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A solution to the problem of predicting the response of an animal to its diet

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Le problème dans la prédiction de la réponse d'un animal à son type d'alimentation

RÉSUMÉ

Le problème est de prédire la réponse (en terme de composition corporelle) d'un animal d'une certaine espèce (en l'occurrence d'un porc en croissance) à une quantité connue d'une nourriture donnée, quand il est gardé dans un certain environnement. On suggère que pour résoudre ce problème on a besoin des descriptions appropriées de ses trois composantes: l'animal, la nourriture, et l'environnement. Les descriptions nécessaires et adéquates de l'animal et de la nourriture, requises pour résoudre ce problème, composent la majeure partie de cet article. Selon la solution que l'on préfère, l'animal est décrit en termes de son état actuel (ou initial) et de trois variables: son taux de croissance (maturation) et son poids à maturité en protéines et en lipides. Les variations dans l'utilisation de la nourriture, les efficacités nettes de l'utilisation des nutriments et les règles de partage pour l'allocation des ressources rares sont supposées être inexistantes, et donc constantes pour toutes sortes de porcs.

Les implications de cette façon de traiter le problème et de décrire ainsi ses composantes, sur la prédiction de la réponse d'une population d'animaux (approche stochastique) forment la dernière partie de cet article. Étant donné le petit nombre de variables proposées, et le fait qu'elles sont simples à mesurer et qu'elles ont une signification biologique, on peut aisément introduire un élément de stochasticité dans les prédictions. Pour ce faire, on a besoin de connaître la nature de la distribution des variables. A ce jour, on dispose de peu d'information sur cette distribution. On peut cependant l'obtenir en convainquant les personnes qui sont intéressées par le recueil des variables génétiques (c'est-à-dire les éleveurs) des mérites de cette approche.

THE PROBLEM

The problem I am concerned with in the present paper is to predict the response of an animal of some kind, in some state, in our case of a growing pig, to a known allowance of a given food, when it is kept in a certain environment; in this case the animal is assumed to consume all its offered diet. When the animal is given free and continuous access to

the food, the problem then is to predict the response over time both in terms of food intake and the change in the animal (and its state). An extended version of the problem is to predict the response of the animal when it is given free and continuous access to two, or more foods. The latter case, although it constitutes a large part of my research effort over the past years (for example Kyriazakis & Emmans, 1991; Kyriazakis *et al.* 1993; Kyriazakis & Oldham, 1993) will not be considered any further here.

The components of the previously stated problem are, thus, the animal (in a given state), the food it is offered and the environment in which it is kept. These three components need to be adequately described in order to be able to predict the response of an animal to its diet. My own interests, in collaboration with others, have centred on the description of the animal (pig), and to a certain extent the description of its food; these two descriptions will be the focus of the present paper. A substantial part of our effort has been directed also towards the definition of the rules that the animal uses to partition scarce resources between its functions, since this was necessary for solving the problem. I have not been concerned with the detailed description of the animal's environment, but I have used that of others, when this was necessary. The latter description has focused mainly on the aspects of the physical environment (Bruce & Clarke, 1979; Verstegen *et al.* 1995), but it has now become clear to me (and to others, for example Black, 1995), that other dimensions of the animal's environment, also, will have to be invoked (for example, in terms of the social and infectious environment) when addressing the problem.

The implications of addressing the prediction of the response of an animal to its diet in this way and describing the components of the system thus, on the prediction of the response of a population of animals to its diet form the last part of the present paper.

A DESCRIPTION OF THE ANIMAL

For the purposes of constructing a theoretical description, the body of the immature pig is seen as consisting of gut-fill and the empty body. The proportion of the body as gut-fill in descriptions of the animal is either ignored (for example Ferguson *et al.* 1994), or is taken to be a constant proportion of the body weight (for example Whittemore & Fawcett, 1979; de Lange, 1995). It is clear, however, that the latter is not the case (Kyriazakis & Emmans, 1995a) and that it is safer if gut-fill is described as a function of the composition of the food and the rate of food intake.

The empty body of the pig is treated as consisting of four components: protein (P), lipid (L), water (WA) and ash (A); the amount of carbohydrate in the empty body is small and it is usually ignored. There are other possible descriptions of the body of the pig (for example, in terms of total DNA content; Pomar *et al.* (1991)), but the previously stated description is preferred here because it relates to measurable components, and it is at one level lower than the level where the predictions are made (since these are at whole-animal level). At time $t = 0$, which is the starting point of a particular time period, the amounts of the respective components (kg) are P_0 , L_0 , WA_0 , and A_0 . When the pig is given a diet, which is a food of a particular composition, at a particular rate of intake for a period of time (e.g. 1 d) up to time t , then its body composition will change to P_t , L_t , WA_t and A_t . One needs, therefore, to describe the rate of change in the four body components, given this particular food intake and, therefore, predict the pig's body composition at time t .

Two kinds of food intake have to be considered here: the one where the animal is able to achieve its maximum output in all four body components, and the other below maximum output (normally a restricted food allowance). The first case implies that there is a maximum (termed potential) in the animal's output, and that there are conditions, termed non-limiting such that its potential can be attained.

Rates of empty-body change under non-limiting conditions

The problem of devising a description of potential rate of protein growth in the pig is at least 20 years old. The first solution of Whittemore & Fawcett (1976), who suggested that the potential rate of protein growth is independent of the animal's state, does not seem appropriate any more (Whittemore, 1994). However, it is surprising how well-embedded it is in current thinking, and it continues to be used in recently developed predictive models (for example Moughan, 1989; de Lange, 1995). The preferred description of the pig's potential growth rate is the one advocated by Emmans (for example Emmans & Fisher, 1986; Whittemore *et al.* 1988), which describes it as a trajectory towards a mature protein weight (Gompertz equation):

$$PR_{\max} = B \times P_0 \times \ln(P_m/P_0), \quad (1)$$

where PR_{\max} is the potential rate of protein retention (kg/d), B is termed the rate of maturing (/d) and P_0 and P_m are the current and mature body protein weights (kg) respectively. The advantages of equation 1 are that it explains the rate of change mechanistically, and that both B and P_m are variables, dependent on the kind of pig (i.e. its genotype), which can be measured as described by Ferguson & Gous (1993). Any changes in the PR_{\max} due to administration of exogenous porcine somatotropin (for example Campbell *et al.* 1989), or other pharmacological agents, are seen as changes in the values of these two variables, in particular the value of B .

The potential growth rates of the other three body components under non-limiting conditions can also be described by the form of equation 1, with the value of B being the same for all four body components (Emmans & Fisher, 1986; Emmans, 1988). It has been shown by Emmans (1988) and Kyriazakis & Emmans (1992a) that this suggestion leads to the well-established allometric relationship between protein and each of the three of the other components. These relationships lead to lipid weight (L_t ; kg) and the rate of maximum lipid growth (LR_{\max} ; kg/d) being described as:

$$L_t = (L_m/P_m) \times P_m \times (P_t/P_m)^b, \quad (2)$$

$$LR_{\max} = (L_m/P_m) \times PR_{\max} \times b \times (P_0/P_m)^{b-1}, \quad (3)$$

where b is the allometric coefficient between lipid and protein, a function of the quantity (L_m/P_m) , i.e. lipid:protein value at maturity. The values of b range between 1.25–2.01 (G. C. Emmans, personal communication).

Equations 2 and 3 can be written for the weight of water (WA_t ; kg) and the maximum rate of water accumulation (WAR_{\max} ; kg/d) as:

$$WA_t = (WA_m/P_m) \times P_m \times (P_t/P_m)^c, \quad (4)$$

and

$$WAR_{\max} = (WA_m/P_m) \times PR_{\max} \times c \times (P_0/P_m)^{c-1}. \quad (5)$$

Table 1. *The constants (common to all pigs) and variables (a pig specific) required to solve the problem of predicting the response of an individual pig to its diet*

All pigs (Genus)	A pig (Species)	Diet
μ, e_p :ME/DCP	P_m , mature protein weight	R, ME:DCP
Maximum e_p , (e_p^*)	L_m , mature lipid weight	
Rules for partitioning a scarce resource	B, rate of maturing	

ME, metabolizable energy; DCP, digestible crude protein ($N \times 6.25$); e_p , net material efficiency of ideal protein utilization above maintenance.

We have recently proposed (Emmans & Kyriazakis, 1995) that the ratio, water:protein at maturity (WA_m/P_m) is a constant across pigs with a value of 3.04, and that the allometric coefficient, c , is also constant at 0.855 (a value which was originally proposed by Kotarbinska, 1969). These two suggestions seemed sufficient to account for the water contents of the empty bodies of pigs of very different genotypes.

Lastly, it is commonly held that the rate of ash growth (A_t ; kg) is constant relative to protein deposition, independent of pig genotype (Kyriazakis & Emmans, 1992*b,c*), such that:

$$A_t = 0.19 \times P_t. \quad (6)$$

It can be seen from equations 1–6 that there are only three variables necessary to quantify animal growth under non-limiting conditions. These are the rate of maturing, B , and the mature weights of protein and lipid, P_m and L_m respectively. All three variables are assumed to be genetic variables and, therefore, differ between different kinds of pigs (Table 1). (In this paper, rates of empty body change following a period of growth under limiting conditions, once non-limiting conditions are restored (e.g. compensatory growth), are not considered. For a treatment of the subject see Kyriazakis & Emmans (1992*a*).)

Rates of empty-body change under limiting conditions

The prediction of protein growth (PR), when the supply of food protein limits it to below its potential, is described in detail on p. 160. Here it is sufficient to say that the rate of protein growth below its maximum depends on the rate of protein supply only, providing the conditions are such that the partitioning rule, determining how an animal allocates its scarce resources, has been met. Under these conditions the rate of lipid growth can be predicted from the rate of energy supply and an energy system. The energy system used in the present paper is the 'effective energy system' proposed by Emmans (1994).

It is now established that the relationship between protein and water in the empty body is not affected by the rate and type of feeding (Kortarbinska, 1969; Kyriazakis & Emmans, 1992*b,c*; Emmans & Kyriazakis, 1995), and that the ash deposition is a constant relative to protein deposition (also unaffected by treatment; Moughan *et al.* 1990; Kyriazakis & Emmans, 1992*b,c*). Therefore, equations 5 and 6 can be re-written to describe the rates of water (WAR; kg/d) and ash growth (AR; kg/d) at $PR < PR_{max}$:

$$WAR = (WA_m/P_m) \times PR \times c \times (P_0/P_m)^{c-1}, \quad (7)$$

$$AR = 0.19 \times PR. \quad (8)$$

In summary the variables, relating to the animal, necessary to quantify how the animal grows under limiting conditions are the rate of maturing, B , and the mature protein weight, P_m .

THE DESCRIPTION OF THE FOOD

Two necessary descriptions of the food offered to the animal have already been raised i.e. the food's energy and protein contents. The former is expressed in terms of the 'effective energy system' proposed by Emmans (1994), which uses the existing metabolizable energy (ME) values for different feedstuffs as its starting point. According to the system, the effective energy content of the food (EEC; MJ/d) is calculated as:

$$EEC = ME_p - (3.80 \times FOM) - (4.67 \times DCP) + (12 \times z \times DCL), \quad (9)$$

where FOM is the faecal organic matter attributable to the food (kg/d), DCP is the digestible crude protein ($N \times 6.25$) of the food (kg/kg), z is the proportion of dietary lipid retained as body fat (for pigs a suitable average value of $z = 1$), and DCL is the digestible lipid content of the food (kg/kg). ME_p (MJ/d) is the classical ME content of the food corrected for zero protein retention, so that:

$$ME_p = ME - a' \times PR, \quad (10)$$

where a' is assumed to be constant and to be close to 5.63 MJ/kg.

According to the system the effective energy required (EER; MJ/d) by the animal for growth and maintenance is described as:

$$EER = MH + (50 \times PR) + (56 \times LR), \quad (11)$$

where MH is the maintenance heat production, which is a function of the animal's current state (P_0 ; kg) and its mature protein weight (P_m ; kg).

The food's protein content may be described either as DCP or digestible ideal protein (DIP; kg/kg). In the latter case the ideal protein content of the food is determined by reference to an empirical ideal amino acid pattern of the body of the pig (Agricultural Research Council, 1981). It is recognized, however, that both scales have limitations associated with them. In the first case, the traditional approach of describing the uptake of protein (or amino acids) from the digestive tract, in terms of crude protein digestibility, is severely limited (Moughan, 1995a), and it would be better if it were described in terms of true ileal digestibility of protein or amino acids. Similarly, it is now well established that there is no single ideal amino acid balance, since the amino acid pattern of the whole body of the pig is influenced by several animal and dietary factors (Kyriazakis *et al.* 1993; Moughan, 1995b). Until these issues are resolved and values exist for true ileal digestibility of amino acids obtained under physiological conditions, DCP and DIP will continue to be used.

Currently, there are no satisfactory scales for measuring the mineral and vitamin supply from the foods, although an attempt has been made to describe them in terms of their content and availability. This description, however, raises important problems, at least for the major minerals (Emmans & Fisher, 1986).

Lastly, apart from energy and nutrients the food also contributes bulk in the digestive tract. Since there is a maximum capacity for bulk in the animal's tract, there will be instances when the rate of food intake will be constrained by the bulkiness of the food.

(The maximum bulk capacity of the animal ($BCAP_{max}$) will also have to be considered as a necessary description of the animal given access to a food which constrains intake due to its bulk.) The bulkiness of foods given to pigs has been expressed in terms of the DM content of the foods (for example Whittemore, 1983), and their undigested organic matter contents (for example Roan, 1991); however, such scales are likely to be inadequate across the complete range of foods. We (Kyriazakis & Emmans, 1995a) have proposed the water-holding capacity of the foods (WHC; kg water/kg dry food) as a suitable bulk scale, since it appears to be the property consistently responsible for limiting their intake of a wide range of foods.

There are obviously other properties of the foods, such as toxicity, that might be important when they are fed to pigs. Although a large proportion of research has been directed towards these latter properties, complete descriptions of feedstuffs do not exist in terms used to describe the nutritional properties described previously. It has to be stressed, however, that the descriptions of a system (which includes the food offered to the animal) should be expanded as much as is necessary for the predictions to be made.

A PARTITIONING RULE

One of the central issues in nutritional predictive models is the form of the relationship between protein (or amino acid or any other nutrient) intake above maintenance, and an individual animal's response in terms of rate of protein growth. Two forms, rectilinear and curvilinear, are commonly used; in both types of relationship the response eventually reaches a maximum, PR_{max} .

It is obviously difficult to distinguish experimentally which of the two forms is more valid, since the same individual animal cannot be tested for its response to nutrient intake more than once, without altering its state (Fuller & Garthwaite, 1993). We and others have favoured the rectilinear form, because of its simplicity (its variables can be ascribed biological meaning and, hence, can be predicted from elsewhere) and, importantly, because of its consequences, i.e. in accounting for the form of the response for a population of individuals to different rates of nutrient intake (see p. 163).

According to the rectilinear form, the animal's response (PR ; kg/d) to ideal protein intake (IPI ; kg/d) above maintenance can be described as:

$$PR = e_p \times (IPI - MP), \text{ when } PR < PR_{max}, \quad (12)$$

where e_p is the net material efficiency of ideal protein utilization above maintenance and MP is the ideal protein requirement for maintenance (kg/d). The questions raised from this relationship are: (1) is e_p constant across different foods and (2) is e_p a function of animal genotype?

The very first modelling attempts (Whittemore & Fawcett, 1976) assumed that e_p was constant and equal to unity. Although this is a safe assumption for the efficiency of protein utilization for maintenance, it probably overestimates the efficiency of protein utilization above maintenance, where a certain inefficiency exists (Batterham *et al.* 1990; Moughan, 1995b) and for which a value of approximately 0.80–0.85 has been assumed. This value has been used in most predictive pig models (e.g. Whittemore, 1983; Emmans & Fisher, 1986; Ferguson *et al.* 1994; de Lange, 1995). However, the previously mentioned assumptions relating to e_p have not proven sufficient to predict satisfactorily

the responses of pigs on very low allowances, and reproduce the results of many pig experiments on their response to protein intake (Campbell *et al.* 1983, 1985*a,b*). For this reason Whittemore & Fawcett (1976) proposed that the previously stated assumptions about e_p hold only when the lipid:protein of the gain (LR:PR_{min}) attains some fixed value, which may be genetically determined. This proposal has been hugely influential and has been inherent in all subsequent predictive models, despite the fact that it was not true in any general sense, since it is well known that pigs can gain protein whilst losing lipid from their bodies (Agricultural Research Council, 1981; de Greef, 1992; Kyriazakis & Emmans, 1992*b,c*).

In an effort to overcome the deadlock created by the LR:PR_{min} suggestion, we (Kyriazakis & Emmans, 1992*c*) proposed a relationship between e_p and energy:protein of the food (R; MJ ME/kg DCP) which seemed to represent adequately preferential catabolism in the pig body:

$$e_p = \mu \times R, \quad (13)$$

where μ is the ratio of the two quantities. This relationship holds until e_p attains a maximum value e_p^* (Fig. 1(a)), which is less than unity. The values for μ and e_p^* estimated from experiments specifically designed to test the proposition are 0.0112 and 0.82 respectively. Although R has been defined in terms of MJ ME/kg DCP, it might be more appropriate to define it in terms of MJ EE/kg DIP. Given this view of e_p , there is no longer a need for a fixed value for LP:PR_{min} (Kyriazakis *et al.* 1994). The proposed relationship (13) still raises the question whether e_p varies with pig genotype? (the term genotype is extended here to encompass both the actual genotype and the degree of maturity, which can be approximated by live weight). Different answers to this question lead to different consequences and, hence, a different family of predictive models (Fig. 1). The simplest and preferred view, is that e_p is constant across pig genotypes i.e. pigs of different kinds retain protein at the same rate on a given diet offered at a rate which is limiting for all genotypes (Fig. 1(a)). A second possibility is that there is a relationship between e_p and PR_{max}, such that as PR_{max} increases so does e_p (Fig. 1(b)); therefore, in principle, the one can be estimated from the other. A third possibility which is the least attractive for devising a predictive model is that no relationship exists between e_p and PR_{max} (Fig. 1(c)). Its consequence is that both variables have to be estimated for a given kind of pig.

While it clearly cannot be established in any general way that there are no differences between genotypes in their use of limiting protein, evidence from our own experiments strongly supports the view that in models of pig growth, it is safe to assume that e_p is the same for different kinds of pigs. We have not found any differences in e_p between male and female pigs of a genotype of pig (Kyriazakis & Emmans, 1992*b,c*) on a given limiting diet, or between the pigs of two very different breeds (Kyriazakis *et al.* 1994; Kyriazakis & Emmans, 1995*b*). Similarly, Noblet *et al.* (1992) have found no differences in e_p between control and somatotropin-treated pigs, given the same food allowances which were limiting for both. There are, of course, experiments whose results contradict the previously-stated view (Campbell & Taverner, 1988; Fuller *et al.* 1995). These experiments, however, do not constitute strong tests of this view since there is some doubt that the treatments were limiting for all genotypes at all times during the experiments (a necessary condition to be met when testing the proposition); for a discussion of this problem, see also Kyriazakis & Emmans (1995*b*).

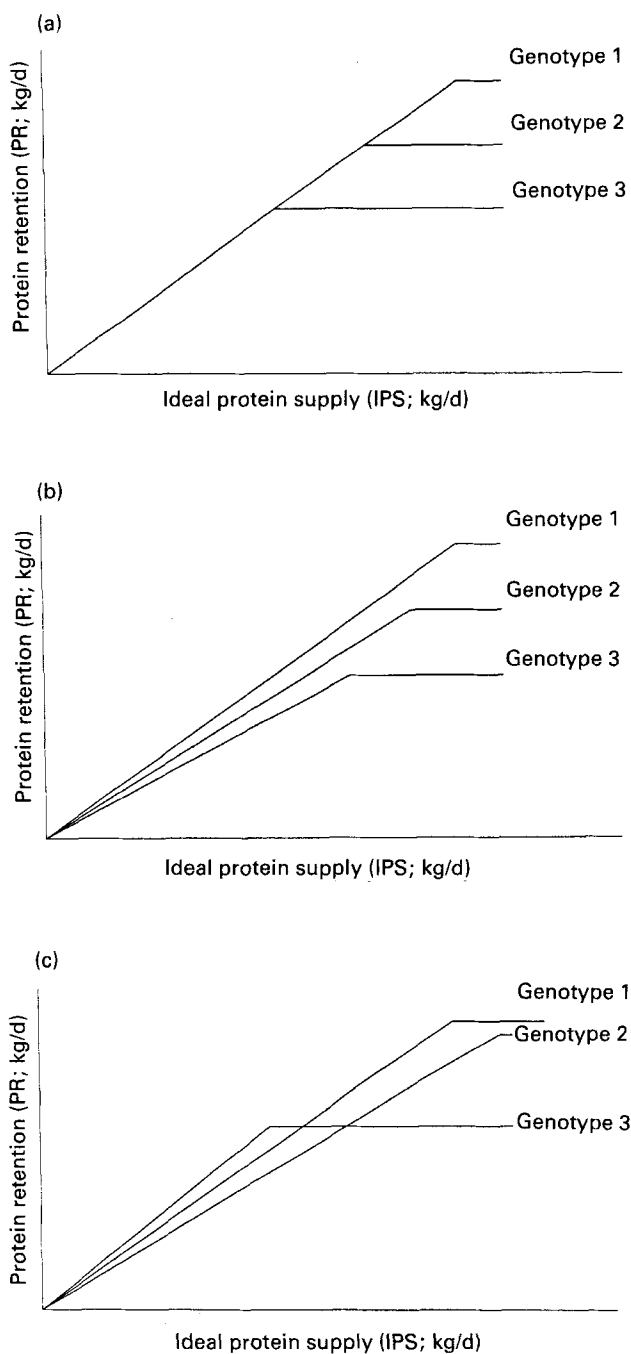


Fig. 1. A representation of the three possible effects (a–c) of pig genotype (here represented by three genotypes) on the relationship between protein retention (PR; kg/d) and ideal protein supply (IPS; kg/d) above maintenance. The slope is the net efficiency of ideal protein utilization (e_p) and the plateau represents the maximum response (maximum protein retention; PR_{max}).

In summary, it has been proposed that the net material efficiency of ideal protein utilization is constant across all kinds of pigs, although it can vary with the food composition (its energy:protein value). A consequence of this suggestion is that animals follow the same partitioning rules when allocating a scarce resource such as protein or energy. Although the present paper addresses mainly the net efficiency of ideal protein utilization, it is suggested that a similar condition to the one proposed previously will hold for other nutrients (i.e. their net efficiency of utilization will be independent of the genotype of the pig).

THE PROBLEM RESTATED: FROM THE PREDICTION OF INDIVIDUAL TO POPULATION RESPONSES

The problem explicitly addressed at the start of the present paper, was that of predicting the response of an individual animal to a known allowance of a given food when kept in a certain environment. For most cases, however, nutritional science is interested in the prediction of the response of a population of animals, rather than that of individuals. It is on populations of animals that most nutritional experiments are carried out and for which requirements are expressed. All existing predictive pig models deal with this problem by treating the response of the 'average' pig as representative of the responses of the whole herd. This approach, however, can lead to systematic errors and does not provide any information about the distribution of the response within the population.

The first task then is to define the form of the relationship between nutrient inputs and the response in a population of animals. It appears that its form is a curvilinear one, whereas the one proposed for the individual's response was rectilinear. It has now been established that the population response to amino acid intakes can be generated from the rectilinear assumptions for individuals (Fisher *et al.* 1973); the same arguments could apply for the responses of individuals and populations to other nutrients. Despite the general acceptability of the latter principle and its formal mathematical treatment by Curnow (1973), there is still considerable confusion regarding the representation of the form of the response of a population of animals; either the responses of groups of individuals are described by rectilinear models (for example Campbell *et al.* 1985*a,b*), or the response of the 'average' individual in the group is described as being curvilinear (for example Black *et al.* 1986; Moughan *et al.* 1987).

In order to introduce an element of stochasticity in the prediction (i.e. to predict the response of a population of animals to their treatment), one needs to know the variables in the predictive system and the nature of their distribution, i.e. their variances and covariances. The greater the number of variables the more difficult it would be to predict the responses of a population rather than of an individual. The variables of the system described in the present paper are those related to the description of the pig: its rate of maturing, B , and the mature weights of protein and lipid, P_m and L_m respectively. I have also suggested that the ratio $e_p:ME/DCP$ is a constant across pigs, as is the maximum e_p (e_p^*). The implication of the latter assumptions is that all pigs follow the same rules when they partition a scarce resource such as energy. A schematic description of the constants and variables required to solve the problem addressed in the present paper is given in Table 1. In Table 1 the Aristotelian classification for an animal has been followed: constants are genus specific, whereas variables are species specific. The more quantities are correctly put into the genus category, the better the predictive model is and the easier the population responses can be predicted.

The three variables B , P_m and L_m are simple to measure (Ferguson & Gous, 1993), and most importantly, they have a biological meaning. The latter is a major advantage over many existing pig models whose variables do not have this property, and, hence, it would not be possible to introduce an element of stochasticity into them. However, there is currently little information that relates to the nature of the distribution of the three variables, although some reasonable assumptions seem to be possible (N. S. Ferguson, R. M. Gous and G. C. Emmans, unpublished results). This lack of information, of course, is a characteristic of all variables defined in existing models which predict the responses of an animal to its nutritional treatment, simply because the people who develop such models tend to be different from those who are interested in the nature of the distribution of genetic variables. The hope, however, is that as the advantages of applying such predictive models become clearer to users, including pig breeders, information will be collected in terms which will be relevant for these predictive purposes (Knap, 1995).

CONCLUDING REMARKS

The present paper addressed the apparently complex problem of predicting the response of an animal or a population of animals (in our case growing pigs) to a known allowance of a given food when they are kept in a certain environment. However, this apparently complex problem can be solved by a rather simple approach. It was suggested that in order to solve the problem one needs to have adequate descriptions of its three components: the animal, the food and the environment. Some problems associated with the description of the food, and to a lesser extent the environment, were discussed and possible solutions (or ways of addressing them) were suggested.

A substantial part of the paper focused on the necessary and adequate description of the animal for the purposes described. The solution offered here represents a first step in achieving this. It is possible, however, that some additional descriptions of the animal might have to be invoked in order to make the predictions more general. We (Kyriazakis & Emmans, 1995*b*) have found, for example, that two very different pig breeds (Chinese Meishan (CM) and Large White \times Landrace (LW \times)) retain the same amount of protein when they are given the same food allowance for the same period of time, but they gain different amounts of lipid. The reason for this is that on controlled feeding CM pigs expend far less energy in physical activity (which is conventionally considered as part of the energy for maintenance) than LW \times pigs do and, thus, they have more energy available for lipid retention. It is clear that this difference in lipid retention would not have been predicted from the framework described in the present paper. It is also worth stressing that any new descriptions which will introduce variables into the system should be done in the terms detailed previously (i.e. should be measurable and have a biological meaning), in order to be able to introduce an element of stochasticity in the predictions. Information on the nature of the distribution of such variables will have to be achieved in collaboration with the people who are interested in collecting them (i.e. animal breeders).

Although this is a single author paper, as is customary for the Nutrition Society Medal, many of the issues presented in the present paper have been pursued in collaboration with others, and in particular with Mr G. C. Emmans. The description of the animal and its food stem from his ideas and this is a small way of acknowledging them.

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