% other minerals (**Misc : SubFat**).

$$\text{ProteinCaDeposition (g)} = (\text{PD}/(\text{Protein} : \text{Musc}/100)) \times (\text{Ca} : \text{Musc}/100) \times 1000 \quad (4)$$

$$\text{ProteinPDeposition (g)} = (\text{PD}/(\text{Protein} : \text{Musc}/100)) \times (\text{P} : \text{Musc}/100) \times 1000 \quad (5)$$

$$\text{ProteinMiscDeposition (g)} = (\text{PD}/(\text{Protein} : \text{Musc}/100)) \times (\text{Misc} : \text{Musc}/100) \times 1000 \quad (6)$$

$$\text{LipidCaDeposition (g)} = (\text{LD}/(\text{Lip} : \text{SubFat}/100)) \times (\text{Ca} : \text{SubFat}/100) \times 1000 \quad (7)$$

$$\text{LipidPDeposition (g)} = (\text{LD}/(\text{Lip} : \text{SubFat}/100)) \times (\text{P} : \text{SubFat}/100) \times 1000 \quad (8)$$

$$\text{LipidMiscDeposition (g)} = (\text{LD}/(\text{Lip} : \text{SubFat}/100)) \times (\text{Misc} : \text{SubFat}/100) \times 1000 \quad (9)$$

where

$$\text{Protein} : \text{Musc (\%)} = 89.010 - 0.03117 \times \text{BW} \quad (10)$$

$$\text{Ca} : \text{Musc (\%)} = 0.02202 - 4.746 \times 10^{-5} \times \text{BW} \quad (11)$$

$$\text{P} : \text{Musc (\%)} = 1.029 - 0.004198 \times \text{BW} + 1.817 \times 10^{-5} \times \text{BW}^2 \quad (12)$$

$$\text{Misc} : \text{Musc (\%)} = 4.184 - 0.005023 \times \text{BW} \quad (13)$$

$$\text{Lip} : \text{SubFat (\%)} = 79.536 + 0.3122 \times \text{BW} - 0.001517 \times \text{BW}^2 \quad (14)$$

Factorial method to determine calcium and phosphorus requirements for bone mineralisation. Phosphorus and Ca requirements are the sum of the maintenance requirement and the amount that should be absorbed to reach soft tissue ash and bone ash potential. It can therefore be expressed on the basis of ATTD or STTD in g per kg of diet.

Mineral maintenance requirements. To obtain ATTD requirement, given that the model simulates requirement for tissue growth with the assumption that there is no excess, deficit or imbalance of Ca or P, only the unavoidable urinary loss is taken into account. In the model, these losses are estimated at 0.5 mg of P and 2 mg of Ca per kg of BW (Bikker and Blok, 2017). To obtain STTD requirement, the basal endogenous sloughing from the digestive tract into faeces is also considered. In the model, the losses are estimated at 190 mg/kg BW (NRC, 2012) for P and at 300 mg/kg BW for Ca (H. H. Stein, personal communication).

Tissue growth requirements. The requirement in Ca and P for tissue growth is the sum of Ca and P deposited into bone (respectively, equations (1) and (2)), protein (respectively, equations (8) and (9)) and lipid (respectively, Equations (12) and (13)).

Model comparison

The ATTD-P, STTD-P and total Ca requirements estimated by the proposed model were compared to those of the previous models of Jondreville and Dourmad (2005), hereinafter called INRA, and by NRC (2012), hereinafter called NRC.

As NRC proposes P requirements in terms of STTD, the ATTD requirement obtained with the current model can be also provided in terms of STTD by correcting ATTD values for basal endogenous losses. Using a simulated default pig generated by InraPorc (van Milgen *et al.*, 2008) for protein and lipid deposition and feed intake, ATTD-P and STTD-P were calculated from the INRA and NRC factorial model equations, respectively. In both models, the Ca requirement is expressed as total Ca determined as a fixed ratio to STTD-P for NRC and to ATTD-P for INRA. Since INRA recommendations are based on reaching 100% of the potential bone mineralisation, whereas the NRC model targets 85% of it, both cases were simulated. Given that Ca requirements are expressed in total Ca, an STTD-Ca digestibility of 70% was assumed for a corn/soybean meal-based diet (González-Vega *et al.*, 2015a; Stein *et al.*, 2016) to calculate the total Ca. Also, given that urinary losses of P considered in the factorial method of INRA and NRC are higher than the unavoidable values used in our model, and these values have been considered for comparison. Models were compared based on the comparison of the body P retention (g/day), ATTD and STTD-P growth requirement (g/kg) and total Ca requirements.

Sensitivity analysis of the model prediction of phosphorus and calcium requirements

In order to verify the accuracy of the proposed model, it was tested for global sensitivity with all of the parameters in a full factorial design with all the possible interactions tested. This analysis is useful for identifying the factors (including interactions) that contribute the most to the variability of the recommendations. It consists of testing the model over the full range of possible values of the parameters. The parameters and their ranges were chosen to simulate field variability. The tested parameters were protein and lipid deposition between −1.5 and +1.5 times (Table 1) their previously reported standard deviations (Andretta *et al.* 2014 and 2016; Remus *et al.* 2019) and bone Ca : P ratios of 2.00, 2.08 and 2.16, with 2.16 being the default value (Nielsen, 1973; Crenshaw, 2001). For bone Ca potential deposition, variation was based on the difference between the default equation (equation (1)) and the individual animal with the highest bone mineralisation in the

Table 1 *Tested parameters and their levels for the global sensitivity analysis on growing pigs*

	30 kg		60 kg		120 kg	
BW	−1.5 SD	+1.5 SD	−1.5 SD	+1.5 SD	−1.5 SD	+1.5 SD
Protein deposition (%)	87	113	84	116	68	132
Lipid deposition (%)	53	147	51	149	78	122
Ca : P Bn (%)	93		93		93	
CaBn (%)	86	114	74	126	60	140

CaBn = Potential Ca deposition in bone; Ca : P Bn = Ca : P ratio in bone.

database (Pomar *et al.*, 2006; Langlois *et al.*, 2016a and 2016b; Gonzalo *et al.*, 2018). All parameters were tested under three scenarios, namely, at BW of 30, 60 and 120 kg. Sobol indices (Sobol, 1993) were calculated to quantify the influence of each tested parameter on the outputs of the model. An objective of 100% bone mineralisation was used for the simulations. This method measures the contribution of each parameter variance to the variance of the outputs. The Sobol indices are defined as:

$$S_{i1,\dots,is}(Y) = Var_{i1,\dots,is}(Y)/Var(Y) \qquad (15)$$

The first-order indices represent the effect of each parameter on the outputs *Y*. The total contribution of each parameter and their interactions to the outputs are expressed as total order indices.

Results and discussion

The current model has been compared to two factorial methods proposed to estimate Ca and P requirements, namely, NRC and INRA. Next step will be to validate in the field knowing that it will be impossible to validate under all conditions (e.g. different shapes of protein deposition).

Body phosphorus retention

The current model evolves more linearly with BW than NRC and INRA models and ended with higher P retention for heavier pigs (Figure 3). This is due to the linear increase in Ca deposition in bones with BW, while the other models are driven by protein deposition or BW gain that follows a Gompertz function. As expected, the INRA model predicted a greater P retention than did the NRC model, since the bone mineralisation criteria were, respectively, 100% and 85%. This difference widens for heavier pigs (10% for 20 kg *v.* 26% for 120 kg BW), since protein deposition, the driver of P deposition in the NRC model, follows a Gompertz function whereas average daily gain, which is more linear, is the main determinant of P retention in the INRA model. Besides, the current model is closer to INRA for an objective of 100% bone mineralisation and closer to NRC for 85% bone mineralisation. However, the current model showed lower retention than INRA (−4% in average for 100% bone mineralisation) and NRC (−5% in average for 85% bone mineralisation) from 30 to 100 kg BW.

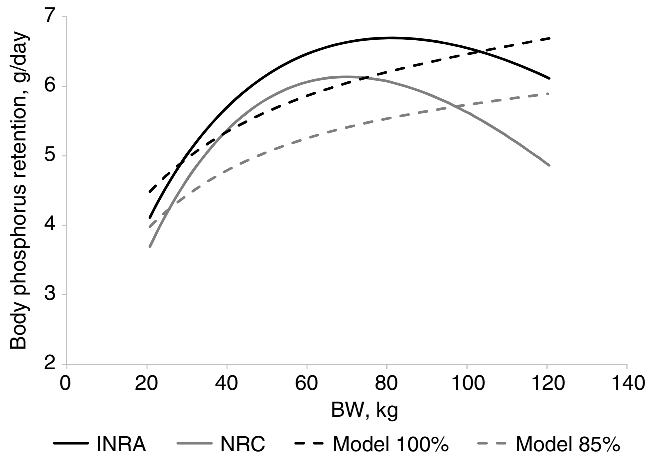

Figure 3 Body phosphorus retention by pigs (g/day) as function of BW according to INRA (Jondreville and Dourmad, 2005), NRC (NRC, 2012) and the proposed mechanistic model for 85% or 100% bone mineralisation.

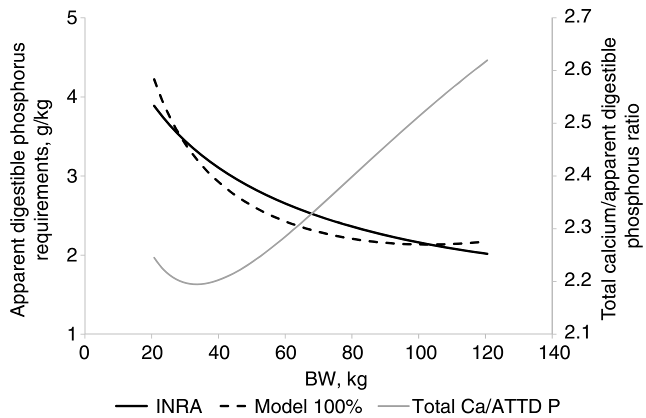

Figure 4 Apparent digestible phosphorus requirements (ATTD, g/kg) for growing pigs according to BW for INRA (Jondreville and Dourmad, 2005) and the current model for 100% of bone mineralisation (Model 100%).

Phosphorus requirement predictions

The comparison of ATTD-P requirement for 100% bone mineralisation and ATTD-P from INRA showed estimated requirements that are really close (Figure 4). However, the relationship between BW and the P requirement is more quadratic with the proposed model with P requirements that decrease more rapidly until 60 kg BW where protein deposition reaches its maximum and then begins to decrease; while Ca, and consequently bone P deposition, continue to increase

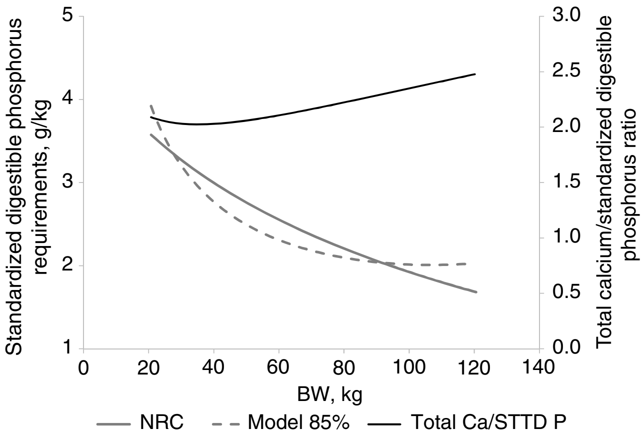

Figure 5 Standardised digestible phosphorus requirements (STTD, g/kg) for growing pigs according to BW for NRC (NRC, 2012) and the current model for 85% of bone mineralisation (Model 85%).

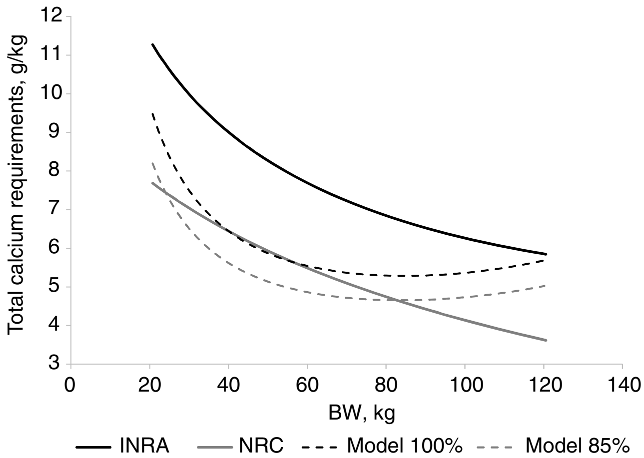

Figure 6 Total Ca requirements (g/kg) for growing pigs according to BW for each INRA (Jondreville and Dourmad, 2005) and NRC (NRC, 2012) models, the current model for 85% (Model 85%) and for 100% of bone mineralisation (Model 100%).

linearly as the BW increases. This model recommended more P than did INRA to meet the 100% bone mineralisation goal from 20 to 30 kg BW (4%) and from 100 to 120 kg (4%). For the comparison of STTD-P obtained by the model for an objective of 85% bone mineralisation, the proposed model recommended lower P requirement (7% in average; Figure 5) than NRC except from 20 to 27 kg (10% at 20 kg) and from 97 to 120 kg (21% at 120 kg) where it estimated higher values. This is consistent with the studies of Vier *et al.* (2019a, and 2019b) that showed greater P requirement than NRC (2012) for both nursery and growing-finishing pigs based on growth performance and maximal bone mineralisation. For growing pigs, these results has been obtained based on a fixed totalCa : totalP ratio, therefore, with a Ca : STTD-P ratio that decreases with the increase in STTD-P. This means that Ca was higher in diet where P was below the NRC recommendation and lower when P was above the NRC recommendations, which may have influenced pig response to STTD-P.

Total calcium requirement predictions

The NRC and INRA models showed a nearly linear relationship between Ca requirement and BW, since Ca was expressed in terms of a fixed ratio to ATTD-P (Figure 6) which in turn was assumed to be linear with BW. In contrast, the current model takes into consideration the deposition of 40% of the absorbed P within the protein pool independently of Ca in comparison to about 60% of P deposited into bone in a fixed ratio with 99% Ca.

With the ATTD-Ca-based model output expressed on a total Ca basis, the average digestibility coefficient for a corn/soybean-meal-based diet considered and Ca endogenous losses (González-Vega *et al.*, 2015a; Stein *et al.*, 2016), this model indicated an increase in the total requirement for animals heavier than 80 kg, reflecting reduced P deposition in body protein as BW increased while the proportion deposited in bone increased (Figure 6). It also sets a lower requirement than the INRA level for 100% bone mineralisation at all BW except for 120 kg BW where they are really close. For 85% mineralisation, the proposed model showed results that are more similar to NRC with lower Ca requirement than NRC from 30 to 85 kg BW (9%) but higher from 85 to 120 kg BW to reach a difference of 38% at 120 kg.

As previously indicated, INRA and NRC used fixed ratio between Ca and P to determine Ca requirements. As well discussed by Bikker and Block (2017), the value adopted as digestibility of dietary Ca has a major impact on the recalculation of digestible to total Ca requirement. For the current simulations, we used 70% based on Stein *et al.* results (personal communication) which is similar to German GfE (2008). Jongbloed *et al.* (2003) adopted a digestibility value of 50% to 60% without and with phytase, resulting in a mean Ca : dP ratio of 2.8 for weaned pigs and of 3.0 for growing-finishing pigs. Besides, due to a lack of information in 2012, the NRC pragmatically adopted a ratio between total Ca and standardised digestible P of 2.15, assuming a high availability of the most inorganic Ca sources. Therefore, better prediction of Ca digestibility considering both feed (e.g. Ca sources, phytase, level of P) and animal (e.g. mineral status) are still necessary to better define its requirement.

Calcium/phosphorus ratios

For 100% bone mineralisation, the current model yielded ratios of total Ca to ATTD-P requirements that increased linearly from 2.2 up to almost 2.6 as the pigs reached their maximum weight (Figure 4). The total Ca to STTD-P ratio for 85% bone mineralisation also increases linearly from 2.0 to almost 2.5 (Figure 5). As stated previously, Ca ratio is fixed for INRA and NRC and is, respectively, of 2.9 based on ATTD-P for INRA and 2.15 based on STTD-P for NRC. The variation in this ratio can be explained in terms of the increasing proportion of deposition in association with Ca (bone *v.* protein allometry), as BW increased.

A high Ca : P ratio in a low-P diet is known to decrease P utilisation (Reinhart and Mahan, 1986; Jondreville and Dourmad, 2005; González-Vega *et al.*, 2016). Although the ratio predicted by the current model is lower than INRA and

NRC, it should be used only with the recommended P predicted by the model; in other words, there is no fixed ratio to implement, and the ratio will depend on the production goal and pig BW, which determines the P requirement. For example, if the goal is less than the full bone mineralisation, the ratio will decrease since less Ca is needed to retain P, given that a higher proportion of the P will be retained in soft tissues independently of Ca. It is noteworthy that according to the model, using a total Ca to ATTD-P ratio dependent on BW and for a given goal (e.g. % rather than potential bone mineralisation) could be advantageous since bone, muscle and fat contribute differently to tissue allometric growth.

In view of the ongoing work on determining digestible Ca ingredient values and requirements (González-Vega *et al.*, 2014, 2015a and 2015b; Merriman and Stein, 2016), the STTD-Ca : STTD-P ratio should be examined. This ratio for 100% bone mineralisation shows the same type of relationship as total Ca : STTD-P with a plateau followed by a linear increase but with lower values: 1.54 at 20 kg and 1.77 at 120 kg. The predicted increased ratio with BW is in agreement with the recent maximised bone mineralisation results (González-Vega *et al.* 2016; Merriman *et al.,* 2017; Lagos *et al.,* 2019), but values although comparable at 20 kg are lower for heavier BW pigs with 1.7 for the proposed model *v.* 2.3 suggested by these authors. The recent study of Vier *et al.* (2019a) when giving 122% of STTD-P recommended by NRC and increasing STTD-Ca : STTD-P showed that the ratio to maximise bone is higher than the one maximising growth performance. They recommended a ratio of 1.75 to 1.82 in growing-finishing pigs to optimise growth performance and bone mineralisation. Lautrou *et al.* (2019b) showed good accuracy in predicting finishing pig whole-body ash with this model indicating that this disconnection is important to consider. Lee *et al.* (2019) also showed an STTD-Ca : STTD-P ratio that has to increase with age to maximise bone mineralisation, which is again consistent with the results of the current model.

It is worthy to note that this ratio is influenced by basal faecal endogenous losses of Ca used to determine STTD-Ca; that is, higher losses increased the ratio. In the current model, faecal endogenous losses was set to 300 mg/kg DMI, but they are very variable between trials (from 123 to 670 mg/kg DMI; González-Vega *et al.*, 2014, 2015a and 2015b; Merriman and Stein, 2016) for unknown reasons (H. H. Stein, personal communication). Moreover, in the current model, the impact of Ca and P deficiencies on feed intake and growth performance is not yet included in the proposed model since the mechanisms involved in the animal responses to deficiencies in these minerals are not well-known and have never been quantified throughout the growth phase. It is therefore not possible to obtain the ratio that maximises growth efficiency with the present mechanistic model. Nevertheless, these recent works showed that although P is provided in sufficient amounts, Ca will have a detrimental effect on the growth performance except in large excess in P (González-Vega *et al.,* 2016; Lagos *et al.,* 2019). Therefore, the low ratio predicted by the current model to maximise bone mineralisation should not interfere with growth performance.

Sensitivity analysis

For all outputs at three BW (30, 60 and 120 kg), the potential Ca deposition was by far the most influencing factor on total Ca requirements, accounting for more than 99% of the observed variance (Table 2). The high sensitivity of the requirements to Ca deposition seems logical considering that 96% to 99% of body Ca and 60% to 80% of body P is found in bones (Crenshaw, 2001; Suttle, 2010). This explains the high effect of the potential deposition to ATTD-P (more than 80%) variance. The influence of the potential Ca deposition in bones on ATTD-P requirements increases with the pig weight and it is the contrary for protein deposition. In fact, young pigs incorporate a greatest proportion of P into soft tissue, explaining the lower sensitivity of Ca deposition in bone. The potential Ca deposition in bone thus plays a major role in establishing the total Ca and ATTD-P requirements. These results show the importance of precise evaluation of the genetic potential of mineral deposition in bones.

Since 99% of body Ca is in bone, protein deposition has almost no influence on the variance of total Ca. However, it does influence ATTD-P variance, 15% for pigs at 30 kg, 6% at 60 kg and 1% at 120 kg based on protein deposition variation in previous trials. The decrease in the influence of protein deposition on P with BW increase coincides with the linear increase in bone deposition. Moreover, the ATTD-P variance associated with protein deposition at 30 kg shows that animal growth will have a major impact on

Table 2 *Sobol indices[1] of the tested parameters that explain part of the total calcium (CaTot) and apparent total tract digestible phosphorus (ATTD-P) requirements for growing pigs at each BW tested*

BW (kg)	30		60		120	
	CaTot	ATTD-P	CaTot	ATTD-P	CaTot	ATTD-P
CaBn	100.00	84.20	100.00	91.33	100.00	98.09
Protein deposition	0.00	15.28	0.00	5.94	0.00	0.83
Lipid deposition	0.00	0.53	0.00	0.64	0.00	0.07
Ca : P Bn	0.00	0.00	0.00	2.00	0.00	0.91

CaTot = Total Ca requirement; ATTD-P = apparent total tract digestibility P requirement; CaBn= Ca deposition into bone; Ca : P Bn = Ca : P ratio in bone.
[1]Sobol (1993), values are percentages of the total variance.

dietary P recommendations. Indeed, if protein deposition is decreased because of any nutrient deficiency, the P requirement will also decrease. This means that P requirement is linked to amino acid and energy intake. As expected, lipid deposition has little impact on total Ca and ATTD-P requirements, since Ca and P deposition in lipids is negligible. Less than 1% of body Ca and P is found in lipids (Nielsen, 1973; Crenshaw, 2001).

The Ca : P ratio in bone had no influence on total Ca requirement. This is to be expected since Ca drives bone ash deposition, so the Ca : P ratio cannot change the Ca requirement. The result is the same for ATTD-P. The Ca : P ratio of hydroxyapatite (most of the mineral in bone) has been estimated at 2.16 (Crenshaw, 2001), which corresponds to 39% Ca and 18% P, the values used in the present model. A Ca : P ratio of 2.00 has been measured using the total bone mass of pigs weighing 90 kg (Nielsen, 1973). The sensitivity analysis nevertheless shows that bone Ca : P did not have a strong impact on the recommendations obtained from the model. Finally, interactions between parameters contributed very little to the total variance of these two outputs.

Influence of dietary calcium and phosphorus on growth performance

Modification of growth through a loss of appetite in case of P deficiency is well-known (Suttle, 2010). As whole-body ashes represent about 3% of BW, this is not due to P deposition itself. Pigs fed with low-P diets frequently have low feed intake, growth rate and sometime feed efficiency. The reduction in feed intake thus reduces protein and energy consumption that can then interfere with growth and feed efficiency. In fact, increasing the available P in these low-P diets increases both feed intake and growth rates but the feed intake reaches normal values before growth rate (Reinhart and Mahan, 1986; Létourneau-Montminy and Narcy, 2013). This suggests that different mechanisms are implicated in these animal responses to dietary P deprivation (Suttle, 2010). To make things more complex, high dietary Ca is known to aggravate symptoms of P deficiency (Létourneau-Montminy *et al.*, 2012; Létourneau-Montminy and Narcy, 2013; Lagos *et al.*, 2019) through a reduced absorption due to the formation of insoluble Ca : P complexes (Narcy *et al.*, 2012). That's why, besides the Ca and P levels, the ratio between these minerals is very important. Moreover, Ca deficiency (Vier *et al.*, 2019a) could also modify growth performance. Besides, overfeeding these minerals also reduced growth performance. Vier *et al.* (2019a) showed that over 130% NRC STTD-P (ratio Ca : P of 1.15) growth performance was reduced while bone is still maximised. It is worthy to note that our model recommendations never exceed this level.

Conclusion

This study proposes the use of a novel mechanistic model for predicting Ca and P requirements for growing pigs with flexible livestock performance goals. The genetic potential of Ca deposition in bone and the deposition of protein in body tissues specified as input parameters is considered to be intrinsic drivers of P requirements. This is the only model that predicts bone growth independently of protein growth, thus allowing allometric growth differentiation of these tissues. This is all the more important since the modern pig body composition and genetic data used for the model parameterisation show that protein and bone growth are independent and evolve very differently as live weight increases. About 70% of P is retained with Ca in bone independently of protein, further reinforcing the relevance of this approach. In fact, this new approach changes the way to estimate Ca and P requirements by growing pigs, and even more for replacement gilts particularly at the end of growth, where the requirements for bone do not plateau as those of protein. Integration of the effect of Ca and P on feed intake and feed efficiency will allow the prediction of requirement that maximise growth performance. However, it needs further studies to understand the underlying mechanisms to mechanistically simulate them in the model. A future study will also be run in order to validate the described model.

Due to technological advancement, farming operations have changed vastly over the past few decades. To profit from the precision afforded by these advanced devices and improve the efficiency, safety and sustainability of agriculture and lessen its negative impact on the environment, the power of data must be harnessed. By allowing the estimation of P and Ca requirements for different bone mineralisation objectives for the moment and in a further version for growth performance, the proposed model offers a more robust approach than the existing models. It also contributes to the science underlying precision feeding (Pomar *et al.*, 2015), a potentially transformative technology and promising tool for ensuring the sustainability of animal protein production by feeding livestock exactly what they need, thereby reducing feed costs and environmental impact.

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Declaration of interest

None.

Ethics statement

Not applicable.

Software and data repository resources

None of the data or the model were deposited in an official repository.

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