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A dynamic growth model for prediction of nutrient partitioning and manure production in growing–finishing pigs: Model development and evaluation[1]

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ABSTRACT: Nutrient loading and air emissions from swine operations raise environmental concerns. The objective of the study was to describe and evaluate a mathematical model (Davis Swine Model) of nutrient partitioning and predict manure excretion and composition on a daily basis. State variables of the model were AA, fatty acids, and a central pool of metabolites that supplied substrate for lipid synthesis and oxidation. The model traced the fate of ingested nutrients and water through digestion and intermediary metabolism into body protein, fat, water, and ash, where body protein and fat represented the body constituent pools. It was assumed that fluxes of metabolites follow saturation kinetics, depending on metabolite concentrations. The main inputs to the model were diet nutrient composition, feed intake, water-to-feed ratio, and initial BW. First, the model was challenged with nutrient partitioning data and then with excretion data. The data had 48 different feeding regimes with contrasting energy and lysine intakes at 2 different stages of growth. The overall observed and predicted mean were 109 and 112 g/d for protein deposition and 132 and 136 g/d for lipid deposition respectively, suggesting minor mean bias. Root mean square prediction error (RMSPE) was used in evaluation of the model for its predictive power. The overall RMSPE was 2.2 and 4.1 g/d for protein and lipid deposition, respectively. The excretion database used for evaluation of the model was constructed from 150 digestibility trials using growing–finishing pig diets that had a wide range of nutrient chemical composition. Nutrient and water excretion were quantified using the principle of mass conservation. The average daily observed and predicted manure production was 3.79 and 3.99 kg/d, respectively, with a RMSPE of 0.49 kg/d. There was a good agreement between observed and predicted mean fecal N output (9.9 and 9.8 g/d, respectively). Similarly, the overall observed and predicted mean urine N output was 21.7 and 21.3 g/d, respectively, suggesting minor mean bias. The RMSPE was 1.9 and 4.1 g/d for fecal and urinary N, respectively. Evaluation of the model showed that the model predicts manure excretion and N content well and can be used to assess environmental mitigation options from swine operations.

Key words: manure, modeling, nutrient excretion, nutrient partitioning, pigs

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INTRODUCTION

One of the goals in animal production is to convert nutrients in feed into useful animal products (meat, eggs, milk, wool, etc.) as efficiently as possible, minimizing nutrient excretion. Accurate and precise estimation of the amount and composition of manure is essential in decision support for a sustainable manure management program. Mathematical models can provide a better understanding of nutrient utilization and excretion in a swine production system (e.g., van Milgen et al., 2008). For assessment of mitigation options for a more sustainable swine production system, models need to predict the composition and amount of nutrient excretion (Dourmad and Jondreville, 2007). Most manure management programs assume linear relations

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connecting dietary variables to animal performance and are too simple and empirical to account for many of the animal–feed interactions that influence the efficiency of nutrient utilization (Rigolot et al., 2010). Therefore, these linear models cannot adequately predict animal performance from given dietary inputs and should be complemented with and eventually replaced by process-based models that describe quantitatively how dietary nutrients are digested, metabolized, and excreted in swine. Although Rigolot et al. (2010) developed a model to estimate manure amount and composition, the model was static; hence, it cannot track the effects occurring during growth. Their predictions should be regarded as averages over a given growth period.

From a biological perspective, nutrient excretion can be viewed as the "residual" and hence prediction of nutrient partitioning between protein and lipid deposition is central. The proposed simulation model (Davis Swine Model) is a mathematical representation of digestive and metabolic processes. Outputs from the animal model can potentially be used as inputs in manure and soil models to estimate farm level emissions.

The objectives of the current study were to develop and evaluate a dynamic model for the growing pig (15 to 125 kg BW) describing 1) energy and nutrient partitioning and 2) manure excretion and composition on a daily basis. Based on the simulated rates of nutrient transactions in the pig, the model is developed to predict growth rate and the chemical composition of growth from weaning to maturity.

MATERIALS AND METHODS

Model Description

The Davis Swine Model is a dynamic, semimechanistic model. The general scheme of the model is given in Fig. 1. The model consisted of 2 submodels: the first represented nutrient digestion and absorption and the second represented metabolism of absorbed nutrients, including retention in the body pools of protein, lipid, and ash. In the digestion submodel, the rates of nutrient absorption were calculated as dietary intake and endogenous secretion minus excretion with feces and fermentation gases, taking apparent digestibility into consideration. The rates of fecal excretion were calculated through apparent fecal digestibility coefficients. A definition of variables and parameters used (with values, if available) are given in Table 1 and a summary of the digestion submodel is given by Eq. [1] to [3] in Table 2. Uptake of ileal digestible nutrients was taken as a starting point with feed intake (**FI**) as one of the major driving forces in the model. Consequently, the model was not able to evaluate the digestive interactions between nutrients or between nutrients and the animal (Strathe et al., 2008). The body tissue metabolism submodel was mainly mechanistic; that is, the behavior of the model is determined by its component parts (nutrients and metabolites) and their interactions (flows of matter).

Inputs to the model were 1) feed characteristics containing DM content; water-to-feed ratio; and chemical composition of DM, particularly CP, 10 essential AA (**EAA**), dietary fiber, starch, sugars, and crude fat; and standardized digestibilities of the individual chemical fractions; 2) animal characteristics containing age at the beginning of the simulation period and genetic capacities for protein and lipid retention (in the form of Gompertz parameters); and 3) environmental characteristics containing temperature in the barn. The model was based on a feed library that contained more than 100 individual feedstuffs based on NRC (1998) tables.

Model outputs were the simulated values of all state and rate variables at any time point during the simulation. From these numbers, the model calculated the predicted animal performance: retention of protein, lipid, ash, and water; heat and methane production; excretion of water; and N and C in feces and urine on a daily basis. These rates were then summed to yield daily rates of manure production. The rates of absorption of EAA, ammonium, short-chain fatty acids (**SCFA**), glucose, and triglycerides were calculated on the basis of CP, EAA, dietary fiber, starch, sugars and crude fat intake, and the standardized digestibilities and fermentabilities of these nutrients. The rate variables describing fecal excretion of protein, fiber, and fat were converted into moles of N and C, using factors given by Strathe et al. (2008).

Absorbed AA were assumed to be either synthesized into body protein or catabolized. Body protein was continuously being turned over and the difference between the 2 fluxes represented the rate of protein retention. Nitrogen from catabolized AA and absorbed ammonium was assumed to be synthesized into urea and excreted in the urine with proportionate amounts of urinary C. Triglycerides absorbed in chylomicrons were hydrolyzed into fatty acids and glycerol. Body fat was synthesized by esterification of fatty acids with glycerol phosphate and the rates of lipolysis into fatty acids and glycerol. The difference between lipid synthesis and degradation represented the rate of body fat retention. Keto acids from AA deamination, SCFA, glucose, glycerol, and long-chain fatty acids entered a common pool of intermediary metabolites. This pool supplies substrates for the de novo synthesis of fatty acids and glycerol phosphate and C for urea and other compounds in the urine as well as fuel for oxidative pathways. The mathematical statements are described in more detail below. Conversion factors for converting kilograms of

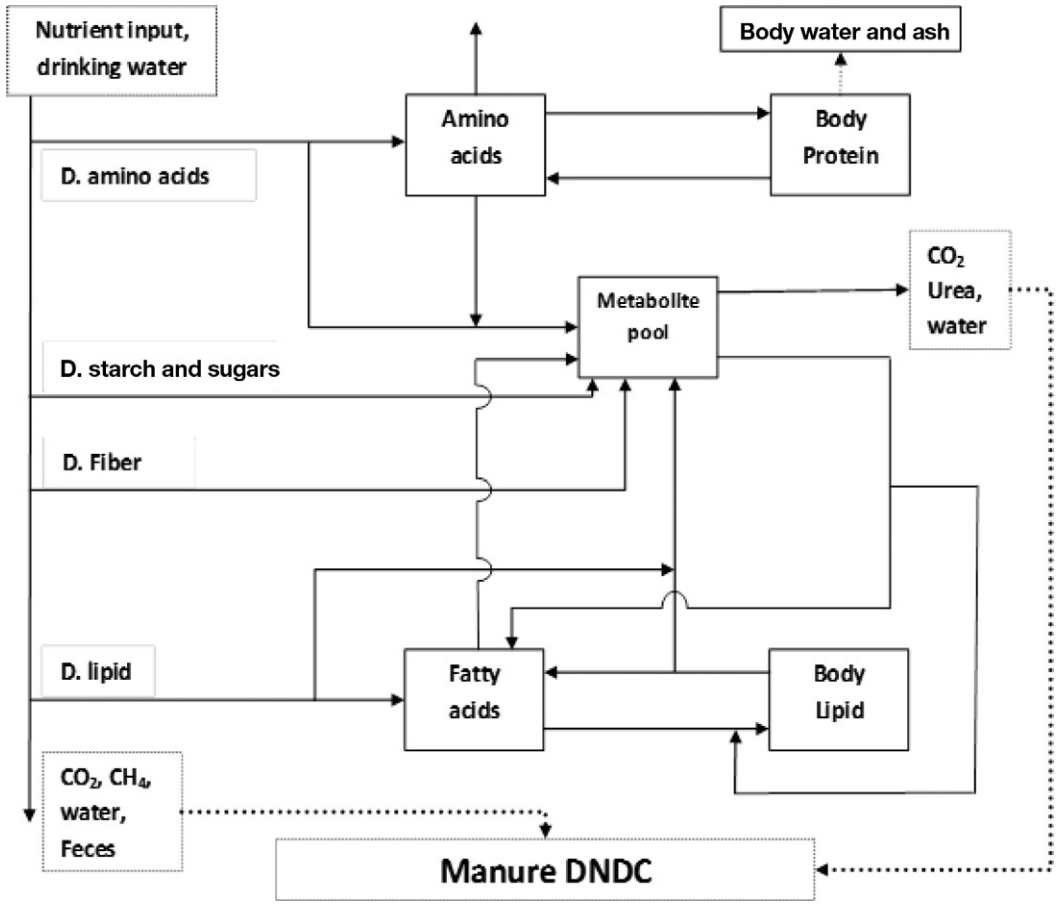

Figure 1. Flow diagram of a dynamic simulation model of growing pigs. Boxes represent state variables and arrows rate variables (mol N/d or mol C/d). The dimensions of the body pools were moles N (body protein) and moles C (body lipid). Metabolite pools were expressed relative to the empty BW (EBW), that is, moles N/kilograms EBW for nitrogenous compounds and moles C/kilograms EBW for carbohydrate and lipid compounds. D. = digestible; DNDC = Denitrification and decomposition model.

nutrients to moles of N and C were described in detail by Strathe et al. (2008). The equations included in the model are given in Table 2.

Body Composition. The chemical composition of the pig at the start of the simulation period was calculated from the initial BW (kg). The Gompertz growth curve was used to characterize potential growth of body protein and lipid. The weights (kg) of lipid, ash, water, and protein were calculated from protein using allometric equations during the growth period. The weights of ash and water were calculated from body protein and protein and lipid were calculated from mass at birth and maturity (Eq. [4] to [7], Table 2).

Feed Intake. Different equation types (linear, power, and exponential) representing FI are available in the literature (e.g., Whittemore et al., 2001). Feed intake was a model input and represented as a function of BW, which was developed based on experiments by Bikker et al. (1994, 1995, 1996). Feed intake in the individual pig fluctuates over time and there is substantial variability between pigs. Moreover, FI in pigs is highly variable across different production circumstances. Feed intake increases with increasing BW according to a multiple of maintenance (M) scale based on the metabolic BW and the energy density of the diet (i.e., $\mathrm{FI} + M \times 0.475 \times \mathrm{BW}^{0.75}/\mathrm{DE}$). The parameter M can be derived from simple on-farm registrations of starting BW (BW_0) and final BW (BW_1), the time (t) elapsed ($t_1 - t_0$), and total FI (TFI) in a given growth phase. A growth phase corresponds to a specific period when a given diet is fed. These periods are generally short, and hence, assuming linear growth for the given growth phase is acceptable. Solving for M yields

$$M = (\mathrm{DE} \times \mathrm{TFI}) / \frac{0.475 \times \left(\mathrm{BW}_1^{1.75} - \mathrm{BW}_0^{1.75}\right)}{(1.75 \times \mathrm{ADG})},$$

where $\mathrm{ADG} = (\mathrm{BW}_1 - \mathrm{BW}_0)/(t_1 - t_0)$.

Protein Metabolism. The protein metabolism and retention were described by a system of differential equations. The amount of protein accumulated was described by a differential equation depending on the function, representing the amount of standardized ileal digestible EAA available above maintenance and the energy state of the pig. A Michaelis–Menten equation (Eq. [11], Table 2) was used to represent protein accumulation in the metabolite pool. The Michaelis–

Table 1. Definition of parameters and variables used in the model

Item	Description	Parameter value	Unit
Ash	Body ash	–	kg
a_1	Gompertz rate parameter for protein (default)	0.0115	per d
a_2	Gompertz rate parameter for lipid (default)	0.0118	per d
b_1	Allometric parameters for ash	0.96	–
b_2	Allometric parameters for water	0.89	–
B_{EAA}	Body content of essential AA	–	g/g
BHP_0	Basal heat production, at 1.5 feed rate	1.82	MJ/(kg $P^{0.60}$ d)
BHP_1	Basal heat production	0.45	MJ/(kg $P^{0.60}$ d)
c_1	Allometric parameters for ash	–1.45	–
c_2	Allometric parameters for water	1.4	–
C_i	Chemical composition of DM, in which i = [CP, dietary fiber (DF), starch (ST), sugars (SU), crude fat (CF)]	–	g/kg
d_{FA}	Differential equation fatty acid pool	–	mol/d
D_i	Digestibility	–	–
d_L	Differential equation of body lipid deposition	–	mol/d
d_P	Decision for minimum rate of protein retention	–	mol/d
d_{TCA}	Differential equation of metabolite pool	–	mol/d
EBW	Empty BW	–	kg
ED	Energy density of the metabolite pool	–	MJ/mol C
FI	Feed intake	–	kg/d
GF	Gut fill	0.05	–
k_{11}	Affinity constant for protein deposition, energy supply	0.17	mol C/kg
k_{16}	Affinity constant for fatty acid synthesis	2.5	mol C/kg
k_{17}	Rate constant for fatty acid catabolism	2.5	per d
k_{18}	Affinity constant for fatty acid retention	0.0001	mol C/kg
k_{21}	Fractional lipid synthesis	0.84	per d
k_{EAA}	Efficiency of utilization of essential AA	–	–
Li	Body lipid	–	kg
L_b	Lipid mass at birth	0.03	kg
L_m	Mature lipid mass (defaults)	73	kg
Pr	Body protein	–	kg
p_0	Basal evaporative heat loss	0.20	–
p_1	Temperature effect on evaporative heat loss	0.012	MJ/(kg $BW^{0.75}$ °C)[1]
P_b	Protein mass at birth	0.22	kg
P_m	Mature protein mass (default)	35.9	kg
RA	Rate of absorption	–	mol/d
$RA_{CF, FA}$	Rate of lipid hydrolysis	–	mol/d
$RA_{CF, GL}$	Rate of glycerol formation from absorbed lipid	–	mol/d
RC	Rate of fatty acid oxidation	–	mol/d
$RD_{L, FA}$	Rate of lipid degradation	–	mol/d
$RD_{L, GL}$	Rate of glycerol usage for lipid degradation	–	mol/d
RE	Rate of excretion	–	mol/d
RH	Total heat production	–	MJ/d
RH_1	Fasting heat production	–	MJ/d
RH_2	Heat of digestion	–	MJ/d
RH_3	Heat of urea synthesis	–	MJ/d
RH_4	Heat of protein turnover	–	MJ/d
RH_5	Heat of lipid turnover	–	MJ/d
RI	Rate of nutrient intake	–	mol/d
RM	maintenance protein rate	–	mol/d
RPmax	Maximum rate of protein retention	–	mol/d
$RR^{(1)}_{AA, P}$	Rate of protein retention – energy dependent	–	mol/d
$RR^{(2)}_{AA, P}$	Rate of protein retention – essential AA dependent	–	mol/d
$RR_{FA, L}$	Rate of lipid retention	–	mol/d
$RR_{GL, L}$	Rate of glycerol usage for lipid deposition	–	mol/d

contintured

Table 1. (cont.)

Item	Description	Parameter value	Unit
RRmax	Maximum rate of lipid retention	–	mol/d
RS	Rate of fatty acid synthesis – energy dependent	–	mol/d
$RS_{FA, L}$	Rate of lipid synthesis	–	mol/d
$RS_{GL, L}$	Rate of glycerol usage for lipid synthesis	–	mol/d
R_{TCA, CO_2}	CO_2 formation	–	mol/d
RWd	Water demand for digestion	–	kg/d
RWe	Water demand for evaporation	–	kg/d
RWf	Water from feed	–	kg/d
RWi	Water intake	–	kg/d
RWo	Water arising from nutrient oxidation	–	kg/d
RWr	Water retention	–	kg/d
RWs	Water demand for synthesis	–	kg/d
T_c	Critical temperature	–	°C
TC_0	Comfort temperature	35.2	°C
TC_1	Comfort temperature	7.02	°C/MJ
TCA	Metabolite pool	–	mol C/d
Wa	Body water	–	kg
Wb	Water balance	–	kg/d

[1]$BW^{0.75}$ = metabolic BW.

Menten equation includes the maximum rate of AA retention in body protein, which was the derivative of a protein growth curve. The value can be obtained from experiments with pigs fed ad libitum optimum composition diets for rapid growth. If neither AA nor energy was limiting growth, protein deposition approached the pig's genetic capacity. This maximum rate was adjusted downward when the metabolite pool was low so interdependence between AA and energy fluxes was taken into account as discussed in detail by Strathe et al. (2008). The AA supply may also potentially determine protein deposition. The supply of 10 EAA and total N were considered in this approach. For each AA, the protein deposition allowed by the supply of available AA was calculated by subtracting the maintenance AA requirement from the standardized ileal AA intake and by multiplying this with the (constant) marginal efficiency of utilization of essential AA ($\boldsymbol{k_{EAA}}$; Table 3). The resulting value was divided by the AA content of body protein to obtain the protein deposition allowed by the AA supply. Calculation of the standardized ileal AA intake is presented in Eq. [2], which implies that the indigestible fractions and specific endogenous AA losses are combined. Requirements for maintenance include the basal endogenous losses and losses due to integuments and basal turnover of protein (Moughan, 1999). The approach depends on the precision with which the parameters (i.e., k_{EAA}) are known or can be calculated. The efficiency parameters can easily be calculated from ideal protein concepts (van Milgen et al., 2008), which are well established in swine nutrition. Furthermore, it should be stressed that when a constant k_{EAA} is assumed as in this case, Eq. [12] (Table 2) gives the AA response according to the linear-plateau concept. Efficiencies were considered constant and hence they represent inevitable AA catabolism. A Michaelis–Menten equation could also be used, implying that the EAA efficiencies were variable, but estimation of affinity constants for the 10 EAA was not straightforward. Finally, a conditional statement was evoked to find the limiting factor for protein deposition. The rate of urinary N excretion was calculated as the difference between ileal digestible N and the realized N retention, representing the rate of AA deamination, plus the rate of ammonia-N formation, resulting from protein fermentation in the hindgut. Consequently, the change of AA pool size in time was 0 (zero pool).

Lipid Metabolism. The maximum rate of fat deposition at a given age was given by the derivative of a Gompertz equation describing a fat growth curve obtained with pigs fed nutritional adequate diets ad libitum. It was assumed that this rate also applies to the de novo synthesis of fatty acids as the animal can synthesize its entire body lipid from glucose, SCFA, and keto acids. Hence, the model did not consider EAA as these were always assumed to be abundant. The change in the pool of body lipid was dependent on 2 flows going into the pool and 2 flows going out of the pool (Fig. 1). The first inflow was the rate of glycerol phosphate incorporation into body fat (esterification), and the second was the rate of fatty acid incorporation into body lipid. The first outflow was the rate of glycerol release from body lipid (lipolysis) and second was the rate of fatty acid release from body lipid (lipolysis). The body lipid was

Table 2. Equations used to describe nutrient digestion, metabolism, and excretion in the model[1]

Equation format[2]	Eq. no.
$RI_i = C_i \times FI \times DM$	[1]
$RA_{i,j} = RI_i \times D_i$	[2]
$RE_i = RI_i \times (1 - D_i)$	[3]
$\text{Ash} = exp[b_1 \times log(\text{Pr}) + c_1]$	[4]
$\text{Wa} = exp[b_2 \times log(\text{Pr}) + c_2]$	[5]
$\text{Pr} = P_b\, exp\{log(P_m/P_b)[1 - exp(-a_1 \times t)]\}$	[6]
$\text{Li} = L_b\, exp\{log(L_m/L_b)[1 - exp(-a_2 \times t)]\}$	[7]
$\text{EBW} = \text{Pr} + \text{Li} + \text{Wa} + \text{Ash}$	[8]
$\text{BW} = \text{EBW}/(1 - \text{GF})$	[9]
$RPmax = a_1 \times \text{Pr} \times log(P_m/\text{Pr})$	[10]
$\text{RR}^{(1)}_{\text{AA, P}} = RRmax/(1 + k_{11}/TCA)$	[11]
$\text{RR}^{(2)}_{\text{AA, P}_i} = (RA_i - RM_i) \times (k_{\text{EAA}_i}/\text{B}_{\text{EAA}_i})$	[12]
$d_P = min(\text{RR}^{(1)}_{\text{AA, P}}, \text{RR}^{(2)}_{\text{AA, P}_i})$	[13]
$d_{AA} = 0$	[14]
$RRmax_{\text{FA, L}} = a_2 \times \text{Li} \times log(L_m/\text{Li})$	[15]
$RS_{\text{TCA, FA}} = RRmax_{\text{FA, L}}/(1 + k_{16}/TCA)$	[16]
$RC_{\text{FA, TCA}} = k_{17} \times \text{FA} \times \text{EBW}$	[17]
$RR_{\text{FA, L}} = RRmax_{\text{FA, L}}/(1 + k_{18}/\text{FA})$	[18]
$RA_{\text{CF, FA}} = RA_{\text{CF}}(52.1/55.1)$	[19]
$RA_{\text{CF, GL}} = RA_{\text{CF}}(3/55.1)$	[20]
$RS_{\text{FA, L}} = RR_{\text{FA, L}}/[k_{21} \times (1 - \text{Li}/L_m)]$	[21]
$RD_{\text{L, FA}} = RS_{\text{FA, L}} - RR_{\text{FA, L}}$	[22]
$RR_{\text{GL, L}} = RR_{\text{FA, L}}/17.4$	[23]
$RS_{\text{GL, L}} = RS_{\text{FA, L}}/17.4$	[24]
$RD_{\text{L, GL}} = RS_{\text{GL, L}} - RR_{\text{GL, L}}$	[25]
$d_{\text{FA}} = (RS_{\text{TCA, FA}} + RA_{\text{CF, FA}} + RD_{\text{L, FA}} - RC_{\text{FA, TCA}} - RS_{\text{FA, L}})/\text{EBW}$	[26]
$d_L + RR_{\text{GL, L}} + RR_{\text{FA, L}}$	[27]
$ED = \sum R_i/(\sum R_i \times CE_i)$, in which i = [keto acids, glucose, SCFA, fatty acids, glycerol]	[28]
$RH_1 = [BHP_0 + BHP_1 \times (M - 1.5)] \times \text{Pr}^{0.60}$	[29]
$RH_2 = k \times \sum RE_i$, *in which* i = [CP, DF, CF]	[30]
$RH_3 = 2 \times 0.078 \times RU - RU \times (0.546 - \text{ED})$	[31]
$RH_4 = 3.5 \times \{a_1 \times (1/k) \times log(P_m - \text{Pr}) \times [P_m/(P_m - \text{Pr})]\} \times \text{Pr}$	[32]
$RH_5 = [RS_{\text{TCA, FA}} \times 2.4335 + RS_{\text{GL, L}} \times 1/3 + (RS_{\text{FA, L}} - RS_{\text{TCA, FA}}) \times 2/17.4] \times 0.078 - RS_{\text{TCA, FA}} \times (10.832/17.4 - \text{ED}) - RS_{\text{GL, L}} \times (1.655/3 - \text{ED})$	[33]
$RH = \sum RH_i$, in which $i = 1, \ldots, 5$	[34]
$\text{R}_{\text{TCA, CO}_2} = RH/\text{ED}$	[35]
$d_{\text{TCA}} = (R_{\text{keto acids, TCA}} + R_{\text{SCFA, TCA}} + R_{\text{glucose, TCA}} + R_{\text{GL, TCA}} + R_{\text{FA, TCA}} - \text{R}_{\text{TCA, FA}} - \text{R}_{\text{TCA, CO}_2} - R_{\text{TCA, GL}} - R_{\text{TCA, urea}})/\text{EBW}$	[36]
$RWi = \text{WFR} \times \text{FI}$	[37]
$RWf = (1 - \text{DM}) \times \text{FI}$	[38]
$RWd = (18.112) \times R_{\text{CP, AA}} + (18/268) \times R_{\text{CF, FA}} + (18.162) \times R_{\text{ST + SU, glucose}}$	[39]
$RWr = exp(c_2) \times b_2 \times \text{Pr}^{b_2 - 1} \times R_{\text{AA, Pr}}$	[40]
$RWo + 0.42 \times R_{\text{AA, TCA}} + 1.07 \times R_{\text{FA, TCA}} + 0.60 \times (\text{R}_{\text{TCA, CO}_2} - R_{\text{TCA, FA}})$	[41]
$RWs = 0.16 \times R_{\text{AA, P}} + 0.07 \times (R_{\text{FA, L}} - R_{\text{TCA, FA}}) + 0.60 \times R_{\text{TCA, FA}}$	[42]
$\text{RWe} = \begin{cases} 0.40 \times p_0 \times RH, & \text{T} \le \text{T}_C \\ 0.40 \times \left\{p_0 + \left[p_1 \times (\text{T} - \text{T}_C) \times \text{BW}^{0.75}\right]/RH\right\} \times RH, & \text{T} > \text{T}_C \end{cases}$	[43]
$T_C = T_{C0} - T_{C1} \times log(RH)$	[44]
$Wb + (RWi + RWf + RWs + RWo) - (RWr + RWe + RWd)$	[45]

[1]Definition of variables and abbreviations used in the equations are given in Table 1.

[2]FA = fatty acid; *M* = Multiple of maintenance; SCFA = short-chain fatty acids.

Table 3. Model parameters, describing essential AA utilization[1,2]

Amino acid	Maintenance, g/kg $BW^{0.75}$ × d	Endogenous, g/kg DMI	Body, kg/kg CP	Efficiencies, k_{EAA}
Lysine	0.028	0.313	0.070	0.72
Methionine	0.008	0.087	0.019	0.64
Sulfur AA	0.017	0.227	0.029	0.51
Threonine	0.017	0.330	0.037	0.61
Tryptophan	0.004	0.117	0.010	0.57
Isoleucine	0.015	0.257	0.035	0.60
Leucine	0.032	0.427	0.072	0.76
Valine	0.020	0.357	0.047	0.71
Phenylalanine	0.017	0.273	0.038	0.82
Aromatic AA	0.028	0.467	0.066	0.75
Protein	0.466	8.52	1.00	0.81

[1]Model parameters are based on van Milgen et al. (2008).

[2]$BW^{0.75}$ = metabolic BW; k_{EAA} = marginal efficiency of utilization of essential AA.

synthesized by esterification of fatty acids with glycerol phosphate and it was assumed that the supply of fatty acids was the rate-limiting step of this process. Few data on in vivo lipid turnover rates in growing pigs have been published. Fractional rates of lipogenesis, lipolysis, and lipid retention in pigs of 80 kg live weight were estimated in 1 study as 2.3, 0.8, and 1.5% of the body lipid pool per day, respectively (Dunshea et al., 1992). It was assumed in the model that the ratio of lipid deposition to lipid synthesis rate decreases linearly from conception to the stage of maximum body lipid mass. Due to limitation of data availability, lipid turnover was only included in the heat production calculations.

Energy Metabolism. The rate of energy input to the pool of intermediary metabolites was the sum of the individual nutrients, that is, keto acids (deamination of AA), acetate, propionate and butyrate (hind gut fermentation), glucose (starch and sugars), glycerol (dietary fat and lipid turnover), fatty acids, and their combustion values (MJ/mol C). These were taken to be 0.546, 0.438, 0.509, 0.546, 0.467, 0.552, and 0.624, respectively (Blaxter, 1989), yielding the energy density of the metabolite pool (**ED**). The ATP cost of catabolism of the substrates has been accounted for as described later in the section. The simulated rate of heat production by aerobic oxidations includes the following components: basal metabolism (related to the mass of body protein), heat of digestion (related to the excretion of fecal organic matter), heat of urea synthesis (related to the excretion of urinary N), heat of protein turnover (derived from the Gompertz parameters), heat of lipid turnover (related to the rates of fatty acid synthesis), activation of fatty acids with CoA, and phosphorylation of glycerol. The basal metabolic rate is linearly related to the plane of nutrition. The basal metabolic rate was represented as a variable with plane of nutrition and hence the model did not use constant estimates of maintenance requirements, which were variable due to metabolic adaptations of the animal to the plane of nutrition (Koong et al., 1982, 1985). Variations in energy expenditures are related to variation in the weight of metabolically active internal organs. Weights of liver and gut and fasting heat production are known to be functions of body size and level of production (Koong et al., 1982, 1985). The heat production related to protein retention was calculated using ATP as the energy currency. The formation of 1 mol of peptide bonds was considered to require 4 mol of ATP together with a further 1 mol for transport across membranes, making 5 mol. Assuming that the ATP cost of protein retention and turnover can be represented in this way, the associated heat production can be calculated. If the average molecular mass of protein AA residues was 112, then the cost of protein turnover would be 44.6 mol ATP/kg protein or 3.5 MJ of heat/kg protein would be produced, assuming 0.078 MJ of heat/mol ATP is produced. The C from the metabolite pool that is not excreted in urine or used for the synthesis of fat was assumed to be oxidized to CO_2, yielding heat. If the C excreted in urine (as urea) or used for fat synthesis contained more energy than the average C in the metabolite pool, heat production would be reduced. Hence, the deductions were calculated as 0.546 – ED (urea synthesis), (10.8/17.4) – ED (lipid turnover), and 1.66/3 – ED (lipid turnover). These calculations were necessary because nutrients in the metabolite pool used for lipid synthesis, oxidation, or excretion were not explicitly specified.

Water Kinetics. The prediction of the growth as described above of each of the body constituents (protein, lipid, water, and ash) and of the whole pig was the necessary first step to estimate the excretion of chemical compounds and water flows through the pig for the prediction of manure volume. Following a factorial approach, a water balance can be established by applying a framework developed by Schiavon and Emmans (2000). The starting point for computation of water balance was taken as 2.5, representing the water-to-feed ratio. Water was gained from feed, which is related to DM content (Eq. [38], Table 2). Water was also gained through nutrient oxidation with contribution from protein oxidation calculated based on the difference between ileal digestible AA consumed and retained and fat catabolism (Eq. [41], Table 2). Additionally, water is gained from protein and fat synthesis including de novo fatty acid synthesis (Eq. [42], Table 2). Water is lost through demand for digestion, which is related to digestibility of CP, crude fat, starch, and sugars (Eq. [39], Table 2). Water is also lost through evaporation related to the heat production

modified by temperature (Eq. [43], Table 2). Finally, water is lost through body water retention related to body protein retention (Eq. [40], Table 2). The daily rates of manure production were calculated as the sum of fecal excretion of protein, lipid, dietary fiber, and ash plus urinary excretion of urea and the water balance. Hence, nutrient and water excretion were quantified using the principle of mass conservation.

Sensitivity Analysis

Global sensitivity analysis to determine sensitivity of the output for variations in input variables and model variables and was conducted using the method described by Saltelli et al. (2008). All parameters were included in the analysis and a parameter matrix ($\mathbf{x}_{ij}$; i = 1, …, 10,000 and j = 1, …, N) where N is the number of parameters constructed with each column representing a parameter and each row representing a draw from normal distributions. The values for each parameter were drawn from N normal distributions, 1 for each parameter, with CV of 2.5% of the original value. Hence, 10,000 simulations were performed with the parameter inputs for each simulation being given by a row from the parameter matrix. The outputs were saved from each run and stored in a model output matrix ($\mathbf{y}_{ik}$; i = 1, …, 10,000 and k = 1, 2, …, N), with the rows being simulations and the columns the outputs from the model. The **x** and **y** matrices were normalized columnwise, with the use of the following equations:

$$X_{ij} = \left(x_{ij} - \overline{x_{.j}}\right) / \sigma_{x.j} \text{ and}$$

$$Y_{ij} = \left(y_{ij} - \overline{y_{.j}}\right) / \sigma_{y.j}.$$

The columnwise mean values of parameter and model outputs are denoted by $\overline{x_{.j}}$ and $\overline{y_{.j}}$, respectively; $\sigma_{x.j}$ and $\sigma_{y.j}$ are the columnwise SD; and X_{ij} and Y_{ik} are the normalized parameter and output values, respectively. The kth set of model outputs ($Yi^{(k)}$) were regressed on the X_{ij}, in which the upper subscript k is used to indicate the kth (k = 1, 2, …, N) regression model, which is given below and fitted using ordinary least squares:

$$Y_i^{(k)} = \sum_{j=1}^{P} \beta_j^{(k)} \cdot X_{ij} + e_i^{(k)}.$$

The error term in the kth regression model is denoted by $e_i^{(k)}$. The betas, $\beta_j^{(k)}$, represent the change in model output SD per 1 unit change in parameter SD, which is estimated for the kth model output. In the standardized regression setting, the model output variance for the kth model output is given by linear relationships in the parameters and can be calculated as

$$\sum_{j=1}^{N} \beta_j^2.$$

This is equal to R^2, the coefficient of determination, and hence the quantity $1 - R^2$ is the fraction of the model variance for the kth model output that is not explained by linear relationships in the parameters. This fraction can be interpreted as the degree of nonlinearity in model output caused by interactions between model parameters. If $R^2 > 0.8$, then β_j^2 will approximate the first order sensitivity indices obtained with variance decomposition methods (Saltelli et al., 2008). The model was deemed sensitive to a parameter if the square of the estimated regression parameter, β_j^2, was greater than 0.01 for any model output. Hence, model sensitivity coefficients that explain more than 1% of the total model variance are reported.

The global sensitivity analysis was conducted for 2 phases of growth (20–50 and 50–100 kg BW) with 2 diets that were either adequate or limiting growth. Lysine was set as the limiting factor because it is the first limiting AA in corn–soybean meal–based diets. The considered model outputs were ADG, average protein retention, average manure production, and average urinary N excretion. It should be noted that urinary C excretion is proportional to urinary N excretion because it was assumed to originate solely from urea. Dietary information was calculated from a feed library and this source also needed to be evaluated. Uncertainty related to dietary inputs was evaluated only in the first growth phase because dietary information was assumed to be applicable to the whole growth period.

Model Evaluation

The model was compared with experimental data by 3 methods: 1) mean values of predicted and observed response variables; 2) plots of observed versus predicted values, presenting the deviation of the perfect prediction (i.e., $y = x$); and 3) root mean square prediction error (**RMSPE**).

Protein and Lipid Retention in Response to Energy and Lysine Intake. Data from several studies collected by Bikker et al. (1994, 1995, 1996) were used to test the model for its predicted response to energy and lysine intake. In the first study (Bikker et al., 1995), pigs were offered feed at 6 levels ranging from 1.7 times maintenance to ad libitum feeding between 20 and 45 kg of BW. The protein and lipid deposition were determined using the comparative slaughter technique. In the second study, pigs were offered feed at either 2.2 or 3.7 times maintenance between 20 and 45 kg of BW followed by 6 levels of feeding from 45 to 85 kg of

BW (Bikker et al., 1996). In the last study considered (Bikker et al., 1994), the lysine requirement for these animals was determined at 2 levels of feeding. To use the data from these studies, an animal profile was created based on the experimental data of pigs fed close to ad libitum (Bikker et al., 1995, 1996). Model parameters, describing the growth potential of the animal (mature protein mass [$\mathbf{P_m}$] and mature lipid mass [$\mathbf{L_m}$] and Gompertz rate parameter for protein [$\boldsymbol{a_1}$] and lipid [$\boldsymbol{a_2}$] accretion) were calibrated to match the genotypes used in the experiments by Bikker et al. (1995, 1996). The values were 30 kg, 90 kg, 0.0185/d, and 0.0160/d for parameters P_m, L_m, a_1, and a_2, respectively

Nutrient Excretion in Response to Dietary Changes. One hundred fifty diets fed in replicates to Danish growing pigs weighing from 28 to 92 kg for a period of 12 d (Vu et al., 2009) were used for independent evaluation. The 2 major drivers of excreted CP and dietary fiber ranged from 87 to 420 and from 48 to 425 g/kg DM, respectively. The inputs to the model were diet ingredient composition, FI (a fixed value during simulation), water-to-feed ratio (fixed at 2.5 for all simulations), and initial BW at the start of simulation. All simulations lasted 12 d and mean rates of nutrient excretion were computed based on simulated values. For these simulations, default values for parameters Pm, a_1, Lm, and a_2 were used because the experimental data was generated over a period of 3 decades and hence defining a genotype is not possible.

RESULTS AND DISCUSSION

Sensitivity Analysis

The standardized regression coefficient method requires the degree of linearization to be satisfactory ($R^2 > 0.80$). If this condition does not hold, which may be the case for nonlinear models with parameter interactions, other global sensitivity analysis methods need to be used. Tables 4 and 5 show that the R^2 were high ($R^2 > 0.95$), which was expected due to the linearization of the model outputs (i.e., computations of averages following a model run). When the diets in both growth phases were adequate, the parameters describing growth potential (P_m and a_1) and body composition (allometric parameters for water [$\boldsymbol{b_2}$ and $\boldsymbol{c_2}$] and gut fill; Table 1) were major contributors to model variance (in all important predictors), which was expected. The main chemical constituents of empty BW (**EBW**) were water, lipid, protein, and ash. Water and ash were assumed to be independent of lipid but closely related to protein. The scaling parameter (b_2) was constant across pig types and represents changes in distribution of protein with increasing EBW and differences in water-to-protein ratios among body pools (De Lange et al., 2003). The parameter c_2 may vary with pig genotype and may need further calibration. Gut fill, the difference between BW and EBW, ranges from 0.03 to 0.10 of BW. Gut fill varies with BW, feeding level, diet characteristics, and time off feed (De Lange et al., 2003). The model used a default value of 0.05, which may be modified by the user. The fasting basal heat production ($\mathbf{BHP_0}$) component of the model accounted for 3 to 4% of the total variance in the rate of protein retention, which can be explained by the relation between metabolite pool and protein retention.

In diets limiting lysine, parameters describing the marginal efficiency of utilizing lysine ($\boldsymbol{k_{Lys}}$) and body lysine content were major determinants of model variance along with the aforementioned body composition parameters. The model assumed a constant lysine content of 0.069 in protein deposition, which may be affected by the protein intake (Bikker et al., 1994). Mahan and Shields (1998) reported that the lysine content in body protein varied from 0.055 to 0.073. This large variation and the knowledge that the AA composition of body protein may be variable and affected by nutrition may require further attention.

Protein and Lipid in Response to Energy and Lysine Intake

The evaluation data had 48 different feeding regimens with contrasting energy and lysine intakes at 2 different stages of growth. The overall observed and predicted means were 109 and 112 g/d for protein deposition and 132 and 136 g/d for lipid deposition, respectively, suggesting minor mean bias. The overall RMSPE was 2.2 and 4.1 g/d for protein and lipid retention, respectively. Figures 2 and 3 show observed protein and lipid retention as a function of ileal digestible lysine-to-energy ratio. The break point for protein retention was predicted to be around 0.64 of ileal digestible lysine/MJ DE. Bikker et al. (1994) reported that these lysine-to-energy ratios were not affected by level of energy intake ($P > 0.05$) and the model reproduces a similar trend. Overall, the increase in protein retention and decrease in lipid deposition rate with increasing ileal digestible lysine or energy intake were satisfactorily simulated. Hence, the model was capable of simulating the interaction between energy and AA supply occurring during growth. In the Bikker et al. (1994) study, the ad libitum FI was approximately 4 times the maintenance requirement, which was considerably higher than FI on the level of 3 times the maintenance requirement. The model showed that as long as the animals' capacity for protein retention was not fully met, protein retention reaches a maximum at

Table 4. Sensitivity coefficients for the growth model, which account for more than 1% of the total model variance. The values for each parameter were drawn from normal distributions, 1 for each parameter, with a CV of 2.5% of the original value[1]

Model output[2]	R^2	b_2	c_2	P_m	a_1	GF	BHP_0	B_{Lys}	k_{Lys}
BW: 20–50 kg									
ADG	0.993	0.444	0.175	0.027	0.058	0.276			
APD	0.975	0.016		0.271	0.655		0.033		
AMp	0.978	0.025	0.209	0.033	0.095	0.57			
AUn	0.984	0.143	0.175	0.15	0.327	0.173			
BW: 20–50 kg									
ADG	0.998	0.378	0.172			0.313		0.071	0.068
APD	0.999	0.02	0.039			0.043	0.037	0.459	0.443
AMp	0.976	0.061	0.248		0.014	0.562		0.02	0.019
AUn	0.996	0.025	0.041			0.046		0.439	0.424
BW: 50–100 kg									
ADG	0.998	0.51	0.116	0.065	0.038	0.27			
APD	0.996	0.024	0.011	0.563	0.376	0.026	0.03		
AMp	0.985	0.215	0.187	0.042	0.045	0.468			
AUn	0.981	0.163	0.101	0.389	0.229	0.112			
BW: 50–100 kg									
ADG	0.995	0.518	0.119	0.046	0.025	0.28			
APD	0.967	0.064	0.03	0.47	0.29	0.055	0.028	0.032	0.033
AMp	0.986	0.224	0.187	0.041	0.047	0.459			
AUn	0.968	0.106	0.067	0.447	0.258	0.074		0.014	0.014

[1]b_2 and c_2 = allometric parameters for water; Pm = mature protein mass; $a1$ = Gompertz rate parameter for protein; GF = gut fill; BHP_0 = basal heat production, at 1.5 feed rate; B_{Lys} = body lysine content; k_{Lys} = efficiency of utilizing lysine.

[2]APD = average protein deposition; AMp = average manure production; AUn = average urinary N.

each energy level and a corresponding minimum lipid deposition when lysine (balanced dietary protein) was no longer limiting. The model predicted that at higher energy levels, protein retention will approach a plateau with similar protein utilization.

Nutrient Excretion in Response to Dietary Changes

The average daily observed and predicted manure production was 3.79 and 3.99 kg/d, respectively, with a RMSPE of 0.49 kg/d (12.9% of observed mean). Figure 4 shows a plot of observed versus predicted rates of manure production with points evenly scattered around the line of unity, suggesting minor bias in prediction. Previous published models predicted total amount of manure (i.e., kg of manure per pig) and not daily rates of manure (e.g., Aarnink et al., 1992; Rigolot et al., 2010) and hence the current model represents an advance in this aspect of manure management. Prediction of manure output resulting from feeding high-fiber diets was challenging because of a varying degree of water binding by the fibrous feedstuffs. Dietary fiber includes a diverse group of molecules with varying degrees of water solubility, size, and structure, which may influence the rheological properties of the gastrointestinal contents, flow of digesta, and the digestion and absorption process to a variable degree (Bach Knudsen, 2001). Modeling these aspects has proven difficult (Strathe et al., 2008) and it

Table 5. Sensitivity coefficients for the dietary inputs into the growth model, which account for more than 1% of the total model variance[1]

Model output[2]	R^2	Lys	ST	DE	M	DM	WFR	CP	DCP	DF	DDF	DCF
ADG	0.984	0.102	0.036	0.473	0.36							
APD	0.979	0.265		0.374	0.335							
AMp	0.994			0.248	0.202	0.357	0.186					
AUn	0.993	0.03		0.157	0.161			0.322	0.323			
AFn	0.998			0.024	0.023			0.022	0.929			
AFc	0.993			0.177	0.172			0.011	0.49	0.038	0.062	0.033

[1]ST = starch; *M* = Multiple of maintenance;; WFR = water:feed ratio; DCP = digestible CP; DF = dietary fiber; DDF = digestible dietary fiber; DCF = digestible crude fiber.

[2]APD = average protein deposition; AMp = average manure production; AUn = average urinary N; AFn = average fecal N; AFc = average fecal C.

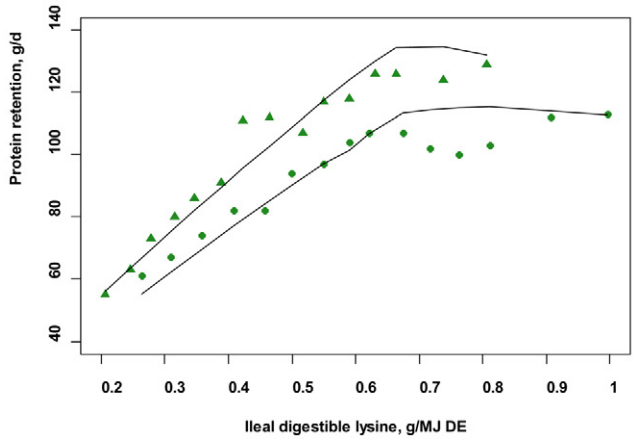

Figure 2. Effect of dietary lysine and energy supply on protein retention in pigs from 20 to 45 kg BW fed at 2.5 or 3.0 times energy requirement for maintenance (Bikker et al., 1994). Simulations with the Davis Swine Model were given by solid lines. The break point for protein retention was predicted to be 0.64 of ileal digestible lysine/MJ of DE calculated with the model.

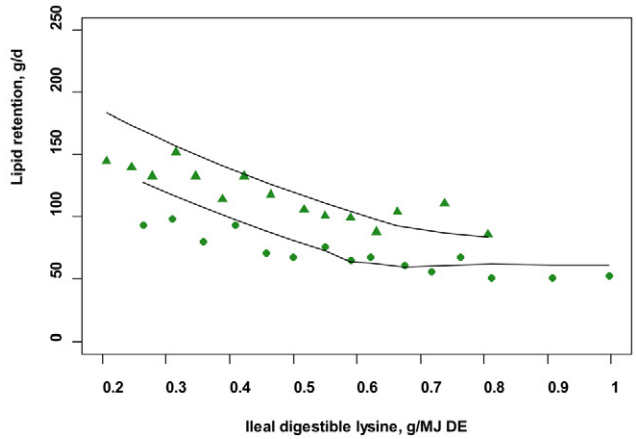

Figure 3. Effect of dietary lysine and energy supply on lipid retention in growing pigs from 20 to 45 kg BW fed at 2.5 or 3.0 times energy requirement for maintenance (Bikker et al., 1994). Simulations with the Davis Swine Model are given by solid lines.

requires an increased number of dietary fractions to be included in the model. Adjustment of animal models to accommodate greater generality has relied on increasing the number of dietary fractions required as model inputs. This notion has led to the development of models that require very detailed feed descriptions that are seldom reported in the literature (Strathe et al., 2008).

There was a good agreement between observed and predicted mean fecal N output (9.9 and 9.8 g/d, respectively) with a RMSPE of 1.9 g/d. Decomposing the prediction error of fecal N excretion into estimating CP content and digestibility suggested that the majority of the error were related to estimation of the CP content in the total mixed ration. Similarly, the overall observed and predicted mean urine N excretions were 21.7 and 21.3 g/d, respectively, suggesting minor mean bias with a RMSPE of 4.1 g/d. There was minor bias in predicted urinary N based on Fig. 5, which shows an even scatter of data around the line of unity.

Prediction of fecal C excretion was associated with higher variation (RMSPE = 38.9 g/d) than similar prediction of N; however, this evaluation was also based on a smaller number of observations (n = 74) from Vu et al. (2009). The overall observed and predicted mean fecal C excretion was 153 and 139 g/d, respectively, suggesting some bias. The deviations from the line of unity increased with the predicted values, indicating that the prediction error was not constant because it depended on the level of excretion (Fig. 6). Dietary fiber was the main factor determining the daily amount of fecal N and C excretion whereas dietary CP was the main factor affecting the daily urinary N excretion. The model predicted positive relation between the C to N ratio in fecal material and dietary fiber, yielding an increase in the methane production in the pigs' digestive tract and potentially a large greenhouse gas production from stored manure.

Model Limitations

The Davis Swine Model requires parameter calibration to specific genotypes and genders (castrates and entire males). Genders and genotypes are represented in the Gompertz parameters, particularly a_1 and a_2. Therefore, genotype sensitive parameters need to be calibrated depending on the user's objective. Furthermore, the Davis Swine Model was developed for pigs kept under optimal sanitary conditions; therefore, it may not respond appropriately to changes in nutrient inputs under high pathogen and viral loads. The present model may not function well at extremely low feeding levels, that is, feed levels below 1.5 times maintenance, which are not relevant for practical applications because most commercial swine operations feed animals at levels of 3 to 4 times maintenance. The predictions of responses

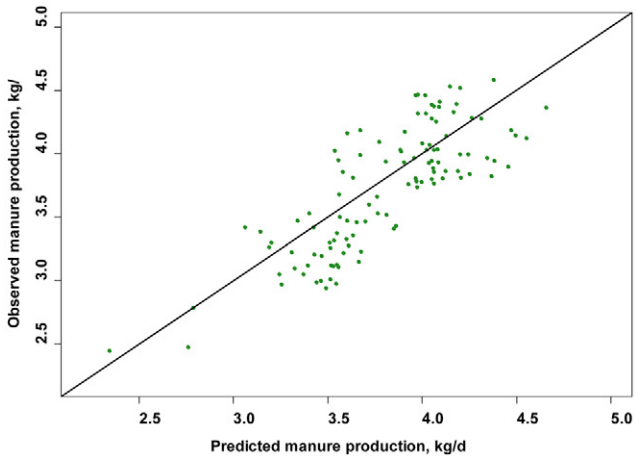

Figure 4. Observed manure production (kg/d) plotted against predicted. A line of unity ($y = x$) is added to the plot.

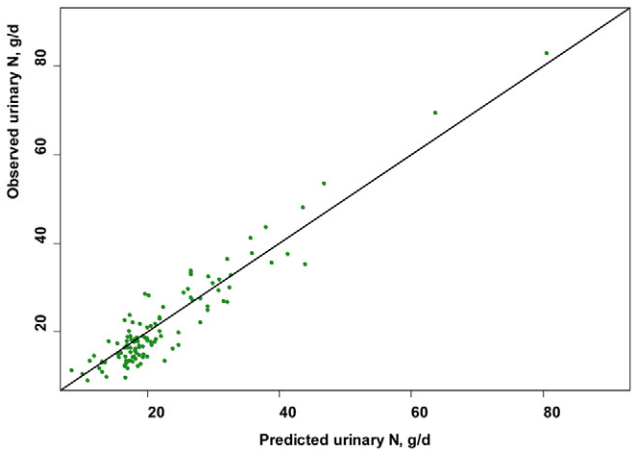

Figure 5. Observed urinary N excretion (g/d) plotted against predicted. A line of unity ($y = x$) is added to the plot.

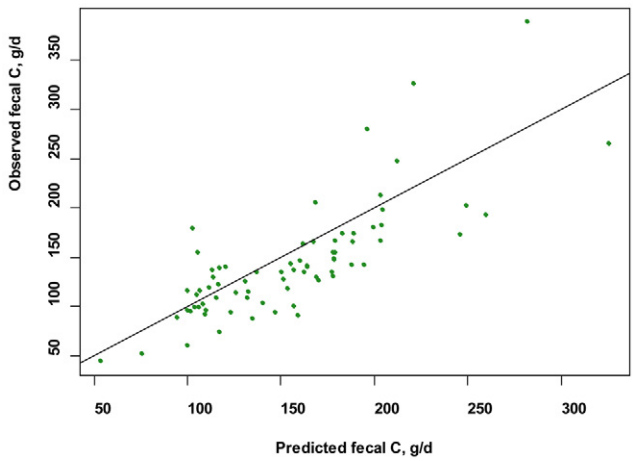

Figure 6. Observed fecal C (kg/d) plotted against predicted. A line of unity (y = x) is added to the plot.

were developed on a daily basis, so it cannot predict the within-day variation in metabolic responses. Finally, it is important to realize that the model predicts the nutritional response for the average animal in the herd. The average animal represents the notion of an "average" or "typical" animal in the herd and hence it was assumed that all pigs have equal growth potentials and were at the same stage of growth. This assumption allows its incorporation into a larger dynamic, deterministic whole-farm model. Furthermore, it does not consider impacts of clinical or subclinical disease, immune system stimulation, social stresses, and other factors that influence growth and nutrient utilization.

In conclusion, the Davis Swine Model is capable of predicting protein and lipid retention in growing pigs under unrestricted or limited nutrient intake. The model was designed to predict manure excretion and composition, which will allow its use as part of a larger whole-farm model for environmental management in swine operations. The model can also be used by animal nutritionists or for teaching nutritional concepts. Finally, the Davis Swine Model can be used to evaluate nutrient utilization by the animal and to test different nutritional strategies.

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