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Consequences of genetic change in farm animals on food intake and feeding behaviour

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Selection in commercial populations on aspects of output, such as for growth rate in poultry, against fatness and for growth rate in pigs, and for milk yield in cows, has had very large effects on such outputs over the past 50 years. Partly because of the cost of recording intake, there has been little or no selection for food intake or feeding behaviour. In order to predict the effects of such past, and future, selection on intake it is necessary to have some suitable theoretical framework. Intake needs to be predicted in order to make rational feeding and environmental decisions. The idea that an animal will eat 'to meet its requirements' has proved useful and continues to be fruitful. An important part of the idea is that the animal (genotype) can be described in a way that is sufficient for the accurate prediction of its outputs over time. Such descriptions can be combined with a set of nutritional constants to calculate requirements. There appears to have been no change in the nutritional constants under selection for output. Under such selection it is simplest to assume that changes in intake follow from the changes in output rates, so that intake changes become entirely predictable. It is suggested that other ways that have been proposed for predicting intake cannot be successful in predicting the effects of selection. Feeding behaviour is seen as being the means that the animal uses to attain its intake rather than being the means by which that intake can be predicted. Thus, the organisation of feeding behaviour can be used to predict neither intake nor the effects of selection on it.

Feeding behaviour: Food intake: Genetic selection

'Prediction is easy; accurate prediction is another thing entirely'. Karl Marx

In the past 50 years commercial populations of several species of farm animals have been selected intensively for different combinations of output characteristics and hardly at all directly for, or against, food intake or any aspect of feeding behaviour. In the present paper we will concentrate on the effects of selecting for aspects of growth in poultry and pigs and for lactation in dairy cows on food intake and, to a lesser extent, on feeding behaviour.

The successful prediction of the effects of selection for output on intake and feeding behaviour implies an understanding of feeding in the base population before selection has occurred. Current views on the understanding and prediction of food intake will be presented briefly. One of these theoretical frameworks will then be used to consider the possible effects of selection on food intake. The view taken here is that it is food intake that is of prime importance to the animal, as it is the food eaten that allows the biological functions to be carried out. Feeding behaviour is seen as the means that the animal uses to achieve its intake and as having little significance in its own right.

Understanding and predicting intake

The approach that we have adopted is shown in Fig. 1 which is taken from Emmans & Oldham (1988). This approach
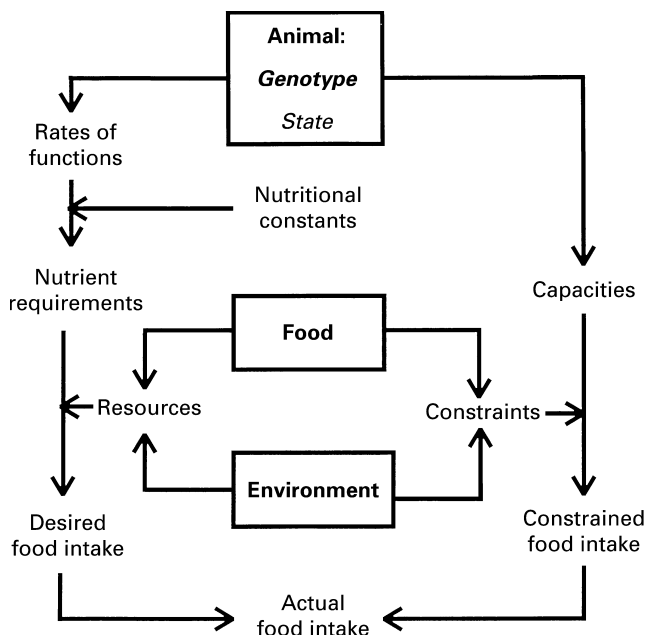

Fig. 1. A schematic representation of the theory that 'animals eat to meet their requirements subject to constraints' (After Emmans & Oldham, 1988).

makes explicit the assumptions that underpin the 'eating to meet requirements subject to constraints' theory of intake that goes back, at least, to Adolph (1947). It has been criticised, especially for ruminants (Grovum, 1987; Tolkamp & Ketelaars, 1992). Other researchers are progressively diluting it (for example, see Forbes 1996; Illius & Jessop, 1996; Ellis *et al*. 1999; Illius & Gordon, 1999; Pittroff & Kothmann, 1999). There is a current attempt to replace it with the view that an animal integrates a set of signals of varying strength in order to decide on its intake. This view is described by Berthoud (2000) and has a superficial attraction; we might imagine that the physiology of intake control could be like this.

This view leads to the research programme that is needed to quantify the effects on the control system of the various factors that influence intake. As a method for the prediction of intake it can, however, have no value. The reason is that the effects of the different presumed signals on the physiology of the animal (and the set of signals must be complete if intake is to be predicted) need to be expressed in a common currency. Only by measuring the strengths of all the presumed signals across a range of cases where intake is also measured can this calibration be done. The data from such experiments could almost certainly then be used to predict intake directly, at least as effectively as they could be used to predict intake through the presumed effects of the intermediate level of the set of signals in the nervous system. Berthoud (2000) recognised the past failure of this approach: 'Behaviors such as searching for and selection and ingestion of food can ultimately only be expressed through specific actions of the nervous system. Almost a century of intense research has, however, been unable to identify clearly the neural substrate subserving these behavioral functions.'

Among those researchers who propose a modification to the original 'eating to meet requirements subject to constraints' framework shown in Fig. 1 are Ellis *et al*. (1999). They state: 'Thus we have a new paradigm emerging in which intake is not strictly controlled by one or the other pathway (e.g. the simple physical or metabolic pathways). Rather, intake is regulated by a milieu of signals indicating costs and benefits.' Illius & Jessop (1996), Illius & Gordon (1999), Forbes (1996) and Pittroff & Kothmann (1999) have adopted a similar position. However, as this 'new paradigm' seems to us to have no prospect of making any contribution at all to the accurate prediction of food intake, we will continue to use the ideas in Fig. 1 in the present paper, which we see as still being fruitful.

One of the attractions of the framework in Fig. 1 is that it allows us, at least in principle, to predict the effects on food intake of changes in the rates of animal functions brought about by selection. The simpler the description of the animal, i.e. the fewer numbers that we need to give a sufficient description of it, the better we can hope to predict the consequences of selection. For any scheme that seeks to predict, it is always worth asking what descriptions of the components of the system (animal, food, environment) are considered to be sufficient to allow this prediction to be done.

The distinction often drawn between 'understanding' and 'ability to predict' is more apparent than real. The test of whether we understand a system is always whether we can make accurate predictions of its behaviour. In the context of food intake we can understand in the high sense of seeing how the system came to be like it is through evolutionary success. Alternatively, we can understand, at least in principle, in the low sense of sufficiently describing the mechanisms of the system so that accurate prediction is possible. Understanding in the low sense has had no success in predicting intake, and there is no immediate prospect that it will have.

We see the problem as being in three parts. The first is to be able to predict intake for a given kind of animal across food compositions and environments. Among the food composition variables are the contents of protein, fat and carbohydrate, the amino acid contents of the protein, and the contents of water and the indigestible, or only slowly-digestible, components such as fibre. The climatic environment can have dramatic effects on food intake and is a relevant dimension, particularly where intake needs to be predicted in climatically-different parts of the world (Knap, 2000*b*). The aim is always to include more dimensions, and wider ranges of them, in the predictive system.

The second problem is to be able to predict what will happen to food intake as some population of animals is selected for some combination of output characteristics, such as growth rate and body composition, or milk yield and composition. To take on this problem implies that we have a satisfactory solution to the first problem. To an animal breeder any change in food intake as selection proceeds is a correlated response that may be in part genetic. Where measurements of intake are available, i.e. the problem is not to predict the future but to account for the past, this correlated response will be available. However, this problem is not the same as the one that we wish to solve. We

want to predict what will happen rather than to account for what has happened.

The third problem, of particular interest to those researchers whose main interest is in feeding behaviour *per se*, is to describe the elements of behaviour contributing to intake. An example would be the statement that:

$$\text{food intake (g/d)} = \text{meal frequency (/d)} \times \text{meal size (g)}. \quad (1)$$

The algebra cannot be faulted. However, the algebraic relationship is sometimes used to argue that the approach to the prediction of intake must be by understanding, and being able to predict, both meal size and meal frequency. This error is logical. Consider the alternative relationship that is also algebraically sound:

$$\text{meal frequency (/d)} = \text{food intake (g/d)/meal size (g)}. \quad (2)$$

We could now see the problem as being that of predicting meal frequency, and the approach as needing to understand and predict both food intake and meal size in order to do this.

The contrast between relationships 1 and 2 lies in part in what we see as our problem. When the animal has 'solved' its problem (in our view the problem of major importance) of deciding how much to eat, it can then solve the secondary problem of how to organise its behaviour in terms of meal size and frequency. Some aspects of feeding behaviour are considered later.

Potential output drives intake

In many schemes to predict animal performance the starting point is food intake. The stated intake is then distributed between functions. The scheme shown in Fig. 1 is different in that the starting point is a description of an animal in terms of its genotype (what kind of animal it is) and its current state. This description allows the rates of its functions to be calculated as potentials (Emmans, 1988). From these potential rates the requirements of the animal for food resources are then calculated using a set of nutritional quantities presumed to be constants. This sub-scheme comprises the left-hand side of Fig. 1. Two sub-problems are identified as: (1) to describe the animal in a way that is sufficient to allow its potential performance to be calculated; (2) to be able to assign values to the nutritional constants.

Efficiency

It is possible that there are no 'nutritional constants' as envisaged in Fig. 1. However, there are two kinds of reasons for behaving as if there were. The first reason is the argument from evolution that existing genotypes are the outcome of the effects of past selection for fitness over long periods of time. An effective chemistry, with little or no residual variation between genotypes, is the expected consequence of this selection. The second reason is that the assumption tends to result in simpler models. A consequence of there being no nutritional constants is that the values of key quantities will vary with genotype, and

perhaps also state, such as degree of maturity. If this is the case then the only approach is to do a very large number of experiments on different kinds of animals in order to estimate the response surfaces that are needed to help in making feeding decisions. While this considerable inconvenience does not mean that there are nutritional constants it does mean that, as a rule of method, we should proceed as if there are until the world tells us that there are not.

The key nutritional quantities in the growing animal are the amounts of energy needed for the retention of 1 kg of both protein and lipid, and the material efficiency with which the first limiting amino acid is retained; the second point will not be discussed further here. Providing that the energy needed is expressed on the effective energy (EE) scale (Emmans, 1994), it seems to be the case that the quantity of EE needed for the retention of 1 kg protein is constant. It was found to be constant across chickens, cattle and sheep (Emmans, 1994), and constant across degrees of maturity when tested using data from cattle and chickens. Allowance for direct lipid retention from food lipid needs to be made in the calculation of the EE coming from the diet (Emmans, 1994).

For lactating cows the key energy quantities are those needed to produce 1 kg each of lactose, milk protein and milk lipid. The EE system has been extended to estimate these quantities as described later (p. 120). The fact that older feeding standards are being successfully applied to cows with the genotype to produce much higher yields than did those from which the quantities were derived (Veerkamp *et al.* 1995) suggests little if any genetic variation in these quantities. Possible effects of genetic variation and selection on maintenance are discussed later (see p. 120).

Maintenance

To maintain its current state an animal needs energy and amino acids as well as other resources. While there is general agreement that between genotypes at maturity maintenance is scaled to (mature size)^k, and that the value of the parameter k is approximately 0·73, there is less agreement about the appropriate measure of mature size for a given genotype. It does appear that using protein weight (Emmans & Fisher, 1986), or lipid-free weight, or mature weight corrected to a constant fatness of 0·2 lipid content (Taylor *et al.* 1986), reduces the variation compared with using live weight. Using protein as the measure of mature size leads to:

$$MN_i \text{ (units/d)} = M_i.P_m^{0·73}, \quad (3)$$

where MN_i is the maintenance requirement of a genotype for a resource i, for which M_i is a constant, and P_m is mature protein weight.

There is less agreement about the relationship between maintenance and immature size for a given animal. The proposal that maintenance is directly proportional to protein weight (Russel & Wright, 1983; Emmans & Fisher, 1986) is attractive. In at least one case, that of normally-growing sheep (Blaxter *et al.* 1982; Emmans, 1987), this proposal is equivalent to the assumption that maintenance is scaled to

live weight$^{0.73}$, the same rule that applies between genotypes at maturity. However, this similarity must be seen as a fortuitous outcome of the particular fattening characteristics of sheep that make protein weight proportional to live weight$^{0.73}$ during growth. For growing chickens maintenance was found to be directly proportional to body protein weight (Emmans, 1994) and this variable was not any simple power function of live weight. The general equation for calculating maintenance across genotypes and degrees of maturity then becomes:

$$MN_i \text{ (units/d)} = M_i.P/P_m^{0.27}. \qquad (4)$$

This equation is analogous to that of Taylor & Young (1968), with protein weights substituted for equilibrium live weights.

There is an implied allowance for physical activity in the value of M_i. As shown later (p. 120) maintenance expenditures can be reduced by selection, in part because of a reduction in activity. In view of this factor it may be better to treat maintenance and activity as different functions.

Potential growth

The huge debate on suitable functional forms for the description of particular sets of actual growth data can be bypassed by concentrating on a form to describe the animal's potential for growth. The term 'potential' is used in two senses (Emmans & Kyriazakis, 1999). The first sense is the classical sense in which there must have been a preceding potential for the 'actual' to be observed. An example is the 'potential energy' that a mass has by virtue of its position. The second sense is that of an upper limit: for example, 'she has the potential to run 100 m in 12 s'. In what follows we are using the term in both senses.

For the immature animal the approach has been to use the Gompertz growth function (Emmans & Kyriazakis, 1999) to describe the way in which the potential to grow varies with size for a particular animal. It has been used with success for broiler chickens (Hancock *et al.* 1995; Gous *et al.* 1999; Mignon-Grasteau *et al.* 1999), turkeys (Emmans, 1989), pigs (Whittemore *et al.* 1988; Emmans, 1989; Ferguson & Gous, 1993*a,b*; Knap, 2000*a*), sheep (Lewis *et al.* 1998) and cattle (Amer & Emmans, 1998). The starting point is the relationship that is assumed to exist between current size and the relative growth rate that can be attained in non-limiting conditions. Where C is the current size of a component of the body, such as protein or lipid, then its relative growth rate, $R = (dC/dt)/C$, is assumed to be given by:

$$R = B.\log_e(C_m/C). \qquad (5)$$

The value of R decreases linearly, at the rate B, with $\log_e C$ to become zero when $C = C_m$, as seen in Fig. 2. The two parameters that describe the animal with respect to this component are C_m, its weight at maturity, and B. An attraction of the function is this simplicity of its having just two parameters.

The components of interest may be either the major chemical components of the body (protein, ash, water and
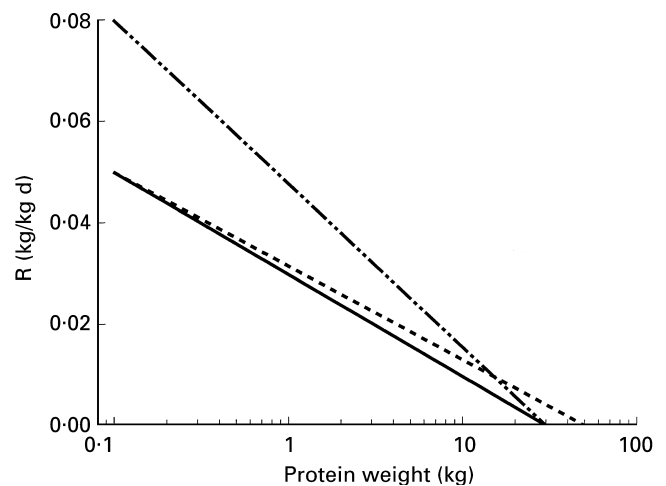

Fig. 2. Relative growth rate (R; kg protein/kg protein d) against body protein weight (kg) in pigs; weight is on logarithmic scale. (——), Before selection; (------) after selection for mature protein weight; (—·—·—), after selection for the rate of maturing with mature weight held constant.

lipid) or organ or tissue groups (Emmans, 1989; Gous *et al.* 1999). The growth rates of the chemical components is of particular interest here, as these are needed to predict requirements (Emmans & Fisher, 1986). It seems to be the case, for the components of the feather-free body of birds (Hancock *et al.* 1995; Gous *et al.* 1999) and of the entire body of pigs (Emmans, 1988, 1989; Knap, 2000*a*), that the value for the rate parameter B is the same for a given animal. For the tissue of greatest economic importance in poultry, the breast muscles, the rate parameter is the same as that for the major chemical components (Gous *et al.* 1999).

It is worth noting that in Fig. 2 no individual point on the line has any particular significance other than the mature size at which the growth rate goes to zero. When, however, equation 5 is re-arranged to predict the absolute growth rate of the component as:

$$dC/dt = B.C.\log_e(C_m/C), \qquad (6)$$

then, as shown in Fig. 3, there is a weight at which the absolute growth rate is at a maximum. When equation 6 is integrated to give the growth curve:

$$C = C_m.\exp(-\exp(-B(t-t^*))), \qquad (7)$$

the time at which the growth rate is at a maximum is t^* where the growth curve has a point of inflection. There has been debate about the effect of selection on the degree of maturity (C/C_m) at which the point of inflection of the growth curve will occur (see Knap, 2000*a*). A more fruitful debate would be about the effects of selection on the underlying relationship between relative growth rate and the current size of the body component (protein weight) that was shown in Fig. 2, as it is this relationship that leads, through algebra rather than biology, to the relationships in equations 6 and 7.

Selection for growth rate, by selecting for weight at an age, seems highly likely to do two things (Emmans &
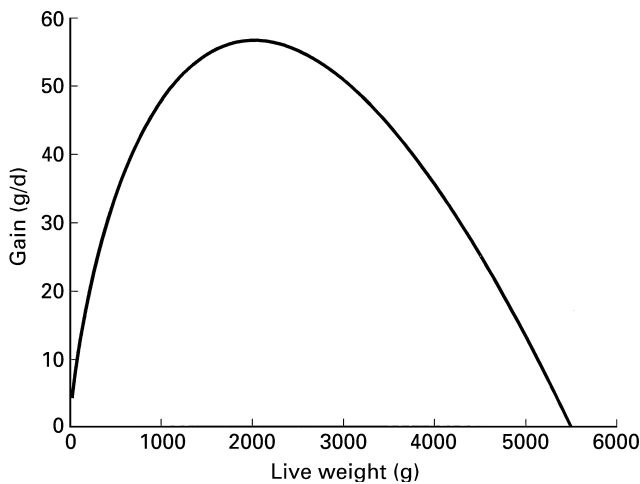
Fig. 3. Growth rate in male broiler chickens in 1975 *v.* live weight, showing that there is a weight at which growth rate has a maximum value.

Kyriazakis, 2000). Selection for size at a high degree of maturity will act mainly to increase mature size, so that relative growth rate is increased at all weights. Inter-species scaling (Taylor, 1980) suggests that the absolute value of the rate parameter B will be decreased as a consequence. On the other hand, selection at a low degree of maturity will act to increase the rate parameter B with little effect on mature size. Real selection programmes in commercial stocks will be somewhere between these two levels; there may also be other effects in the selection programme that contribute to changes in the values of the two parameters under selection. However, it does seem highly unlikely that the form of the genetic relationship between the relative growth rate and the current size of the body component will be changed as selection proceeds. It is possible that, if the environment fails to be modified in an appropriate way to keep up with the effects of selection, then the phenotypic form of the relationship between the relative growth rate and the current size of the body component may be observed to change. The solution is not to seek more complex growth functions to describe actual growth but to change the environment, including the nutritional environment, to match the needs of the improved genotype.

From equations of the form of equation 6, and the values of the parameters for a particular animal, the rates of growth of the relevant components can be predicted for that animal in a given state. With protein (P) and lipid (L) assumed to be the only components that require organic resources from the diet, it is the growth rates of these two components that are needed for the prediction of energy and amino acid requirements. The growth rates of these components can be predicted using equations of the form of equation 6 as:

$$dP/dt = B.P.\log_e(P_m/P), \tag{6a}$$

$$dL/dt = B.L.\log_e(L_m/L). \tag{6b}$$

The genetic parameters are the mature weights of the two components (P_m and L_m) and rate parameter B. It is

convenient (Emmans, 1988; Knap, 2000*a*) to use $L_m/P_m = LPR_m$ as the second parameter, rather than L_m, to describe mature fatness rather than mature fat weight. The sufficient set of parameters to describe the animal becomes P_m, LPR_m, and B. Selection is then seen as acting by changing the values of these parameters.

Lactation

Potential milk production, for our present purposes, can be seen either as milk or as the organic components of lactose, protein and fat. A function originally used to describe potential yolk production in hens (Emmans & Fisher, 1986) has also been used (Oldham & Emmans, 1989) to describe potential milk production. It was found to be useful for dealing with the effects of parity on the way in which yield changed with time from calving (Friggens *et al*. 1999). The function is the product of three terms. One term describes the size of the system, u, which changes with time from calving, t. The second term describes the competence of a unit of the system, p, which also changes with t. The final term is a, a scalar. The rate of yield, dY/dt, is then given by:

$$dY/dt = a.u.p. \tag{7}$$

With $u = \exp(-\exp(g_o-b.t))$, a Gompertz growth function, and $p = \exp(-ct)$, an exponential decay function, the potential lactation function becomes:

$$dY/dt = a.\exp(-\exp(g_o-b.t)).\exp(-c.t). \tag{8}$$

Interestingly, the form for the lactation curve derived by Dijkstra *et al*. (1997), using arguments based on the presumed mechanistic basis of the growth of the mammary gland, was found by Friggens *et al*. (1999) to be mathematically equivalent to equation 8. Rook *et al*. (1993) compared the ability of several functions of the form of equation 7 to describe actual lactation curves. As the actual data used came from cows fed in a wide variety of ways it is not surprising that the form seen as being appropriate to describe potential by both Friggens *et al*. (1999) and Dijkstra *et al*. (1997) did not do well on this test. The use of actual data to compare the ability of functional forms to describe potential, whether as growth, yolk material or milk, needs to be done only after careful consideration of the nature of the data to be used. When this procedure was done Friggens *et al*. (1999) found the functional form of equation 8 to be satisfactory.

The form for milk production in equation 8 can also be used for each of the components (lactose, protein and fat). The usual patterns of the changes in composition with time from calving can be generated by an appropriate choice of values for the four parameters for each component.

Requirements for the potential to be met

Energy will be the only resource considered here, but similar arguments apply to amino acids (Emmans & Fisher, 1986; Emmans, 1989) and minerals. The requirement is the sum of the separate requirements for maintenance and

production. The choice of a scale of energy on which the requirements are assessed is important. The EE scale (Emmans, 1994) has several desirable properties. The starting point is metabolisable energy, which is corrected appropriately for the digestibility, fermentability and protein and lipid contents of different foods. The corrected scale is EE on which the requirements for a unit of function are constant across foods. A further assumption is that the requirement for a unit of a function, such as protein and lipid retention, is constant at all levels of feeding. This assumption is contrary to the alternative one of a continuously-diminishing marginal efficiency (Wiegner & Ghonheim, 1930; Blaxter & Boyne, 1978; Tolkamp & Ketelaars, 1992). Some of the arguments against this view have been presented elsewhere (Emmans & Kyriazakis, 1995). The linear assumption made here has at least some experimental support (Emmans, 1994). The values of some of the key quantities in the system, such as the EE needed to retain 1 kg protein, appear to be constant across the main farm species and across degrees of maturity (Emmans, 1994).

The requirement for EE by the growing animal ($EEREQ_g$) is calculated, as in the traditional factorial system, as the sum of the requirements for maintenance and each of the productive functions. For growing animals the energy needed is the sum of the requirements for maintenance, protein retention (P) and lipid retention (L; Emmans, 1997) and can be calculated as:

$$EEREQ_g \text{ (MJ/d)} = M_e.P/P_m^{0.27} + z_1.P.\log_e(P_m/P) + z_2.B.L.\log_e(L_m/L), \quad (9)$$

where the values of the energy constants have been estimated to be M_e 1.63 MJ/unit, z_1 50 MJ/kg and z_2 56 MJ/kg (Emmans, 1994). The way in which $EEREQ_g$ changes with time can be predicted by making L a function of P and P a function of time. The full set of equations is given in Emmans (1997).

The EE requirements for the components of milk production have been estimated using extensive published (van der Honing, 1975) and unpublished (Y van der Honing, personal communication) calorimeter data from cows. The data were used to estimate the EE needed for milk-protein production, given the other assumptions of the system and that the EE requirements for milk lactose and milk fat production were 18 and 56 MJ/kg respectively. The estimate of 33 MJ EE/kg milk protein leads to the EE requirement for milk production ($EEREQ_1$) as:

$$EEREQ_1 \text{ (MJ EE/d)} = M_e.P/P_m^{0.27} + dY/dt.(0.018lac + 0.033pro + 0.056fat), \quad (10)$$

where lac, pro, and fat are the milk contents (g/kg) of lactose, protein and fat respectively.

Lactating cows can, and usually do, change the weights of protein and lipid in their bodies in systematic ways through lactation. Gains in protein and lipid have the same coefficients as those shown in equation 9; the yields of EE from losses are 13.5 MJ/kg for protein and 39.6 MJ/kg for lipid (Emmans, 1994).

Possible effects of selection

Efficiency

Selection for outputs in farm animals has been successful (Emmans & Kyriazakis, 2000) in increasing the rate of growth and, where judged to be important, reducing fatness at a weight as in pigs (Knap, 2000a). Milk yield in dairy cows has steadily increased within a breed with little change in milk composition. There have been increases in output, therefore, that must be due to an increase in intake, unless there has been an increase in efficiency, a decrease in maintenance or some combination of these effects. The evidence is consistent with the simplest view that all, or virtually all, the changes in output can be entirely accounted for by an increase in intake. Possible changes in maintenance are discussed below. However, there is no indication that the amounts of energy needed to retain 1 kg protein or lipid, or to produce 1 kg lactose, protein or fat in milk, have been changed under selection for output characteristics.

Maintenance

Taylor et al. (1986) proposed that selection for higher rates of output, particularly for milk production, would lead, as a direct genetic consequence, to an increase in maintenance. The evidence produced in support of this proposition was of two kinds: a feeding experiment and a literature review. The review of the literature in which beef, dual-purpose and dairy breeds of cattle were compared was inconclusive. It was recognised that apparent differences in maintenance between breeds could arise because they were compared at different levels of fatness. The feeding trial data showed that the animals of the two dairy breeds had 1.25 higher scaled maintenance than the two beef breeds at the same condition score. As Wright & Russel (1984) had found that total lipid content at a given condition score was higher in a dairy breed than in a beef breed, it is not possible to argue that the difference is due to the dairy cows being leaner at a given condition score. The observed differences between breeds may be associated with different levels of milk yield (Taylor et al. 1986), and it is thus possible that continued selection for high milk yield will increase maintenance cost; however, this possibility has not been established.

It is possible to reduce maintenance in laying hens by selecting for low residual food intake (Luiting & Urff, 1991a,b). Much of the change is due to a reduction in physical activity. In fast-growing poultry and pigs, and in high-producing dairy cows, the contribution of maintenance to total intake is much smaller than it is in hens, and there is probably a lower level of physical activity. Selection for lower maintenance either directly or indirectly is thus of less quantitative importance in these animals than it is in hens (Emmans & Kyriazakis, 2000).

A possible effect of selection for milk yield on maintenance is an important issue. Measurements of maintenance in both males and females of different genetic potentials for milk production would be justified. When combined with measurements of body composition at different degrees of maturity such data would help to resolve the issue.

Selection for growth rate could also, in principle, have associated effects on maintenance, but there is no indication that this process has happened in broiler chickens (Emmans, 1994).

Growth rate

Fig. 2 showed that selection could be expected to increase both mature size and the rate of maturing. The consequences for energy requirement, and hence food intake on good foods, are predictable through equation 9. The effects can be large when many generations of intensive selection are involved. Fig. 4 shows the predicted effects on food intake at a weight in male broiler chickens over the 50 years of selection since 1950 (Emmans & Kyriazakis, 2000). Calculations show that the intakes of current broilers are those predicted from their performance and the EE system; the same pattern was found for highly-selected turkeys (Emmans, 1989). Other consequences of such selection are predicted and discussed by Emmans & Kyriazakis (2000).

Selection against fatness

As the consumers of pork and bacon reduced the level of fatness that they preferred, the breeders of pigs responded by selecting for reduced levels of genetic fatness in their stocks. Over the past 25 years at least they appear to have been dramatically successful (Knap, 2000a). The weight of lipid : weight of protein at maturity has fallen from about 4 to about 1, a huge change in mature composition. A consequence is that the rate of lipid retention at a weight has been much reduced, with the further consequence of a reduction in the energy requirement at a weight. This entirely predictable effect is sometimes greeted with surprise (Campbell, 1988). This effect on intake is offset to some extent by the increase in the rate of protein retention that has also been achieved (Knap, 2000a). Where both effects can be quantified the effects on intake can be predicted. Other effects of such selection can also be predicted (Emmans & Kyriazakis, 2000).
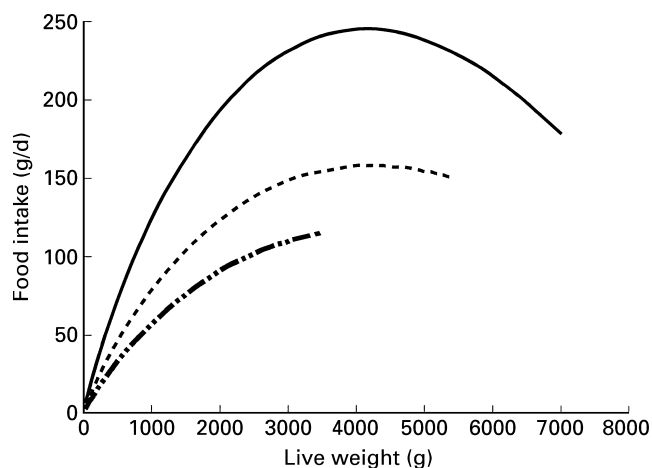

Fig. 4. The predicted food intake of commercial male broiler chickens *v.* weight in different years. The effects of 50 years of selection are shown. (—·—·—), 1950; (------), 1975; (——), 2000.

Lactation

Dairy cows have been selected largely for increased milk yield in their first lactation, with some specific emphasis on yields of protein and fat. The heifer lactation shows a much lower rate of decrease with time from calving than do later lactations (Friggens *et al.* 1999) and, perhaps for this reason, the effect of selection for increased yield has been largely by increasing the value of the scalar a in equation 8. Where there is no effect on milk composition, and even where there are, the effects of such increases in output on energy requirement for milk production can be predicted from equation 10.

It is possible that selection for higher yields, particularly where diet quality has not been improved sufficiently to cope with the increased potential output, could lead to an increase in loss of energy from the body, particularly in early lactation. As such loss provides energy for milk production, the rate of this supply needs to be taken into account in the prediction of total requirement and hence intake. More work is needed in the area of being able to predict state changes during lactation.

Organisation of feeding behaviour

Average daily intake is, in a purely formal sense, the result of the average number of meals and the average intake per meal as given in equation 1. However, the relationship between daily intake and meal patterns can be approached in two different ways. Average daily intake can be considered to result directly from the animal's short-term decisions with regard to initiation and cessation of feeding. Several authors have stressed the importance of knowing the rules that govern short-term feeding behaviour for intake prediction (Forbes, 1985; Gill & Romney, 1994). An immediate consequence of this view is that modelling of these short-term decisions is seen as being necessary in order to predict average daily intake.

On the other hand, meal patterns can be seen as the combined consequence of the average daily intake that the animal is seeking and the experimental conditions. This approach assumes that a given animal genotype in a given state with access to a given food has some average daily level of intake that it seeks. The argument is the same whether the intake is predicted according to the framework depicted in Fig. 1, or by some other means such as the maximisation of efficiency (Tolkamp & Ketelaars, 1992). The animal will then use some eating pattern, which is not necessarily constant, which allows it to obtain the level of intake that it seeks. This approach allows for a great deal of variation in eating patterns: (1) between individuals under given conditions; (2) within individuals between periods (e.g. from day-to-day); (3) within individuals between different (experimental) conditions, while average daily intake is not (necessarily) affected. This approach requires the quantification of the effects of the relevant animal, food and environmental variables to predict average daily intake, and does not rely on models of short-term feeding behaviour to predict food intake under most conditions.

In farm animals there is considerable evidence for large variation in the values of the parameters used to describe

short-term feeding behaviour (i.e. the number of daily feeding bouts, bout duration and feeding rate) between animals that have very similar average daily intakes. Animals with similar average daily intakes can vary about fourfold in the individual average number of daily visits to a feeder, and the individual average intake per visit when kept under identical conditions (Nielsen, 1995; Nielsen *et al*. 1995; Friggens *et al*. 1998; Tolkamp *et al*. 2000). An example is shown in Fig. 5. Although the variation decreases when visits are clustered into meals, some animals may still have twice the number of meals (with half the average intake per meal) than other animals that consume similar amounts (Tolkamp *et al*. 2000). Within individuals, similar variation in number of eating bouts and average intake per bout has been recorded between days during which daily intake was similar (Nielsen, 1995).

There is much evidence that changes in experimental conditions that have no effect at all on average daily intake can be accompanied by very large changes in short-term feeding behaviour. An example is that either an increase in the number of animals in a group with a constant number of feeders, or a decrease in the number of feeders for a given group size, almost invariably leads to considerable changes in feeding behaviour. The number of recorded feeding bouts, bout duration and feeding rate are affected, while average daily intake is unaffected (for pigs: Nielsen, 1995; Nielsen *et al*. 1995; for dairy cows: Harb *et al*. 1985; Elizalde & Mayne, 1993; for beef steers: Gonyou & Stricklin, 1981; Corkum *et al*. 1994). Large effects of changes in experimental design on feeding patterns that leave average daily intake unaffected have also been observed for rats (for example, see Collier & Johnson, 1990, 1997).

In the study of Elizalde & Mayne (1993) it was found that silage intake was unaffected when the number of cows per feeder was increased from three to seven. This increase led to an increase in feeding rate (from 42·1 to 65·3 g DM/min), a decrease in feeding time (from 253 to 174 min/d) and to an increase in feeder occupancy (from 53 % to 85 %). Such
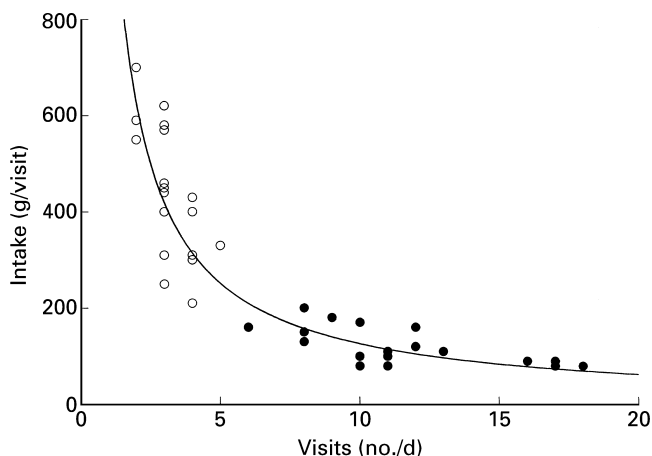
observations show that animals can respond flexibly to a wide range of changes in conditions with large changes in short-term feeding behaviour while maintaining the same average daily intake. Attempts to predict average daily intake under such circumstances via models of short-term feeding behaviour seems unlikely to be successful, because intake is independent of the form that short-term feeding behaviour takes. Of course, in the limit, even very flexible animals may not succeed in maintaining intake, as was found by Elizalde (1993) when the number of cows per feeder was increased from seven to nine, which led to a decrease in average daily intake. While such effects can occur, this finding does not justify the insistence on the use of short-term feeding models for the prediction of daily intake in all other circumstances.

Most attempts to predict intake for grazing animals are based on models of the same form as equation 1, for example:

$$\text{food intake (g/d)} = \text{grazing time (min/d)} \times \text{biting rate} \\ \text{(/min)} \times \text{bite size (g).} \qquad (11)$$

Bite size can be broken down further into a number of other measures, e.g. bite depth (cm), bite surface area (cm^2) and food density (g/ml), all in relation to some sward characteristics such as height or bulk density (for example, see Laca *et al*. 1992). The mathematics are impeccable. However, once more it appears that for an animal of a given size and with certain mouth characteristics that is grazing a given sward, its 'feeding motivation' can have a large effect on each of the parameters in equation 11. For example, restriction of daily grazing time for dry or lactating sheep led to considerable increases in instantaneous intake rate, mainly as a result of increased bite size, while daily intake was not necessarily affected (Iason *et al*. 1999).

Other researchers, working within the framework exemplified by equation 11, have come to similar conclusions. The values of the parameters in equation 11 for a given animal grazing a given sward will depend on whether or not the animal is hungry, whether or not the animal is lactating, etc. The behaviour will depend on the intake level the animal apparently desires, or on its 'feeding motivation' (for example, see Newman *et al*. 1994; Penning *et al*. 1995). The best estimate of the 'feeding motivation' of a given animal on a given sward is the actual measurement of daily intake. However, if the 'feeding motivation' and, therefore, actual intake must be measured before the values of the parameters in equation 11 can be set, we can no longer speak of a system of intake prediction. What is left is a verification of whether measurements, or estimates, of the parameters of food ingestion agree with the observed daily intake. Such models can have no value for predicting the effects of selection on food intake of farm animals (Kyriazakis & Emmans, 1999).

Fig. 5. The mean food intake per visit *v*. the number of visits to the feeder in the day. The data are for two pigs (○,●) for each of 18 d. (———), The combinations of intake per visit and number of visits per d that result in a daily intake of 1260 g. The same mean intake was achieved by both pigs but by different means (Neilsen *et al*. 1995).

Discussion

Animals need resources from their food in order to maintain themselves, grow, accumulate fat reserves, reproduce and, in the case of mammals, lactate. In order to get the resources at the rates needed to meet their presumed requirements they

have to eat the food, or foods, that are available at rates such that these requirements are met. It has been found to be useful to see the animal as eating to meet its requirements as shown in the left-hand side of Fig. 1 (Emmans, 1997). In the present paper the emphasis has been on 'eating to meet requirements' rather than on the 'subject to constraints' part on the right-hand side of Fig. 1, because of the context of what will happen under selection for outputs.

If animals are selected for increased output under conditions where their potential output is already unattainable then, given the framework in Fig. 1, selection would be only for an increased capacity to deal with constraint that is limiting intake. There would be cases where this would be useful. If the environment is hot, and nothing can be done about it, then it is sensible to select animals that can grow and produce at higher rates in hot conditions because they have a higher capacity to lose heat. If energy from forage is cheap relative to that from concentrates (although this is not always the case) then it is sensible to select cows that have a higher capacity for forages so that they can eat more of such foods and hence produce more milk. However, in many cases it is possible to provide economically the resources that the improved genotype needs to fully express its potential and, in such cases, it is the potential for output that is relevant for predicting intake.

We have argued that the energy, and other resources, needed to allow the greater potential outputs to be realised, will be eaten by the animal, providing that the conditions are such that it can do this. It is thus the potential for output, including maintenance as an output in this sense, that drives intake and which needs to be known in order to predict intake. As animal breeders continue to select farm animals for higher levels of output it is important to be able to predict the other consequences of such selection. In the present paper the focus has been on the prediction of food intake, as this is a crucial first step to considering other consequences. Among the other consequences are effects on heat production and the required nutrient balance of the foods needed by the changed genotypes, that are discussed elsewhere (Emmans & Kyriazakis, 2000).

While selection that leads to changes in food intake must lead to changes in short-term feeding behaviour (for example, either meal size or meal frequency must increase) we see such changes as incidental rather than as causing the change in intake. We have taken the position that the detailed short-term feeding behaviour of the animal is the means that it uses to, or to attempt to, attain the intake that it needs to meet its requirements. Examples were given of the flexibility that can be shown in the values of the parameters that describe short-term feeding behaviours and on the high intrinsic variation that is present between animals. It is by focusing on the prediction of intake in a general way, including the prediction of the effects of genetic selection, that we feel that progress will be made.

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