An Analytical Model of Animal Growth

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Abstract

The purpose of this study was to explain some aspects of ontogenetic growth in pigs by analysing the relationships between variables that are significant to the development of animals. The novelty of the study is a new modelling approach to the growth problem, with the attention that has been paid to both a new set of variables, and an analytical discrete-continuous hybrid model, innovative for the field. This is a first species-specific hybrid model for animal growth formulated in discrete-time difference equation technique. The efficiency of the model is not only due to the modelling technique but also due to a set of relevant variables, especially a feed conversion coefficient, which provides a link between macro and micro physiological scales. The model is based on functional relationships between relevant variables acquired from experimental data analyses, and field observations. The concept explains some aspects of growth in pigs from 30 kg to 600 kg, which is considered the maximum individual weight for a boar, and further growth up to a species maximum weight. The model predicts that boar can reach their maximum individual weight of 600 kg when 6,40 years old and are required to consume 62,51 kg of feed to put on the last kilogram. The phenotypes that can attain their maximum individual weight go through bifurcation of the growth trajectory, a transform in the growth mode. After bifurcation, the smallest number of the phenotypes go on the growth trajectory that leads to a set of species maximum weights of over 1205 kg, and the greatest number of phenotypes continue to live until aged 24,90 years, provided their maximum weights do not change. The study includes growth rate equations, identifies species maximum weight phenotypes, and produces insight into pig longevity. The results suggest that species maximum weight growth trajectories are phenotype-dependant. A modified discrete-time difference equation technique combined with standard continuum methods is an appropriate formalism to model ontogenetic growth in animals.

Keywords: Animal development; growth dynamics; maximum weight; life span; difference equation; hybrid model

Introduction
Ontogenetic growth

In animal development, growth is an indispensable process, and is probably the most specific and variable trait studied that entails many if not all levels of individual phenome. Morphogenesis, reproduction, senescence, and many other biological events occur alongside or during the course of growth. Development is a continuous process, and sometimes the "trait" that we are interested in is actually the growth process itself (Rice, 2008). Numerous factors influence the growth of an individual. These are internal, such as inherited qualities and physiological particulars, and external, such as environmental conditions.

Over the last century, there has been moderate progress in the development of novel growth theories; however, a number of growth functions have been created (Dumas *at al*. 2008) and applied in industry (de Lange *et al*. 2001). At the same time, there are few if any models, designed to describe growth solely in pigs. In most cases, one of the considered theoretically universal animal growth functions has been used (Schinckel & de Lange, 1996). The most frequently applied mathematical function to model growth in animals is reportedly the Gompertz equation (Strathe *et al*. 2008) and the von Bertalanffy equation is considered most suitable to model individual growth (Dumas *et al*. 2010). To evaluate pigs' genetic potential for growth in industrial conditions, the Gompertz equation was suggested (Wellock *et al*. 2004).

Although the present range of growth functions seems to serve the purpose well (Birkett & de Lange, 2001), a call for new, advanced, biologically meaningful (Hirst & Forster, 2013; Boukal *et al*. 2014), next generation models exists. A unified mechanistic theory of growth remains elusive, a synthetic explanation is still needed for how and why growth rates vary as body size changes (Sibly *et al*. 2015). The reason for this is the apparently insufficient levels of qualitative and quantitative understanding of the related growth processes the models reveal (Dumas *et al*. 2010). The purpose of modelling growth in animals is to integrate the existing knowledge about the process, and apply mathematical methods to identify the qualitative and quantitative features, which are as yet unknown, likely to remain out of sight, or prove empirically unapproachable.

Animal growth models

Despite a considerable amount of accumulated experimental data, understanding of the biological processes that cause and control growth is far from complete, and theoretical tools have not been developed to resolve the issues that need to be addressed (Houle *et al*. 2010). The tools are thought concepts, models or theories that can convert the accumulated experimental

data into knowledge (Brenner, 2010). These concepts can be formulated either in verbal or in mathematical form. The mathematical formulation is preferable due to the clear advantage of yielding analytical analyses. Moreover, biological interactions and processes are often nonlinear, and this is where intuitive, verbal reasoning may let us down; whereas mathematical methods allow us to analyse diverse biological processes (Baker *et al*. 2009).

Many animal growth models currently used in science and industry are built upon an equation first invented by Pütter (Boukal *et al*. 2014). A range of such models entails the Pütter equation and several derivatives of it, such as the well-known growth functions the von Bertalanffy, the Gompertz, logistic, and some others. These growth functions were produced when solving ordinary differential equations, by which certain speculative proportionalities between growth rate and animal weight were specified, without reference to the biological species studied. The functions obtained after solving the equations were termed general or universal growth functions. The resulting models specify animal growth dynamics, based on what is considered reasonable or believed to be true.

While some authors have considered the von Bertalanffy's law as one of the most universal biological patterns (Sousa *et al*. 2008), others who are more sceptical have argued that the universal growth functions provide only retrospective curve fitting with little, if any biological insight (Pittroff and Cartwright, 2002). If the derived functions are sufficient and practicable for general purposes, they remain inadequate for scientific explication of the complex variables that cause the growth of numerous biological species. It follows that a different approach is required: at first focus on species-specific growth models and then, applying acquired knowledge, formulate a unified concept of growth across species. The study offers a first analytical model to implement this approach.

Hybrid model for animal growth

There are recognised difficulties in applying mathematical methods to model development in animals. Living organisms entail not only the notion of biological function or purpose but also the notion of growth and development that differentiates biology from other natural sciences. Moreover, growth and development facilitate the increase of structural and functional heterogeneity in animals. Growth is an essential process in development that has been identified as a significant factor in the production of spatial heterogeneity (Maini *et al*. 2012), which complicates its mathematical modelling.

The two most classical modelling techniques of biological phenomena are continuous-time, and discrete-time models. A number of biological objects do not fit either formalism; such systems contain

heterogeneity, where some phenomena are continuous while some are discrete. The modelling of this kind of systems would then naturally involve two different parts, a continuous one in ordinary differential equations, and a discrete one in difference equations, yielding what is called a 'hybrid' system (Mailleret *et al*. 2009). Hybrid modelling in biology has mainly been applied to couple continuous and discrete formulations. Although hybrid models are not new, the methods and approaches keep on developing, as well as the field of applications that keep widening (Stéphanou & Volpert, 2016). In this field, neither a hybrid model for animal growth was published nor an appropriate modelling technique specified. Hybrid dynamical systems combine evolution equations with state transitions; when the evolution equations are discrete-time, also called map-based, the result is a hybrid discrete-time system (Cao & Ibarz, 2010).

This reasoning suggests a possible explanation for the potential efficiency of modelling in animal growth by the discrete time modelling technique. If animal growth phenotype is a rapidly changing and not smooth function with many variables, then evidently, a discrete time model can outline the coarse dynamics of the same process without taking into consideration some implicit microscopic level events that take place in the chosen discrete time unit.

Difficulties cause not only intrinsic heterogeneity of biological objects but also different growth rates of different organism parts. Accordingly, in order to go beyond the limitations the growth functions impose (Boukal *et al*. 2014), it is necessary to extend the present range of methods, and develop the existing potentials of hybrid models (Hasenauer *et al*. 2015). For this purpose, a modified discrete-time difference equation technique combined with standard continuum methods would be an appropriate formalism.

The model's description

In this study, a hybrid modelling technique is applied. This is an attempt to formulate and analyse a hybrid model of animal growth, which combines the well known, though modified discrete-time difference equation technique, and standard continuum methods.

The study provides a partial explication of the changes in traits associated with the growth under nonindustrial conditions. However, the variables considered in the study are chosen to represent the underlying biology, but direct measurements of these variables are often difficult in practice. The model is a species-specific exercise constructed by considering relationships between variables analysed in experiments and field observations, without the inclusion of any theoretical premise.

In the model, discrete time and continuum modelling techniques are combined to set up a scheme, which develops as time proceeds, and therefore is considered as a dynamical system. A big advantage of the model is the absence of unknown speculative parameters; the parameter estimation problem does not exist. Most models for animal growth are based on events taking place at the macroscopic level. This model has variable Z, a feed conversion coefficient, which provides a link with microscopic levels metabolic processes and, as a result, a coupling of different biological scales has been established.

Mathematically, the model is formulated as a set of partial difference equations with discrete chronological time. A marked quality of the model is its formulation to enable the relevant information to be concentrated in a parameter, and not in the initial and boundary conditions, as is usually the case with models of continuum dynamics. Growth in the pig under nonindustrial conditions was modelled from 30 kg up to a species maximum weight.

Material and methods
Data set

The data set was obtained from experiments on growing domestic pigs, LW, fed from 30 ± 6 kg up to 96 ±4 kg live weight. The pigs were housed and fed under non-industrial conditions, either in a pig testing station or in research facilities. The animals were kept loose in groups of up to four to a pen, or individually in pens, fed a dry balanced feed with unlimited access to water contingent on the experiment design, *ad libitum*, or a constrained diet, in accordance with the current body weight, adjusting the feed quantity once a week. Besides the experimental data set, records available from research pig-breeding farms, as well as the wild pig data publicly available from some European national parks, were used.

The growth processes are discussed and modelled in terms of body weight, daily gain, and a feed conversion coefficient. The performance of a phenotype, a trait, is regarded as a biological function of the underlying causal factors. The identification of such factors or variables is a separate task to complete prior to formulating a model. The quality of the model is contingent upon the choice of the variables. The two main variables used in the model, parameter K, an invariant, and Z, a feed conversion coefficient are not conventional biological traits, cannot be directly measured in animals, and are dimensionless.

The model's variables

'M' stands for an individual animal current live weight, measured in kilograms.

$M = \{M \in \mathbb{R}_+ \mid 30 \leq M \leq 600\}$, Individual maximum weight, $M = M_x = 600$ kg

'm' is animal initial considered weight, measured in kilograms, $M \geq m$, $m_o = 30$ kg.

't' is chronological current time, measured in days starting from animal birth.

$t = \{t \in \mathbb{N} \mid 0 < t < \infty\}$, $\Delta t = 1, 2, 3 \ldots n$, $n \in \mathbb{N}$.

't_o' is starting time, correspond m_o, $t_o = 90$ days.

'K' is a parameter, nondimensional.

$K = \{K \in \mathbb{R}_+ \mid 1 \leq K < 11\}$, $K_o = 1$.

'Z' is a current feed conversion coefficient, dimensionless.

$Z = \{Z \in \mathbb{R}_+ \mid Z_o \leq Z < \infty\}$, $(Z = \infty) \rightarrow (M = M_x)$. Z_o correspond m_o.

Results
Growth up to 600 kg

Analysis of the experimental data identified some functional relationships between variables, which form the model's base. Parameter 'K' proved to be an invariant that is equal for the same-weight animals during rapid growth between $m_o = 30$ kg and $M = 100$ kg regardless of individual pig daily gain. It is considered that the relationships hold up to $M_x = 600$ kg. The parameter 'K' has the following form:

$$K = \frac{M \cdot t}{m_o(2t - t_o)} \tag{1}$$

Equation (1) may be written in many forms; however, the two following equations are usually used:

$$\frac{M}{m_o} = 2K - 1 + \frac{(t - Kt_o)}{t}. \tag{2}$$

$$\frac{1}{m_o} \cdot \frac{\Delta M}{\Delta t} = \frac{\Delta K}{\Delta t} + \frac{K}{t}. \tag{3}$$

From the same data set, the following relationship was found:

$$\frac{t - Kt_o}{t} = -\frac{(2K - Z) \cdot (K - 1)}{ZK}. \tag{4}$$

Substituting (4) into (2) and after obvious transformations, one get

$$\frac{1}{m_o} \frac{\Delta M}{\Delta K} = \frac{2K + 1}{K} - \frac{2}{Z}. \tag{5}$$

From (1) and (5) follows:

$$\frac{\Delta K}{\Delta t} = \frac{1}{t} \cdot \left[\frac{ZK^2}{Z(K+1) - 2K} \right] \tag{6}$$

In this section, equation (5) will be analysed. Equation (5) is valid not only for rapidly growing animals, but also for the animals that reached individual maximum weight, M_x, but not species maximum weight. At this stage, it is necessary to calculate Z_x to derive relevant relationships. As the first step, it is shown how to find parameter 'K' under the condition $M = M_x = 600$ kg. In formal notation: $K|_{(M=Mx)} = K_x$. Data analyses acquired from pig-breeding farms where mature boars were kept proved that (7) converges as $M \to M_x$, and the following limit holds:

$$\lim_{M \to Mx} \left(\frac{2K-1}{K+1} \right) = \sqrt{3}, \text{ where } (K \to K_x)|_{M \to Mx}. \tag{7}$$

It follows from (7) that under condition ($K = K_x$), $K_x = 5 + 3\sqrt{3} = 10{,}19615$.

The next step is to calculate Z_x, $Z|_{(M=Mx)(K=Kx)} = Z_x$.

Substituting K_x and M_x into (5) one obtains $Z_x = 62{,}51$. Z_x an analytical expression that will be presented in sections below. One should notice that Z_x and K_x are constants both linked to $M_x = 600$ kg. Z_x has a clear biological interpretation. It specifies the quantity of feed in kilograms needed for a boar to put on the last kilogram to reach its individual maximum weight $M_x = 600$ kg. K_x specifies the association between M and t at M_x. K_x provides the means to calculate the time at which M_x was reached.

From ($K_x = 10{,}19615$)($M_x = 600$) follows that $t|_{(M=Mx)(K=Kx)} = t_x = 6{,}40$ years, is in agreement with field data. This means that under the model conditions, boars can reach M_x in 6,40 years, consuming 62,51 kg of feed to put on the last kilogram. This result is experimentally testable.

It was shown that equation (5) applies not only to model weight dynamic during the period of rapid growth, but is also correct up to the point an animal reaches maximum weight, M_x.

After individual maximum weight, M_x is reached, animals do not grow. It means that live weight M_x does not change and, as a result, feed conversion, Z becomes infinity, $(t > t_x)|_{(M=Mx)} \to (Z=\infty)$. Under the above constraint, and considering equation (5), it follows:

$$\lim_{z \to \infty} \left(\frac{1}{m_o} \cdot \frac{\Delta M}{\Delta K} \right) = \frac{2K+1}{K}, \text{ where } (K \to K_1)|_{Z \to \infty} \tag{8}$$

From (8) under condition ($K = K_1$) follows, $K_1 = K|_{(M=Mx)(Z=\infty)} = 10{,}04975$. This result allows calculation of the time that corresponds to K_1, presented below.

It follows from ($M = M_x$)($K = K_1$), that $t|_{(M=Mx)(K=K1)} = t_1 = 24{,}90$ years. The time t_1 may be named 'obtainable life span'. The main condition to reach t_1 is that M_x remains constant between t_x and t_1. It is possible to show that not

all phenotypes can reach t_1. Those phenotypes that can achieve their individual maximum weight, M_x can live until aged 24,90 years, provided their live weight M_x remain constant. However, t_1 is not a species maximum life span. It follows from the model, that theoretical maximum life span in the pig is 49,31 years, not analysed in this article.

The following relationship was found from data set analyses:

$$\frac{t}{t_o} = \frac{2K-1}{K+1} \cdot \Delta Z + 1$$

Results found earlier suggest that if the following condition holds $t|_{(M=Mx)(K=K_1)} = t_1$, than follows

$$\frac{t}{t_o} = \frac{2K-1}{K+1} \cdot \Delta Z + 1 \rightarrow K^2, \quad \lim_{K \to K1}\left(\frac{t}{t_o}\right) = K_1^2 . \tag{9}$$

It follows from (9) that $t|_{K \to K_1} = t_1$, $t_1/t_o = K_1^2$.
Considering equations (1), (5) and (6), it follows

$$\frac{1}{m_o} \cdot \frac{\Delta M}{\Delta t} = \frac{1}{t} \cdot \frac{m_o[Z(2K+1)-2K]}{m_o[Z(2K+1)-2K]-MZ} . \tag{10}$$

The condition that (10) reaches maximum is: $m_o(Z(2K+1)-2K)-MZ = 0$. It means that the relationship that maximises (10) is

$$\frac{M}{m_0} = 2K+1 - \frac{2K}{Z}, \ Z_o = 1. \tag{11}$$

On the other hand, taking into consideration (10) one can see that there is no growth if $Z(2K+1)-2K = 0$. It means the condition under which animals do not grow at m_o is $Z_o = 2/3$. This is an unexpected result, counterintuitive and allegedly puzzling, attributable to the nonlinearity of the growth process. Formal, linear, empirical logic says that Z may not be less than 1. This fact has some important implications.

In the sections above it is demonstrated that in experiments, collected data analyses and the model provide correct relationships between variables. The identified relationships extended beyond the experimental data domain, show results consistent with field observations.

The model predicts that boar can reach an individual maximum weight, M_x 6,40 years old. Phenotypes that can reach M_x can live up to $t_1 =$ 24,90 years, provided M_x remains constant between t_x and t_1.

The constants: K_x, K_1, M_x, t_x, t_1, will be important tools in further analyses. Below, the main facts are summarised.

$$\frac{M_x}{m_o} = 2K_x - \frac{4}{K_x} \tag{12}$$

$$\frac{M_x}{m_o} = 2K_1 - \frac{1}{K_1} \tag{13}$$

$$\frac{t_x}{t_o} = \frac{K_x^2}{4} \tag{14}$$

$$\frac{t_1}{t_o} = K_1^2 \tag{15}$$

$$\frac{1}{m_o} \cdot \frac{\Delta M}{\Delta t} = \frac{1}{t} \cdot \frac{m_o[Z(2K+1) - 2K]}{m_o[Z(2K+1) - 2K] - MZ} , K \leq Kx, Z \leq Zx.$$

$$\frac{1}{m_o} \cdot \frac{\Delta M}{\Delta t} = \frac{1}{t} \cdot \frac{ZK(2K+1) - 2K^2}{Z(K+1) - 2K} , \text{ where } K \leq Kx, Z \leq Zx. \tag{16}$$

$$\frac{1}{m_o} \cdot \frac{\Delta M}{\Delta t} = \frac{1}{t} \cdot \frac{K_x(2K_x+1)}{K_x+1} , \text{ where } K = Kx, Z = \infty. \tag{16a}$$

$$\frac{1}{m_o} \cdot \frac{\Delta M_x}{\Delta t_x} = \frac{4}{t_o} \cdot \left[\frac{Z_x(2K_x+1) - 2K_x}{K_x \cdot Z_x} \right] \cdot \left[\frac{K_x - 1}{K_x^2 - 4} \right], Z = Z_x, K_x > 2. \tag{17}$$

Due to the definition of the feed conversion coefficient, between $Z_x = 62{,}51$ and $Z = \infty$ there is a tiny indefinable border. In simple words, after the instant M_x is reached, $Z = \infty$. Passage to the limit procedure, for example ($Z \to \infty$), should be regarded a mathematical abstraction, and not a workable definition.

Growth up to species maximum weight

In this section, species maximum weight will be defined. It is understandable that the species maximum weight is greater than M_x. However, I start with M_x, considering it variable. Taking the K_x as variable into consideration as well, consider (1) and (14) as a system. The equation that follows is given by

$$K_x^2 - \frac{K_x \cdot M_x}{2m_o} - 2 = 0 \tag{18}$$

There is a standard procedure of how to find the maximum M_x. The condition that M_x in (18) has maximum is $dM_x \backslash dK_x = 0$. It follows max $M_x = M_{xx1} = 4m_oK_x = 1223{,}538$ kg. A sufficient condition for the maximum to exist, is $d^2M \backslash dK^2 < 0 \mid_{(M=Mx)(K=Kx)}$, is fulfilled. There is an inflection point (IP) on the M_{xx} growth trajectory. From $d^2M_x \backslash dK_x^2 = 0$, it follows that inflection point, $M_{xx|ip} = 2m_oK_x = 611{,}769$ kg. The inflection point on the M_{xx} growth trajectory, most likely the last one, was expected. This time, $M_{xx1} = 1223{,}538$ kg was found by applying continuous methods, and the same result will be obtained below by applying the difference equation technique. Similarly to

in the analyses above, in searching for species maximum weight, M_x was considered variable, and accordingly K_x and K_1. Consider (12) and (13) a system; after multiplying and rearranging, it follows:

$$\frac{1}{m_o} \cdot \frac{\Delta M_x}{\Delta K_x} = \frac{(M_x \cdot K_x + m_o) + m_o(4K_x^3 - 10K_x - 5)}{m_o(4K_x^3 - 5K_x) - K_x(M_x \cdot K_x + m_o)}. \tag{19}$$

The condition under which (19) reaches maximum is: $m_o(4K_x^3 - 5K_x) - K_x(M_xK_x + m_o) = 0$. From this follows:

$$\max M_x = M_{xx3} = \frac{2m_o(2K_x^2 - 3)}{K_x} \tag{20}$$

Numerically, $M_{xx3} = 1205{,}884$ kg, is different to M_{xx1}. The average of M_{xx1} and M_{xx3} is M_{xx2}, is given below:

$$M_{xx2} = \frac{m_o(4K_x^2 - 3)}{K_x} \tag{21}$$

Therefore, there are the following three species maximum weights, obtained by applying both continuous and discrete methods:

$$M_{xx1} = 4m_oK_x = \quad 1223{,}538 \text{ kg} \tag{22}$$

$$M_{xx2} = \frac{m_o(4K_x^2 - 3)}{K_x} = \quad 1214{,}711 \text{ kg} \tag{21}$$

$$M_{xx3} = \frac{2m_o(2K_x^2 - 3)}{K_x} = 1205{,}884 \text{ kg} \tag{23}$$

I can remind the interested reader that the heaviest reported domestic boar was 1157 kg (Mayer, 2009).

It follows from the model that $K_{xx} = 10{,}09807$ is a new constant related to M_{xx}. The relation between K_{xx} and K_x is given by

$$K_{xx} = K_x - \frac{1}{K_x}.$$

The related time, $t|_{(M=M_{xx})} = t_{xx} = 12{,}69$ years. $t_{xx}/t_0 = (K_x \cdot K_{xx})/2$.

A possible interpretation is that (21), (22) and (23) are species asymptotic maximum weight phenotypes. A most unusual feature was that in order to find out the phenotypes, a combination of discrete and continuous methods was needed. Neither of the methods can produce the result separately. It seems that the information about the phenotypes was spread over different biological levels, or different scales, and conceivably had diverse biological meanings. The next point to underline is the procedure by which the phenotypes were found. The essential starting point was in field observations found M_x. It was chosen as the most frequently observed boar maximum weight. However, species maximum weight, M_{xx} does not directly follow from M_x. Nevertheless, by considering M_x as variable, and applying

both discrete and continuous methods, the phenotypes were identified. This implies that the biological information about species maximum weight is also present in those animal genomes, which never reach it. It is in line with general notions about the process, and suggests the existence of a gene or process that either stops or enables the trajectory $M_x \rightarrow M_{xx}$.

Rapid growth

The aim of this section is to concentrate on the rapid growth, which occurs between 30 kg and 100 kg live weight in domestic pigs. In this weight range, a maximum growth rate is observed, and during the rapid growth, physiological and anatomical traits undergo fast change that requires additional attention. General equations (10) and (16) for growth are inconvenient for this purpose; therefore, a restricted model for rapid growth was built.

The mathematical base for the rapid growth model is a system derived from (2) and (4). The following equation is a good approximation of rapid growth $M \backslash m_o = 2K$-1. However, to apply (2) and (4), the following system is to consider:

$$\frac{M}{m_o} = 2K - 1 \tag{24}$$

$$\frac{t - Kt_o}{t} = 0 \tag{25}$$

$$\frac{(2K - Z)}{ZK} = 0 \tag{26}$$

The system of (24), (25) and (26) equations suggests that equations (2) and (4) were rearranged and considered differently. From (24) follows

$$\frac{\Delta M}{\Delta K} = \frac{2M}{2K - 1}, 100 > M \geq m_o. \tag{27}$$

From (25) follows

$$\frac{\Delta K}{\Delta t} = \frac{K^2 \cdot t_o}{t^2}, 100 > M \geq m_o. \tag{28}$$

From (27) and (28) follows

$$\frac{\Delta M}{\Delta t} = \frac{2K^2 m_o t_o}{t^2}, \ 100 > M \geq m_o. \tag{29}$$

$$\frac{\Delta M}{\Delta t} = \frac{2MK^2 t_o}{(2K - 1) \cdot t^2}, 100 > M \geq m_o. \tag{30}$$

Considering (25), (26) and (27) one more growth equation is given by

$$\frac{\Delta M}{\Delta t} = \frac{2KZm_o}{(Z - 2K)t + ZKt_o}, Z > K, 100 > M \geq m_o. \tag{31}$$

The above growth rate equations (29), (30) and (31) are only some of many possible under the restricted model. Below, a more advanced approach will be shown, which entails speculation about the growth genetic aspect. Considering (27) and (30), it follows

$$\frac{\Delta K}{\Delta t} = \frac{K^2 t_o}{t^2} + \frac{t - Kt_o}{gtt_o}, 100 > M \geq m_o. \tag{32}$$

In (32) 'g' is a speculative parameter, regarded as a genetic factor, which is thought to specify a particular growth phenotype. In this paper, 'genetic factor' is not discussed further. From (27) and (32) follows

$$\frac{\Delta M}{\Delta t} = \frac{2m_o}{t} \left[\frac{K^2 t_o}{t} + \frac{t - Kt_o}{gt_o} \right], 100 > M \geq m_o, (g \in \mathbb{Z}) \vee (g \in \sqrt{\mathbb{Z}}+) \ .$$

Discussion
Growth dynamics

It is widespread opinion that the growth rate in many mammals has a sigmoid form (Li & Wu, 2010). This growth curve form is considered universal and is modelled by a number of growth functions (Barberis *et al.* 2011). The form results from growth dynamics, where it has one maximum and presumably two inflection points, either side of the maximum. In most cases, the rest of the curve is not specified, assuming it is smooth, monotonic, and asymptotically ends up at the animal maximum weight point.

This picture is tentatively accepted as a working hypothesis and has been frequently reproduced while modelling the growth of farm animals. The model can produce more precise growth dynamics, both in the rapid growth stage and in its final phase.

Maximum weight

The last part of the growth curve has a considerably different dynamic; the curve is neither smooth nor monotonic. There are two maximum animal weights, namely an individual one, and a species maximum one. They differ considerably, but only some phenotypes are biologically capable of reaching the species maximum weight.

Moreover, there is an inflection point on the growth trajectory between the two maximum weights. The inflection point suggests that the growth trajectory is modelled correctly, mathematically accurately, and biologically reasonable. At this inflection point, ($M_{xx|ip}$) the growth cessation stops and the growth process starts again.

Under the model conditions, the phenotypes, which are able to reach their individual maximum weight, go through a transformation in the growth mode. It means that on the growth trajectory M_x at the point (M_x, Z_x, K_x, t_x), bifurcation takes place with two new growth trajectories to develop. On one trajectory ($M{\rightarrow}M_x{\rightarrow}M_{x|t_1}$), animals continue to live up to 24,90 years, provided their individual maximum weight, Mx remains unchanged. On another trajectory ($M{\rightarrow}M_x{\rightarrow}M_{xx}$) phenotypes continue to grow to reach the species maximum weight, M_{xx}. What happens when the animals reach individual maximum weight is that the growth temporarily stops until a new growth mode is initiated, which takes the animal development on the next possible trajectory from that starting point. An important precondition for the growth to continue ($M_x{\rightarrow}M_{xx}$) is an inflection point on the growth trajectory. The inflection point can be thought of as a point on a curve, where the growth trajectory qualitatively changes. It takes approximately three months for the species maximum weight growth trajectory before it passes through the inflection point, $M_{xx|ip}$. However, from the presented results it is difficult to deduce why growth stops, and starts after a while again, or how the growth mode has been changed; additional analyses is needed. The mechanism underlying growth dynamics regulation has been less well studied. There is little doubt that genes play an important part in the growth processes. However, little is known about how genes influence growth during development to shape animals of predetermined species-specific sizes.

Growth variables

Animal current weight, M dynamics was modelled by parameter K, an invariant, and variable Z. Individual animal maximum weight, M_x is defined by parameter K_x and variable Z_x; species maximum weight M_{xx} is modelled by the parameter K_x, K_{xx} and variable Z_x, Z_{xx} ensuring uniform modelling. variab

It suggests that parameter K and le Z are significant for modelling all stages of growth. Variable Z, a feed conversion coefficient, was not accounted for in theoretical studies. However, it not only provides a link with the microscopic levels of metabolic processes, but is also essential for modelling the dynamic of animal growth, and is indispensable to finding necessary facts. The model offers means for the direct calculation of Z. Although some calculations are possible, and some functional relations are clarified, the question about the animal weight balance equation is still open. This is partly due to the fact that the dynamic of variable Z is sparsely understood. From the model it follows that the closer Z is to unity, and the greater extent ($\Delta Z < 0$) the growth mode is developed to, the higher growth

rate is. This seems reasonable; it is in line with feed conversion formal logic. However, equations (5) and (11) indicate the contrary. If in these equations Z is set equal to 1, a meaningless result is obtained. This suggests that the dynamic and functions of Z are more complicated than was expected. Consider the result showing that there is no growth in the Z_o range from $Z_o = 2\backslash3, \ldots 3\backslash4, \ldots$ up to $Z_o = 0,95$, that corresponds to the weight range from m_o to M_x, respectively. If this logic is followed, there should be $\min Z, 0 < Z < 2/3$, that would indicate the level of animal body conversion in order to maintain organism functions under animal weight decrease conditions. A growing organism is an autonomous open system, and can probably maintain its optimal functions in many alternative ways. Summarising the section above it is possible to state that the maximum growth rate is achievable not only when Z tends to unity, but also under other, yet unknown conditions.

If Z is a difficult variable, then parameter K is more complicated. K is remarkably informative and useful, however with complex dynamics. I shall briefly explain the general concept of applying parameter K. There are two options to utilise information in an open, autonomous system. The first option is dynamical, which entails definitions of initial and boundary conditions that entirely determine the process. The second option is parametrical, which entails nonspecific initial conditions, and not informative boundary conditions, and can be applied to a dissipative system with a stable trajectory. In this case, dynamic and structure of the system are completely determined by the parameter. However, the parameter or parameters should be informative enough to manage the process. The model is an attempt to implement this approach. Parameter K and variable Z are regarded as the parameters, which determine an animal's growth in the course of its life span. Parameter K dynamic can be conditionally divided into two sets. One K set ($K \rightarrow K_x \rightarrow K_{xx}$) is associated with animal growth ($m \rightarrow M \rightarrow M_x \rightarrow M_{xx}$). These sets are tightly related to set ($Z \rightarrow Z_x \rightarrow Z_{xx}$). The second K set ($K \rightarrow K_x \rightarrow K_{xx} \rightarrow K_1$) is associated with animal longevity ($t \rightarrow t_x \rightarrow t_{xx} \rightarrow t_1$). This suggests that K is sufficiently informative to model both longevity and growth. The above-mentioned sets are interrelated; however, the relation is not at all straightforward. Although there is insufficient understanding about dynamics of K and Z, these variables are essential for modelling and analysing animal growth.

Species maximum weight phenotypes
Taking into consideration the above modelling results the following interpretation is proposed. If genetic determination of growth is denoted by the interaction of phenotypes $Y°P°G$, the whole growth process, up to species maximum weight M_{xx} is obtained, in terms of phenotype sets is

given by $Y°P°G \Rightarrow W$, $W = \{$ AA, Aa, aa $\}|_{M=Mxx}$, where W is an ordered set of asymptotic species maximum weight phenotypes $\{$ M_{xx1}, M_{xx2}, M_{xx3} $\}$, respectively. This interpretation is in agreement with dissipative systems theory saying that dynamical system phase trajectories that start from diverse initial points end up in a single attractor. Under the model conditions, this attractor is the set W. This suggests that in an animal phenome, the number of body weight phenotypes asymptotically reduces to one set with three species maximum weight phenotypes, regardless of the initial distribution of phenotypes. This result is consistent with the general notion about growth genetics and supports the opinion that genetic determination of phenotype changes during individual growth (Houle *et al.* 2010). It is in line with notions about the genetics of animal development, however the results above imply that the hypothesis according to which the combined action of many genes with small effects explains quantitative traits development is not the only one to consider. It seems that a limited number of genes can explain the development of a quantitative trait well.

The study fails to answer the question as to what determines species or an individual animal maximum weight. Species maximum weight was found considering the individual maximum weight as a variable. The causation is direct; it is the individual maximum weight that entails information about species maximum weight. This implies that the biological information about species maximum weight is also present in those animal genomes, which never reach it.

Pig longevity

Under the model conditions, pigs can reach the individual maximum weight, $M_x = 600$ kg in 6,40 years; species maximum weight, M_{xx} in 12,69 years. Obtainable life span in the pig is 24,90 years, and species theoretical maximum longevity is 49,31 years. It suggests that most pigs can live barely longer than 25 years. This result is supported by field observations. There was only one reported case about a 27 year old pig (Hulbert *et al*. 2007). It follows from the model that the obtainable life span can be reached provided that the maximum individual weight M_x remains constant.

Conclusion

The study suggests that both rapid growth and species maximum weight growth trajectories are phenotype dependant. The biological information about species maximum weight is also present in those animal genomes, which never reach it.

The phenotypes, which are able to reach their individual maximum weight, go through bifurcation in the growth mode with two new growth trajectories to develop.

Species maximum weight is represented by a set with 3 asymptotic phenotypes, and is 1205,88 kg, 1214,71 kg, or 1223,53 kg.

Most pigs live less than 25 years, and only few phenotypes can live longer.

A modified discrete-time difference equation technique combined with standard continuum methods is an appropriate formalism to model ontogenetic growth in animals.

The results can be considered as boundary conditions in the differential equations representing the lower, metabolic level processes.

The details of growth causation turn out to be so complex, and nonlinear that no animal weight balance equation can be formulated at this stage.

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