

Characterization of pig genotypes for growth modeling

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ABSTRACT: The models dealt with herein are driven by descriptors of pig growth potential and environment, predicting growth from their interaction. Growth potential parameters relate to resource intake and partitioning to maintenance, protein (P) deposition (PD), and lipid (L) deposition (LD); these parameters quantify genotype (breed, etc.). Simulation of a pig's growth requires characterization of its potential in terms of the associated model parameters. This requires a set of parameters that fully describe the potential, measurement of resource input, and partitioning in a genotype, and using these measurements to quantify those parameters for that genotype. Resource partitioning is commonly covered by potential PD, required LD, and ME_m. Description of the first two features commonly requires three parameters. The ME_m here is restricted to a neutral environment without functions for coping with stressors, which would require extra parameters. Nutrient intake is best modeled as resulting from nutrient requirements and from constraints to physical up-

take, be they external or genetic. Intake and partitioning observations must reflect potential; environmental load must be minimized. Repeatedly measuring whole-body P and L and ad libitum ME intake over a sufficiently wide maturity range (for example from 10 to 175 kg of BW) requires serial slaughter trials with chemical analysis or in vivo techniques such as ultrasound. The latter allow for the description of individual growth patterns and for quantification of variation in addition to mean levels. Parameters can be estimated in three ways. First, P and L observations can be fitted to P and L growth functions. Then, ME_m comes out as the remainder of the ME budget, given valid assumptions about PD and LD efficiency. Second, observed feed intake, growth, and body composition can be fitted to their simulations (parameter calibration, inverted modeling) to avoid P or L measurement. This requires serial data and iteration to match resource requirements to allowance. Third, differential nutrient restriction techniques can be used.

Key Words: Genotypes, Growth, Models, Pigs

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J. Anim. Sci. 81(E. Suppl. 2):E187–E195

Introduction

Characterization of pig genotypes as it is dealt with here should produce input parameters for a specific group of growth models. The genotype's potential for protein (P) and lipid (L) deposition drives these "potential deposition" models: Deposition is predicted from this (fixed) potential and quantification of environmental load. The latter term signifies the suppressive effect of external factors (nutrition, climate, etc.) on the potential's expression. Genotype characterization is difficult here because it is unclear if pigs are fully expressing their potential. Other models ("operational accretion" models, not covered here) do not assume a fixed poten-

tial, and must be parameterized by measuring animals in the environment to be simulated. This type of genotype characterization has been dealt with by Schinckel and De Lange (1996). The difficulty is that it is unclear if the environment has been representative for the target setting.

The genotype is broadly defined here as a type of pig that differs genetically from others. Depending on required detail, this could be a breed (e.g., Duroc vs. Pietrain), a strain within a breed (e.g., PIC's PB427 vs. Belgian herdbook Pietrain), or an individual within a strain. For many deterministic applications, genotype characterization aims at a breed or strain in some stage of its development, and the simulated pig is its typical representative (e.g., the average PB427). Characterization is done by specifying the population means of genotype-specific parameters; together, these represent the relevant part of the population potential. Stochastic simulation deals with individual pigs, and characterization must specify not only population means but also

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Received August 7, 2002.
Accepted June 11, 2003.

(co)variances to generate replicates. Either action requires a concise set of model parameters that fully describe the potential, real-life measurement of resource input and partitioning in a genotype, and using those measurements to quantify those parameters for that genotype.

Resource Intake

When modeling is used to support the understanding of the growing pig as a biological input-output system, it is not very useful to deal with nutrient intake as an input parameter or as a characteristic of an external rationing scheme. Instead, voluntary intake can be modeled as an output parameter. It can be driven by nutrient requirements due to genotype-specific deposition processes (related to resource partitioning, as discussed in the next section) and body maintenance. Such drives are described by Black et al. (1986) and Emmans (1997). Additionally, intake can be constrained by environmental factors such as feed composition (bulkiness, as discussed later in this section; nutrient density), climate (particularly by hot conditions as in Black et al., 1986; Knap, 1999; and Wellock et al., 2003), health (reviewed by Knap and Bishop, 1999; tentatively modeled for a specific disease by Black et al., 1999) and social conditions (such as group size with limited feeder capacity), and/or by animal-intrinsic factors related to effective gut size and feed intake capacity. The latter would require a genotype-specific model parameter, interacting with current body size and characteristics of the feed, such as “bulkiness.” This was described by Ferguson et al. (1994) as a function of organic matter digestibility, and by Whittemore et al. (2003a) as a function of water-holding capacity. The associated genotype-specific parameter (the capability of the pig to deal with feeds with high bulk content) can be measured in real life as described by Whittemore et al. (2003b). When required in the simulation, voluntary intake can be overridden by any kind of rationing scheme after it has been calculated.

Resource Partitioning: Deposition

Resource partitioning in growing pigs is commonly modeled in terms of body maintenance requirements (ME_m), potential protein deposition (PD), required (alternatively called minimal/essential/inevitable/desired) lipid deposition (LD), and surplus lipid deposition, roughly in that order of precedence. Although published “potential deposition” models at first glance seem to differ widely in the way they describe potential PD and required LD , most (such as Whittemore and Fawcett, 1974; Moughan and Smith, 1984; Black et al., 1986; Emmans, 1988; De Greef, 1992; Walker and Young, 1993; Kyriazakis et al., 1994; Quiniou et al., 1996; Möhn and De Lange, 1998; Van Milgen et al., 2000) use essentially the same basic algorithm with two to four genotype-specific parameters. Any energy left after these

two processes and body maintenance have been covered is commonly used for surplus lipid deposition. Differences between genotypes in resource partitioning are then due, in the first place, to variation in the parameters of the potential protein and required lipid deposition rules.

The focus here is on the rules for both processes described by Emmans (1988), not because these are necessarily superior to alternative rules but because they have attractive mathematical features that work well in examples such as the following ones. Emmans modeled potential protein deposition by describing potential protein mass as a Gompertz function of age:

$$P = P_{\infty} \times e^{-e^{-b \times (\text{age} - t_p^*)}} \quad [1]$$

where P is body protein mass as the genotype “desires” it to be at a particular age, P_{∞} is potential mature protein mass, t_p^* is the x-coordinate of the sigmoid’s point of inflexion, and b is the specific growth rate $(dy/dt)/y$ in that point of inflexion. The derivative of this function gives the potential rate of protein deposition (PD , in kg/d), which, in the point of inflexion (at $P = 0.368 \times P_{\infty}$ for the Gompertz function) reaches its maximal value of $PD_{\max} = b \times P_{\infty}/e$ (e is the natural logarithm base).

According to Emmans’s rules, body lipid follows a similar pattern. Assuming full allometry between potential protein and desired lipid (not between actual protein and actual lipid: surplus LD is not dealt with here, nor is a lower LD than desired in the case of nutrient restriction) leads to a common rate parameter b for both fractions, and desired body lipid mass is modeled as:

$$L = L_{\infty} \times e^{-e^{-b \times (\text{age} - t_L^*)}} \quad [2]$$

The points of inflexion t^* cancel out of the derivatives of [1] and [2]. This leaves three parameters for this model to describe the genotype’s intrinsic drive for protein and lipid deposition (not necessarily its operational levels): b , P_{∞} , and L_{∞} .

It must be stressed again that Eq. [1] and [2] are not sufficient to predict actual protein or lipid deposition in pigs under practical conditions; that requires a set of nutrient partitioning rules to deal with the effects of unbalanced or insufficient diets and of environmental load. Emmans’s assumption of full allometry between potential protein and desired lipid is difficult to verify. Knap (2000b) analyzed serial slaughter data from the literature to obtain estimates of b , P_{∞} , and L_{∞} for a wide range of pig genotypes (see the “Observations” section that follows), checked for differences between separate b_P and b_L estimates, found these to be nonsignificant ($0.53 \leq P \leq 0.97$), and concluded that those data presented no reason to abandon the assumption. One of the analyses in the “Serial Measurements” section below shows similar trends, although to a lesser degree. Abandoning the assumption of full allometry would mean

that Eq. [1] and [2] need to be solved for four parameters (b_P , b_L , P_∞ , L_∞) rather than three. This illustrates a crucial point of systems modeling: Reduction of the number of parameters to be estimated may lead to the introduction of strong assumptions. Finding the right balance between the two is often a matter of subjective judgement and always a matter of debate.

Resource Partitioning: Maintenance

The energy requirements for body maintenance (ME_m) vary within animal populations, with a phenotypic CV of approximately 0.1 and a heritability of about 0.3 (reviewed by Knap, 2000c). They are commonly modeled as a simple function of body weight (e.g., $ME_m = \alpha \times BW^\beta$) or body protein mass, which implies maintenance of a body in environmentally neutral, unchallenging conditions without the need to switch on additional coping functions (Whittemore, 1983; Cleveland et al., 1983; Baldwin and Hanigan, 1990). Those functions would include the following: 1) service functions (Gill and Oldham, 1993), such as circulation, coordination, respiration, and excretion, 2) protein turnover and active transport of molecules across cell membranes, and 3) physical activity at its basic level. Differences between genotypes can be conveniently modeled in terms of variation in the above parameter α , which then becomes the fourth genotype-specific model parameter (where necessary in conjunction with β) to describe resource partitioning. The ME requirements for protein turnover and membrane transport are related to body composition, but not to such an extent that they have important consequences for the between-animal variation in ME_m (Knap, 2000a). Assuming little variation in service functions, much of the ME_m variation must then be due to variation in basic activity levels.

Additional maintenance functions include activity above the basic level and functions to cope with climatic, immunological, and social stressors. When such functions are switched on, the parameters α and/or β in the above equation for ME_m can become strongly inflated and difficult to handle. Such cases are more usefully dealt with by dedicated routines that model the additional function as such (see the references for constraining factors in “Resource Intake”) and leave neutral ME_m unchanged. This may require one or more additional genotype-specific parameters, such as the one for immunocompetence in Figure 1.

Observations

When observations on resource intake and partitioning are to properly reflect the animal’s growth potential, they must be collected under minimal environmental load so that additional maintenance functions are not triggered and do not act as a resource sink. Hot climatic conditions, infectious conditions, and overcrowding can suppress energy intake so that the requirements of potential deposition cannot be fulfilled.

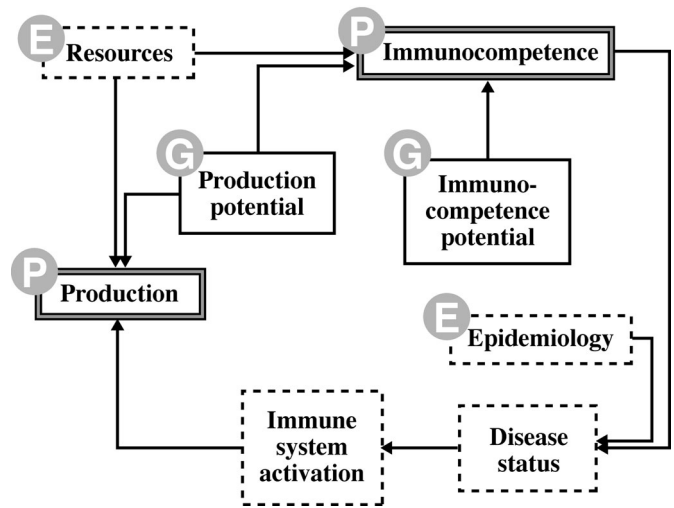


Figure 1. Genetic (G), environmental (E), and phenotypic (E) entities involved in the relation between live-stock production and infectious disease. After Knap and Bishop (1999).

On the other hand, when energy intake is increased (such as in cold climatic conditions), neutral ME_m will be overestimated if the environmental load is not properly measured and adjusted for (which is difficult).

Fitting the three genotype-intrinsic parameters (b , P_∞ , and L_∞) that drive potential protein and lipid deposition (Eq. [1] and [2]) to observed data requires measurement of whole-body protein and lipid mass and ad libitum ME intake at various stages of developmental maturity, with a wide enough maturity range to allow for a meaningful fit of the sigmoid curve. An example is in Knap (2000b), where serial slaughter data from the literature were analyzed to obtain genotype by sex-specific estimates of the above parameters for a wide range of pig genotypes. The nature of such data (serial slaughter and chemical analysis of body composition, with a single data point per animal) leads to estimates of the b , P_∞ and L_∞ population means only (the animals referred to here had not been raised in conditions that allow for direct comparison of those estimates across genotypes).

Prediction of the within-population variation requires longitudinal analysis as described in the next section, with serial in vivo measurements per animal—for example, with ultrasound, electrical conductivity, x-ray, or isotope dilution techniques (Forrest et al., 1989; Allen, 1990). The prediction of such variation is of foremost interest in the context of animal breeding, where differences between individual animals are the central theme. Kinghorn (1998) and Knap (2000c) provide further discussion, whereas Pomar et al. (2002) show why the modeling of variation may be of interest outside an animal breeding context.

Serial Measurements

To illustrate the concept of pig genotype characterization based on serial within-animal measurements (also

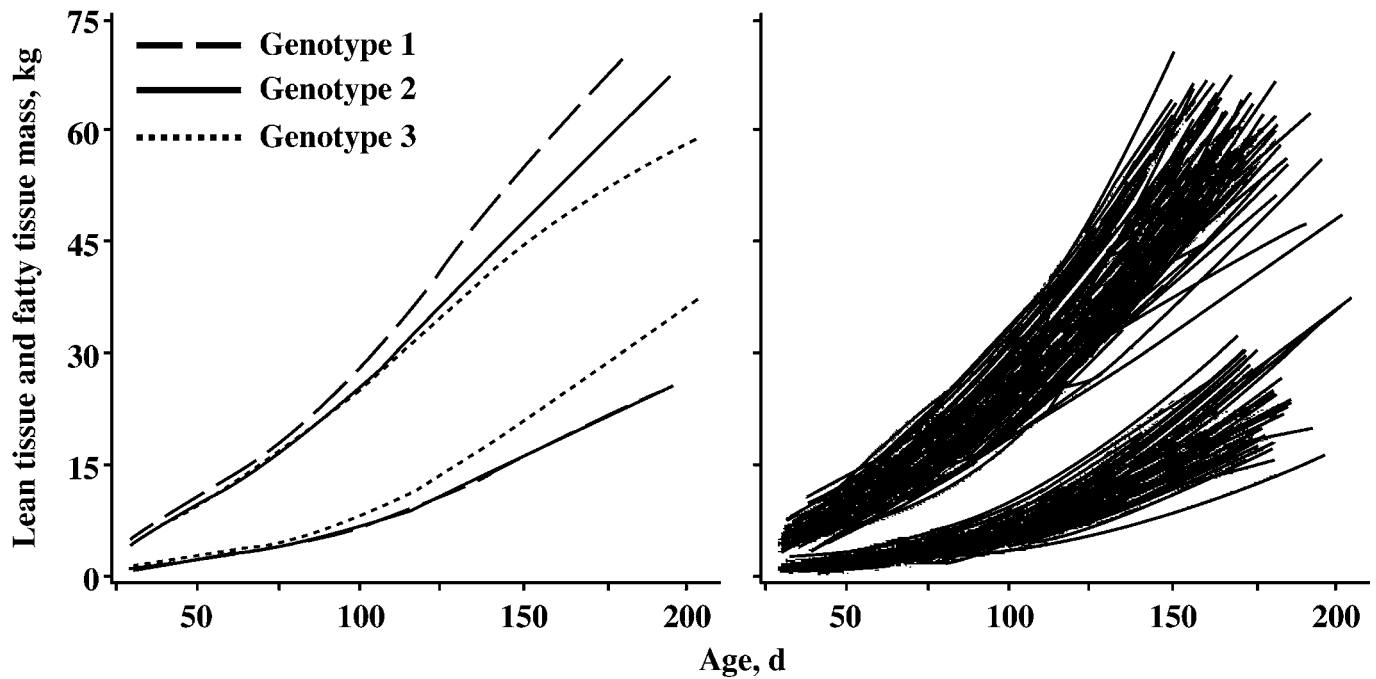


Figure 2. Lean (muscle plus viscera) tissue (top) and fatty tissue mass (bottom) measured by x-ray computer tomography in 141 pigs of three genotypes in relation to age. Lines are spline interpolation plots; data from Kolstad (2001). Left: genotype means; right: individual pigs. Genotype 1: modern Norwegian Landrace (NoL); Genotype 2: modern Norwegian Duroc; Genotype 3: cross of Genotype 1 with 1975 NoL.

referred to as longitudinal measurements) of body composition, data from two experiments are used, as described by Kolstad (2001) and Landgraf et al. (2002).

The data of Kolstad (2001) were collected with a different aim than carrying out the current analysis. These data comprise computer tomography x-ray observations of body muscle mass, lean viscera mass, and fatty tissue mass in 141 pigs of three genotypes and two sexes. Computer tomography scans were obtained at five body weights in the range of 10 to 105 kg. The development of observed total lean tissue mass (muscle plus viscera) and fatty tissue mass in relation to age is shown in Figure 2.

These graphs show that at this end weight of 105 kg, most pigs had barely reached the point of inflexion of their growth curves with the associated PD_{max} and LD_{max} levels; this may indicate that nutritional conditions had been limiting the expression of potential deposition rates. As a consequence, attempts to fit sigmoid equations to the individual lean and fatty tissue data failed, and the parameters of Eq. [1] and [2] could not be estimated.

Instead, for each pig that reached an end weight over 70 kg, second- or third-degree polynomials of lean and fatty tissue mass were fitted as a function of age, and the derivatives of these were used to determine maximal tissue growth rate within the range of observations; an important disadvantage of this method is that it is difficult to quantify the accuracy (standard error) of the predictions. The PD_{max} and LD_{max} can then be predicted

assuming that lean tissue contains 19% protein and fatty tissue contains 75% lipid at the stage of maximal protein deposition, following the results obtained by Wagner et al. (1999) from carcass dissection of pigs in the same body weight and body fatness range as Kolstad (2001). These results, which underestimate the true potential levels because many of these pigs had not attained their maximal growth yet, show effects ($P < 0.01$) of sex and genotype on PD_{max} and LD_{max} . The genotype by sex means and between-animal standard deviations of these traits are in Table 1.

The specific growth rates (b in Eq. [1] and [2]) were calculated (and likely overestimated) by dividing PD_{max} and LD_{max} by their estimated contemporary P and L mass. Table 1 shows that b_P and b_L differ between genotypes ($P < 0.02$) but not between sexes ($P > 0.4$). All of the b_P predictions are somewhat lower than their associated b_L values ($P < 0.0001$). This means that realized LD was not allometric to realized PD , which suggests again that these pigs had been fed an unbalanced diet, and potential deposition was not expressed.

All these traits show CV well over 10% (in seven out of 24 cases over 20%), much higher than Knap's (2000a) suggested CV for b (3%) and PD_{max} (6%). The P_{∞} values that can be (under)estimated from the PD_{max} and b_P values in Table 1 ($P_{\infty} = PD_{max} \times e/b_P$) range from 17 to 30 kg; the lowest values (for genotype 3) are indeed unrealistically low. The corresponding L_{∞} values are 1.4, 1.9, and 3.1 times higher (for genotypes 1, 2 and 3, averaged over sexes), which is fully in the range found by Knap (2000b).

Table 1. Statistics of maximum protein and lipid deposition (PD_{max} , LD_{max}) in growing pigs^a and of the associated specific growth rate parameters (b_P , b_L)^b

Genotype	Gender ^c	n	PD_{max} , kg/d		LD_{max} , kg/d		b_P , $kg \cdot d^{-1} \cdot kg^{-1}$		b_L , $kg \cdot d^{-1} \cdot kg^{-1}$	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	m	20	0.133	0.0185	0.193	0.0408	0.0120	0.00140	0.0148	0.00225
1	f	22	0.121	0.0215	0.244	0.0451	0.0135	0.00286	0.0159	0.00227
2	m	22	0.102	0.0168	0.212	0.0635	0.0114	0.00228	0.0136	0.00178
2	f	28	0.096	0.0118	0.243	0.0463	0.0118	0.00237	0.0142	0.00207
3	m	8	0.100	0.0181	0.282	0.0674	0.0138	0.00343	0.0141	0.00214
3	f	8	0.079	0.0088	0.286	0.0440	0.0126	0.00293	0.0134	0.00096

^aApproximated in a subset of data from Kolstad (2001). Genotype 1 = modern Norwegian Landrace (NoL); Genotype 2 = modern Norwegian Duroc; Genotype 3 = cross of Genotype 1 with 1975 NoL.

^b b_P quantifies the growth rate of body protein in the point of inflexion of its sigmoid growth curve (where it attains its maximal level, PD_{max}) as a proportion of body protein mass at that time: $b_y = (dy/dt)/y$.

^cm = castrated males, f = females.

Landgraf et al. (2002) reported on magnetic resonance measurements of body muscle mass and fatty tissue mass in eight pigs of a commercial three-way cross; in the course of the same experiment, 442 female and castrated male pigs were subjected to measurement of deuterium (D_2O) dilution to estimate total body water mass (and from that, lipid and protein mass; Susenbeth, 1984) at six body weights in the range of 15 to 140 kg. This higher end weight had been expressly chosen to avoid the problems with fitting sigmoid functions to the data that were encountered with the previous dataset, expecting that the pigs would have reached a reasonable proportion of their mature weight at 140 kg.

Presented here are the results of a preliminary analysis of the D_2O dilution measurements in 14 of these pigs. Eq. [1] and [2] were fitted to the data of each individual pig using the MODEL procedure of SAS (SAS Inst., Inc., Cary, NC) as in Knap (2000b). Iterations did not converge in one of these 14 cases. Six other cases produced very high standard errors for the estimates of P_∞ (five times), L_∞/P_∞ (five times), b (three times), and PD_{max} (once), but most estimates fell within the range of the results from the remaining seven cases, which produced estimates for P_∞ ranging from 27.7 to 40.7 kg, for L_∞/P_∞ ranging from 1.95 to 3.49 kg/kg, for b ranging from 0.0089 to 0.0128 $kg \cdot d^{-1} \cdot kg^{-1}$, and for PD_{max} ranging from 0.118 to 0.137 kg/d. Overall, the estimates of the 13 “converging” pigs amount to mean values \pm standard deviations of $P_\infty = 34.4 \pm 5.12$ kg, $L_\infty/P_\infty = 2.83 \pm 0.76$ kg/kg, $b = 0.0104 \pm 0.0015$ $kg \cdot d^{-1} \cdot kg^{-1}$, and $PD_{max} = 129 \pm 10.5$ kg/d, rather fat and slow-growing compared with the sire lines analyzed in a similar way by Knap (2000a) but within the realistic range. The CV are 15, 27, 14, and 8%, respectively, again higher than suggested by Knap (2000b). The observations and fitted curves are in Figure 3. Applying Eq. [1] to body weight resulted in a mean estimate of the asymptote at $BW_\infty = 240$ kg.

Taken together, the results of these analyses of the Kolstad and Landgraf data suggest that there is substantial between-animal variation in the traits that Emmans (1988) chose to drive his growth model. Mea-

surement of these traits on the individual animal level is feasible with the use of x-ray or isotope dilution techniques but requires data collection over a wide body weight range; based on the latter data set, 140 kg seems just sufficient to allow for a satisfactory fit of sigmoid functions in pigs with an asymptotic weight of 240 kg, and a sigmoid describes protein deposition better than lipid deposition. Based on the former one, 105 kg is certainly insufficient.

The predicted P_∞ , L_∞/P_∞ , and b values from these two datasets show much more between-animal variation than suggested by Knap (2000a). In that study, the output of a stochastic growth simulation model (mean values and between-replicates variation of growth rate, feed intake, and body protein content) was compared to literature findings, and the CV (input variables to the model) of P_∞ , L_∞/P_∞ , and b were altered until a satisfactory match was achieved. Those input parameters were assumed in the simulation model to be independently and normally distributed with uniform distribution characteristics both across replicates and over time. By contrast, the variation found in the present analyses was estimated directly from real data (even though the estimation is a double prediction: protein and lipid mass were predicted from x-ray or D_2O dilution readings), the results were fitted to polynomial or sigmoid functions, and the parameters of these were further analyzed separately. As such, the variance of these predicted values includes the true residual variance, variance due to inaccuracy in the prediction equations for protein and lipid mass, variance due to lack of fit (particularly the six cases with high standard errors in the Landgraf data), variance due to unstable convergence and small numbers of observations, and bias (particularly the cases with end weights considerably below the points of inflexion in the Kolstad data). Clearly, both approaches can be improved. First, by fitting the stochastic model to consistent data (like the Kolstad and Landgraf data) rather than to a conglomerate of literature values. Second, by analyzing the data with multivariate random regression techniques to predict the parameters of interest and to estimate their

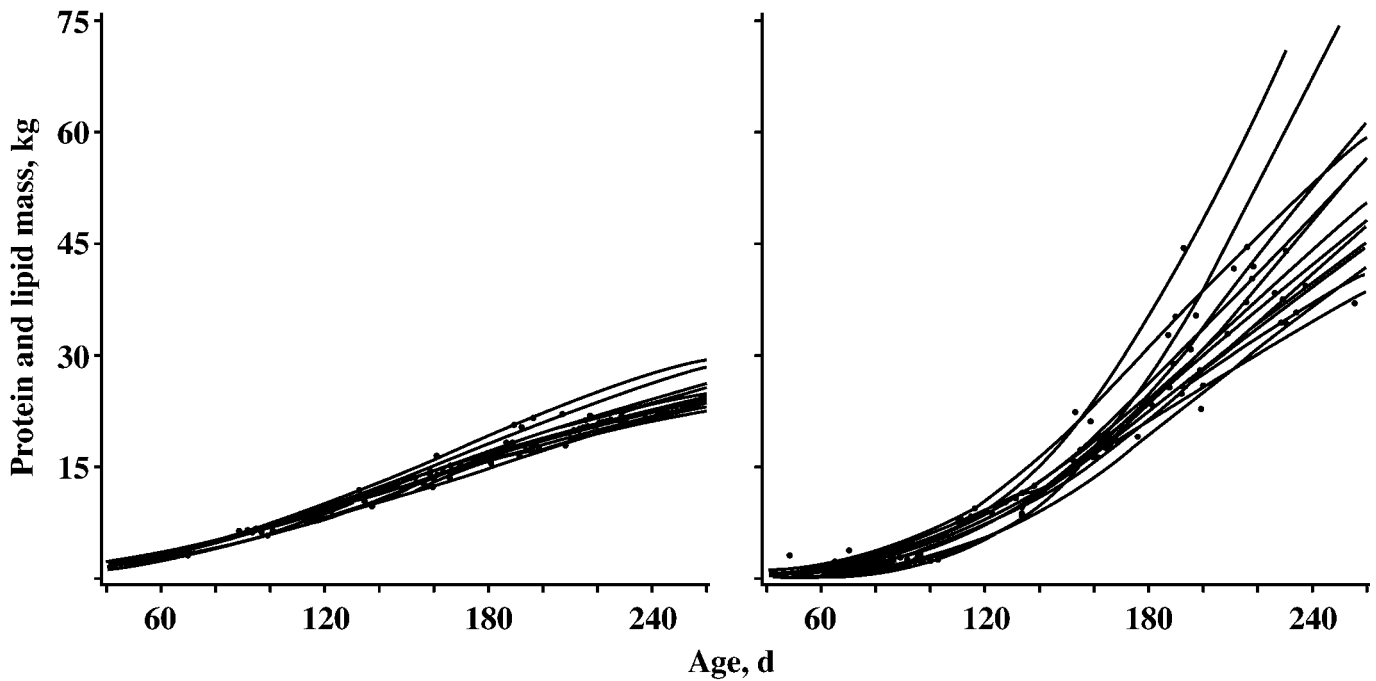


Figure 3. Protein (left) and lipid mass (right) measured by D₂O dilution in 14 pigs in relation to age. Dots are observations, lines are Gompertz curves fitted according to Eq. [1] and [2]; data from Landgraf et al. (2002).

(co)variation simultaneously, taking proper account of their interdependence.

Not surprisingly, fitting population-level sigmoid equations to pooled observations of P and L as determined in serial slaughter trials (as in Knap, 2000b) is much less demanding than fitting individual animals. Another issue is whether it is possible, in practice, to feed and house a growing pig in such a way that its growth potential is fully expressed. Both the Kolstad (2001) and the Landgraf (2002) results show deviations from the allometric double Gompertz model implied in Eq. [1] and [2], which suggests that imbalanced diets have suppressed potential protein deposition in these pigs or that this model is not the appropriate descriptor of the potential, or possibly both. See Knap (2000a,b) for more discussion on the same issue.

Inverted Modeling

An alternative to the direct measurement of model parameter-related traits is “inverted modeling,” or “reverse simulation” as it was called by Bourdon (1998). In animal science, this notion goes back to Baldwin (1976), who suggested that estimates of model parameters could be obtained as follows: “assign initial values to unknown parameters in the model; compute, using these values and diet input data, ... body energy change estimates; compare these computed estimates with experimental data for each diet input and compute from this comparison, an error of estimate; and allow a computer routine to systematically adjust parameter values in ... iterative solutions until differences ... between

computed and real data are minimized.” This approach is an iterative one. The model is “inverted” in the sense that phenotypic observations on traits that conventionally would be model output are now used as input to obtain prediction errors that are iteratively minimized by changing the value of some model parameters, and the final values of these parameters are the output of this iterative process. The procedure is similar to “fitting of equations to data.”

A more elegant way of obtaining the same would be to algebraically rework the model equations, to end up with the fundamental parameters (rather than the observations) on the left-hand side, and coding this inverted model as a new computer program. The most important advantage of this analytical approach is that the resulting program directly produces a unique solution without any need for iteration. As a consequence, analytical model inversion has attracted much attention from a wide variety of scientific and engineering disciplines. The problem with this approach is that many differential equation systems, which is what growth models essentially are, cannot be inverted analytically without serious difficulties. Many of those problems are “ill-posed,” having no solution, a series of nonunique solutions, or solutions that are unstable relative to the delivered input (Tikhonov and Arsenin, 1977).

If an analytically inverted pig growth simulation model could be provided with input in terms of final body weight and backfat depth and cumulative feed intake, and with a description of the average nutritional and climatic conditions during the growth period, that

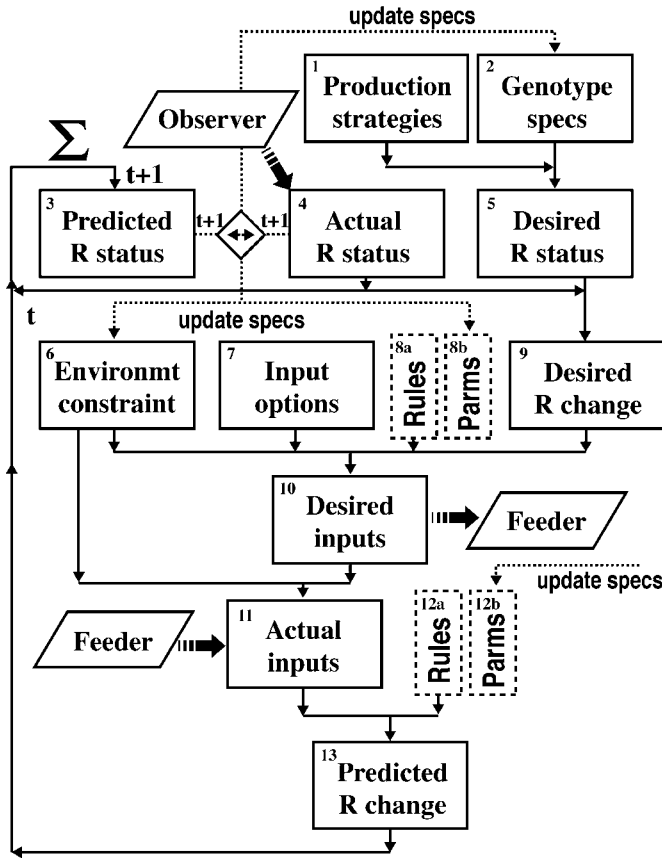


Figure 4. Iterative resource (R) status diagnosis and diet prescription.

model would likely produce a range of possible genotype characterizations that match those phenotypic and environmental specifications. All those genotypes would eventually realize the specified phenotypic performance, but they may differ in the way they arrive there. An iterative (rather than analytical) inversion approach would yield a flat optimum in this case, with the same inconclusive results. What is required in such a case is a more exhaustive description of the phenotype (and of the associated environmental conditions) to make the matching process in the inverted model more powerful. This would require serial measurement of phenotype and environment along the growth trajectory, providing the system with more animal-intrinsic information to help it focus on animal-intrinsic model parameters.

This process is illustrated in Figure 4, where the symbol “R” is used to denote resources; the general principles have been described by Wathes et al. (2001) and Whittemore et al. (2001). The model itself comprises rules and parameters, as in entities 8ab and 12ab in Figure 4. It is assumed that the animal’s genetic make-up (specified in Entity 2) results in a metabolic drive to reach a certain resource status (body mass and composition, heat production) at any point in its development. That is, an animal-intrinsic potential development pattern over time is assumed, which leads

to a genetically desired resource status (Entity 5). This potential pattern will only be achieved in a nonlimiting environment (in terms of stress and nutrient supply). In most cases, the actual resource status (Entity 4) will deviate from the desired situation; the animal is then assumed to adapt its nutrient input (or its interactions with stressors) to reduce this deviation. In addition to the genetically desired status, the pig producer’s production strategies (specified in Entity 1) may have specific desires with regard to the pig’s developmental pattern, often contradictory to genetic desires.

The system must be able to observe, at any given time, the pig’s actual resource status, determine its desired resource status, compare the two to estimate the pig’s desired change in resource status (Entity 9), and work out the required resource input, taking into account the available options for nutrient intake (Entity 7) and the limiting effect of current environmental factors (specified in Entity 6). This required resource input must then be translated into a specification of dietary requirements (Entity 10), which is output to the feeder. An important part of this translation is the relationship between pig appetite, required performance, and diet nutrient density. The required nutrient input may be further constrained by limiting environmental factors (stressors, bulkiness of the feed; specified in Entity 6). The model must therefore receive information from the feeder about the pig’s actual nutrient consumption (Entity 11) and predict from it the realized change in resource status (Entity 13). The predicted realized change in resource status can then be added to the actual resource status that was measured in the current time step, which gives the predicted resource status (Entity 3) for the coming time step. The loop of the system is closed during that time step when this prediction is compared to its realized (observed) value.

This comparison allows for “iterative status diagnosis.” When predicted values deviate from realized ones, some of the information that made the system arrive at that prediction must have been wrong. Apart from measurement errors by the observer and the feeder, there may be errors in the parameters used in the model calculations (entities 8b and 12b), the specification of the pig’s genetic make-up (Entity 2), or in the specification of limiting environmental factors (Entity 6). These three entities can then be updated (as by “update specs” instructions in Figure 4) by simultaneous examination of factors potentially affecting the observation—expectation difference. This would result in estimates of model parameters, genetic specifications and environmental specifications that become gradually more accurate as the pig grows and its accumulating information becomes available for retrospective analysis.

Pig growth models assume different relations between PD and feed protein intake, between LD and feed energy intake, and between PD and energy intake. This situation can be exploited for growth parameter estimation: Targeted over- or undersupply of feed energy and/or protein can be used to bring the animal in a specific

stage within those relationships, allowing for uncomplicated measurement of parameters such as ME_m , PD_{max} , genetically desired LD, and the regression of PD and LD on energy intake. These differential nutrient restriction techniques can be implemented through Entity 7 in Figure 4.

Implications

Simulation of the growth of pigs of a particular genotype with "potential deposition" models requires specification of the model parameters that drive body maintenance and potential growth of body protein and lipid. In stress-free nonlimiting environments this requires four to six parameters: maintenance metabolizable energy requirements, two to four parameters to describe potential protein and lipid growth, and one to describe effective feed intake capacity. These can be estimated by fitting observed body protein and lipid mass to growth functions or by inverted modeling, fitting observed feed intake, growth rate, and body composition to their simulated values by calibrating model parameters. In a stressful or limiting environment, more parameters will be needed to describe the coping strategies of a particular genotype. A model requires functions to deal with such parameters to allow for a proper fit of data measured in such environments and avoid biased estimates of the potential parameters.

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