A QUANTITATIVE BIOLOGY OF THE PIG

A Quantitative Biology of the Pig

Edited by

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Foreword

This book is a good idea. It is about quantification, and taking a systems approach to the biological study of a particular organism – the pig. It is also full of good ideas. It is a commissioned challenge set by the Editor to the world's foremost scientific teams of this generation. They have risen to that challenge and produced an important book that will become an instant classic. It is both compulsive and compulsory reading.

Why is this book so badly needed?

First, because science must be understood in order to be correctly applied. This requires not empiricism and anecdote but rather rigorous underlying theory. Theory is difficult, much more difficult than doing an experiment and reporting the results.

Second, the application of science through the technology of pig production is coming to depend upon two principles: quality assurance and integrated management control systems. Both these require full and quantitative understanding of the whole of the process, and completion of all the links in the chain of knowledge into a closed loop.

It has taken many years for these needs to be recognized, and many more for them to be addressed. The work is by no means complete; but this book establishes the ground rules, points the way and gets well down the track.

Animal science has had insufficient theoretical analysis, and an excess of empirical experimentation. The latter is fine for short term fixes but the former is the only way forward for long-term advance. This is not to say that the next steps in science are just thinking about things – quite the reverse. Better and more penetrating experiments are required to yield quality data upon which unifying constructions of understanding can be built. It is a characteristic of this book that the authors have seen the need to provide the robust experimental knowledge-base so greatly needed if accurate scientific interpretation is to be achieved.

This book is of its time and ahead of its time. It will change the reader's perception of the issues, it will influence future thought and work. It is an important book, and I am delighted to be associated with it. I congratulate and thank the Editor and all the authors for this work.

Colin Whittemore, NDA, BSc, PhD, DSc, FIBiol, FRSE
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1998

I

Describing the Elements of the System

Introduction

1

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Why 'a Quantitative Biology of the Pig'?

The science and practice of pig production has changed dramatically over recent decades, so that the 'modern pig industry bears little or no resemblance to that of only a few decades ago' (Whittemore, 1993). These changes have arisen from the need to consider novel issues and alternatives regarding the quality of the end product, the welfare of the animals and the environmental impacts of pig production. They have been achieved through improvements and modifications in the breeding, feeding, housing and management of pigs. One of the greatest challenges that has arisen from these changes is the need for extremely accurate decision making, which can only be achieved by considering simultaneously the effects of many interacting factors which influence the outcome of a pig production system: 'Meat of a *given quantity* and *definable characteristics* requires to be produced from feedstuffs of *quantifiable* nutritional value when given to *specific* pig genotypes in *describable* environmental, managemental and economic circumstances' (Whittemore, 1993; my italics).

The tradition in the practice of pig science has been to focus mainly or only on the factors which appeared to have an overwhelming influence on the system in question. For example, it has been, and unfortunately still is customary to investigate the effect on a response by varying a small set of experimental variables; with all of the uncontrolled factors, and the way in which the components of the pig production system (such as pigstock and feedstuffs) change, such an approach has little or no chance of success in predicting the future, and in helping us to be accurate in our decisions

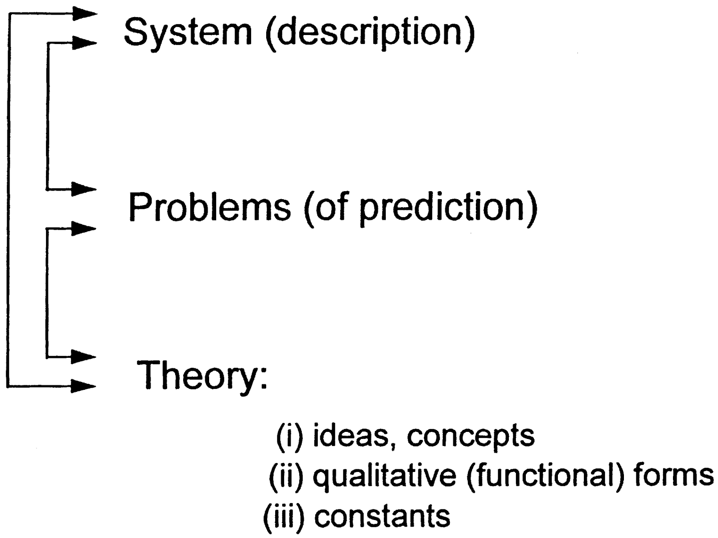

Fig. 1.1. A process for theory construction and methodology for research. (Adapted from Emmans and Oldham, 1988.)

(Emmans, 1996). Fortunately, these complex interactions between the component factors can now be approached through simulation modelling, using biological principles and mathematics, which provides a means of focusing on the issues under consideration. Model building, however, requires a satisfactory theory which underlies the behaviour of the system to be simulated: 'In many senses a model *is* a theory' (Emmans and Fisher, 1986). The aim of this book is to develop theories or models dealing with the biological processes which underlie pig production. By doing so alternative theories in the field are inevitably considered and compared with the offered ones. These theories, like any good theory, are put into quantitative terms so that their predictions can be made explicit and compared with outcomes from the real world (see below).

The Need for a Theory in Pig Biology

A theory arises from the need to be able to predict the behaviour of a system, and represents an idea or a concept of how a system operates. Although theories always form the basis of predictions in biological systems, this is not always obvious in agricultural systems, such as that of pig production. Emmans and Oldham (1988) suggested that the process of theory construction is done at three levels (Fig. 1.1). Once we have an idea of how a system operates, then the next step is to choose logical and functional forms which represent the theory qualitatively. The third level is to identify the variables, and find the values of the constants of the theory's functional forms, so that the theory is put in quantitative terms. The values of the constants are found by making measurements in the real world by experiments.

An application of the above process to an important task in pig production systems, that of describing quantitatively and being able to predict how the voluntary food intake of pigs changes from weaning to maturity, is provided here as an example. The concept is that food intake initially increases as the pig increases in size and the rates of gain of lipid-free body and fat are also increasing, and eventually reaches an equilibrium when the pig has achieved its mature size. The task then is to choose a function which describes adequately this pattern, and this may range from a simple regression equation to a more sophisticated set of functions (see Chapter 10). The choice should be based on the criterion of generality, i.e. how well the form describes various sets of data, and not how well some particular set of data is described by different functional forms without questioning the data. It may be found eventually that the chosen form is not adequate in describing the food intake of new breeds of pig, as these are introduced into the system, or of pigs manipulated by endocrine agents or immunological means. It would then need to be replaced with an alternative, better function(s) which would be able to describe quantitatively the change in the food intake of pigs.

The quantitative theories presented in this book have the above process inherent in their structure. The choice of the level at which these theories are developed (e.g. whole animal or metabolic, empirical or mechanistic) was offered to each individual author, but it was greatly dictated by their subject matter. Similarly, the form of presentation of the functional forms which represent each theory, varies among different chapters which deal with different biological processes. This is mainly a reflection of the diverse scientific backgrounds of the contributors of each chapter, but also of the fact that in some cases the specific values of the constants related to the functions representing a particular theory are yet to be determined experimentally. In these latter cases the value of the constructed theories will lie not in their immediate predictive ability, but in the identification of their existing shortcomings. Theories are both evolving and dynamic in their nature; their true value lies in the identification of the *problems* associated with their construction, rather than in the provision of the correct answers to these *problems*.

The Book Structure

In order to be able to predict the behaviour of any system we need both a predictive theory and a description of the system. As Emmans (1996) pointed out the theory and the description of the elements of the system are not independent, since different theories call for different descriptions of the system. For this reason Part I of the book addresses explicitly descriptions of the elements of the system, which form the broad subject of this book.

In pig production systems their three obvious components are the pigs, the food offered to them and the environment in which they are kept. Chapter 2 examines the underlying biological traits which describe genetic populations of pigs, while Chapter 3 provides an overview of the chemical and physical characteristics of pig foods, and discusses how such a description may assist in developing a quantitative understanding of pig biology. A specific description of the foods offered to pigs, in relation to their 'energy' contents is in part revisited in Chapter 15. Chapters 4 and 5 deal with the descriptions of the environment in which pigs are kept while some conventional descriptions of it are provided, e.g. in terms of its thermal and physical characteristics; some other, less usual descriptions are also invoked. These include tentative descriptions of the infectious (Chapter 4) and the social environments (Chapter 5), and to a certain degree of their interactions, since it is becoming increasingly evident that these have a profound influence on the system under question. For example, it is now suggested that the reduced voluntary food intake seen in group housed pigs, relative to that of their individually kept counterparts (Chapple, 1993), cannot be accounted for through the effects of the climatic environment (i.e. ambient temperature, humidity, airspeed).

Part II of the book deals with the quantitative descriptions and predictions of the biological processes in the pig from its conception and birth, to slaughter. They are divided, in the traditional manner, into: mating, pregnancy and prenatal growth (Chapter 6), lactation and neonatal growth (Chapter 7), and (postweaning) growth and body composition (Chapter 8). The physiological controls which underlie these processes, and an attempt to define them in quantitative terms, are addressed in Chapter 9. This is done by attempting to answer questions such as how sensitive is a process responsive to a regulator (i.e. hormone)? and, what is the relative importance of each regulator within the whole animal? By doing so this chapter becomes the link between the whole animal and its underlying metabolic processes, which are addressed in Part III of the book.

In pig production systems the ultimate interest lies in the ability to predict the outcome of feeding a group of pigs in a particular way. This can be achieved through our knowledge of the amount of food either offered to or voluntarily consumed by the pig, and our ability to predict the fate of food within the animal (metabolism). Part III addresses these two issues by first describing quantitatively the voluntary food intake of pigs given access either to a single food or to more than one food as a choice (Chapter 10). The digestion and absorption of the food and its associated nutrients are described in Chapter 11 and subsequent chapters deal with the fate of the most important group of nutrients within a food, i.e. minerals (Chapter 12), amino acids (Chapter 13) and carbohydrates and lipids (Chapter 14). Chapter 15 addresses the fate of energy consumed within a pig, and by doing so it provides a concluding link with its preceding chapters.

In Place of Conclusions

One can claim to understand how a system works only if one can successfully predict its behaviour. As discussed above this can only be achieved by developing theories which are then tested, criticized and eventually replaced. It has now been over two decades since the first attempt to represent quantitatively one of the biological processes in the pig, that of growth (Whittemore and Fawcett, 1974). The intervening twenty years have demonstrated, rather strongly, the importance of developing theories or models in making progress in pig science (as will be discussed in the final chapter). I do not, however, wish to give the false impression that the development of theories or model construction is relevant only to scientific endeavours. There is a tendency to consider theories as being appropriate only for the environment in which they have developed. However, it is the characteristic of good science that scientific and practical issues are or should be different aspects of the same thing.

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2

Describing the Pig

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Introduction

Genetic selection for improved pork production efficiency has resulted in substantially different pig populations. In the past four decades, vastly different performance testing and selection programmes have been implemented by government agencies, regional cooperatives and seedstock companies (David and Johnson, 1982; Schinckel *et al.*, 1985; De Vries and Kanis, 1994). Initially, selection focused on the more highly heritable postweaning performance traits including growth rate, feed conversion and carcass lean percentage. Different testing procedures, selection criteria and selection intensities have resulted in substantially different absolute and relative rates of genetic changes for postweaning performance traits. Application of BLUP (Best Linear Unbiased Prediction), hyperprolific sow selection schemes and importation of Chinese breeds has resulted in renewed interest in the genetic improvement of more lowly heritable reproductive traits.

Several swine models have been developed which integrate our knowledge of the effects of genetic potential, nutrient intake, and environmental conditions on pig growth and reproduction. These models can be used to identify alternative means to improve the efficiency of pork production and to estimate daily nutrient requirements for pigs of different ages and genetic groups when managed under a range of environmental conditions (de Lange and Schreurs, 1995). For an effective application of swine growth models, the growth potential of pig genotypes must be accurately characterized (Schinckel and de Lange, 1996).

Researchers have primarily concentrated on the evaluation of commonly measured performance traits. To understand the biological changes which have occurred as a result of past selection practices and direct future genetic changes, genetic evaluation must be directed towards quantifying the underlying biological traits rather than conventionally measured performance traits. The differences observed between genotypes for measured performance traits, i.e. growth rate, feed conversion and per cent lean, are susceptible to nutrient intake and environmental interactions. Evaluation of the underlying biological traits, when used as inputs to swine growth models, allows the prediction of differences in performance traits given the nutritional and environmental limitations present. This chapter examines the underlying biological traits which describe genetic populations of pigs.

Growth Performance

Protein accretion potentials

Estimation of empty body protein accretion rates is the primary characteristic needed to describe the growth of pigs. The growth of all other non-fat body components including water, carcass lean and ash can be modelled as functions of protein accretion (Whittemore, 1994).

The growth of protein mass to time is best described as a sigmoid growth curve with respect to time. The sigmoid growth curve has two principal segments, the first of increasing daily growth rate or accelerating phase of growth and the second phase of decelerating growth (Brody, 1945). The point of inflection between the two growth phases is the point at which maximum protein accretion occurs. When protein mass (*Pt*) is fitted to a sigmoid function of time (*t*), daily protein growth is estimated as $\partial Pt/\partial t$. The inflection point is mathematically defined as the point in which the second derivative of protein mass with respect to time equals zero. Secondary parameters include the maximum protein accretion rate, the age at which maximum protein accretion was achieved, the protein mass at the inflection point as a ratio of mature protein mass and mature protein mass.

There are two primary methods in which protein accretion can be mathematically estimated. The first is to describe protein mass as a sigmoid function of age. The second method is to describe protein accretion as the product of the live weight growth rate and the rate of change in protein mass relative to live weight.

Protein mass data can be fitted to either fixed or variable inflection point functions. Fixed inflection functions assume that maximum protein accretion is achieved at a constant percentage of mature protein mass. The Gompertz equation, a fixed inflection point function, has been widely used to describe pig growth (Whittemore, 1994; Emmans, 1995a). The Gompertz equation has the form: $P_t = \hat{P}_t \,.\, e^{-e^{-B(t-t^*)}}$ where B is the rate parameter, P_t is present protein mass, $\hat{P}_t$ is predicted mature protein mass, t is time (age) and t^* is the