The multifactorial nature of food intake control[1]

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ABSTRACT: Three approaches to predicting and understanding food intake by beef cattle are discussed and compared. Although many physiological factors are known to be involved in intake control, these are not sufficiently quantifiable to form an adequate basis for intake prediction. Prediction equations derived from observed effects of animal and feed factors on intake are useful within the range of conditions under which the data were collected, but they do not predict adequately outside this range. The concept of an intermediate approach to intake prediction and understanding is presented, suggesting that proportional deviations of resource supplies from the feed (e.g., energy, protein, fiber) from the animal's optimal supply ("requirement") generate discomforts. These, when squared and added, yield a total discomfort signal, which the animal minimizes. The fact that feed intakes by individual animals fluctuate considerably from day to day provides a means whereby animals can assess whether an intake somewhat higher or lower than their current average intake will improve their well-being. Examination of intake data from beef cattle fed grass silage suggests that intake is controlled over a period of several days. It is concluded that different levels of understanding of the control of voluntary intake are needed for different reasons, and that no single approach will serve all purposes.

Key Words: Beef Cattle, Physiology, Prediction, Voluntary Intake

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Introduction

Beef cattle are almost always fed ad libitum to maximize growth rate and profitability. Intake control involves energy because changes in energy requirements of the animal and/or in the digestible or metabolizable energy content of the diet cause intake to change in the appropriate direction. For example, results summarized by Baumgardt (1970) show that beef cattle decrease their DMI as the concentration of DE increases (Figure 1a). It appears as if DE intake is being held constant (Figure 1b), but closer examination shows that DE intake systematically decreases by a small amount as DE concentration increases (Figure 1c) (see also Grovum, 1987). It seems highly unlikely that animals eat in order to achieve constancy in the supply of only one of the many resources provided by feed.

With forage-based diets, beef cattle, as other ruminant animals, increase their DM intake as the rate and extent of digestion increases. This has been attributed to a physical limit to intake and, because of its slow rate of digestion and correlation with forage intake in sheep, NDF has been used to account for the bulkiness of feeds. However, there is large variability in NDF intake of forages (Ketelaars and Tolkamp, 1992), which strongly suggests that bulk is not the only factor affecting forage intake.

We can conclude that intake is controlled and that energy- and bulk-sensing mechanisms are involved. Many other factors are also implicated in the control of intake, including nutrients (such as amino acids, minerals and vitamins), disease, and environmental conditions and social pressures in a multifactorial manner. In order to use information on these factors, it is necessary to construct a conceptual framework as to how intake might be controlled. The rest of this review will examine three approaches: physiological, empirical, and teleological.

Physiological Approach

Numerous metabolites, hormones, and nervous pathways have been proposed to act as signals in providing the central nervous system (**CNS**) with information about nutrient status (Forbes, 1995). Many of these have first been proposed for simple-stomached animals and then adopted for ruminants (e.g., distension of the digestive tract, cholecystokinin [**CCK**], leptin). Other signals are not effective in ruminants (e.g., glucose), whereas yet others are peculiar to ruminants (e.g., VFA, rumen-degradable protein [**RDP**]). As each new candidate

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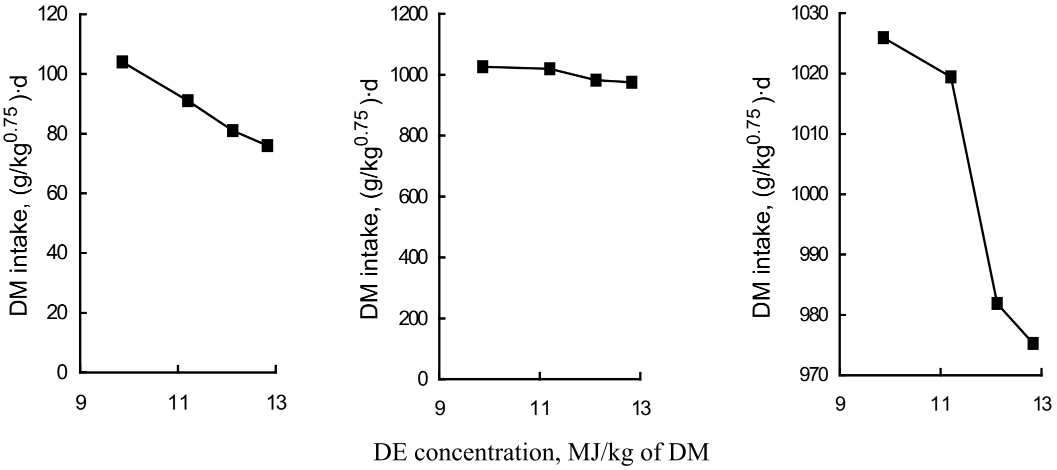

Figure 1. Intake of pelleted feeds of different DE concentrations by growing beef cattle (Montgomery and Baumgardt, 1965): a) DMI; b) DE intake; c) DE intake on an extended scale.

comes along, previous favorites tend to be forgotten. However, a role for CCK is no less likely now than it was in 1973 when its effect on intake was first reported. It is likely, therefore, that the physiological mechanisms controlling intake are complex and truly multifactorial. Diagrammatic representation of the factors thought to be important is probably the best way of integrating them into a scheme of intake control (e.g., Blundell, 1991) since attempts to quantify models of such complexity are likely to end in unstable solutions (France and Thornley, 1984). In many cases, there are no adequate experimentally derived equations with which to build quantitative models based on physiological factors, such as those outlined above. Thus, whereas studies of the detailed physiology of the control of food intake will continue to reflect aims to prevent obesity in human beings, they are unlikely in the short term to provide practical solutions for the formulation of animal feeds.

Empirical Approach

Given the limitations in ability to account for the many factors that control appetite, empirical equations have been developed to predict intake with different types of beef cattle in different types of production situations (CSIRO, 1990; AFRC, 1991; NRC, 1987; 2000). These equations are developed by collecting and analyzing data to produce equations that can be used for prediction of DMI in formulating diets, predicting performance, etc. Information is typically used that is measurable in production situations.

The NRC (1987) published comprehensive compilations of equations on prediction of feed intake in beef cattle. The graphs presented there are plots of various equations that have been proposed to predict DMI in beef cattle, and in some cases, show considerable discrepancy between the predictions of equations from different sources. No validation is presented, in common with most published prediction equations (Pittroff and Kothmann, 2001), and, as always with this type of approach, predictions of intake are limited to the range in which the observations on which the equations are based were made. However, NRC (2000) gives some validation of the use of the equation for growing yearlings:

$$\mathrm{DMI} = \{[\mathrm{SBW}0.75 \times (0.2435\mathrm{NE_m} - 0.0466\mathrm{NE_m}^2 - 0.1128)]/\mathrm{NE_m}\}$$

where DMI is measured as kilograms per day, SBW is starting body weight in kilograms, and $\mathrm{NE_m}$ is given in Mcal/kg of DM. In one comparison with experimental results from cattle fed high-energy diets, this equation accounted for 76% of the variation, with an overall prediction bias of 0.16% and standard error of Y of 0.34kg. Other data sets were less well fitted, but adjustment factors for body fat, breed, feed additive, environmental temperature, and mud were calculated to adapt the basic equation to different management situations.

Looking at the numerous factors with which intake is correlated, and which presumably affect intake, there can be no doubt that the control of voluntary food intake is multifactorial. In the NRC (1987; 2000) approach, such factors as the sex of the animal and the use (or not) of anabolic agents are applied to the predictions based on live weight and dietary energy concentration as multipliers. There are interactions, however. For example, the reduction in the DE concentration of a medium-quality diet for an animal with low nutrient requirement results in it eating more since it is not at the “physical limit,” whereas for an animal with a high nutrient requirement, a reduction in the DE concentration causes it to eat less since it is already eating to its physical capacity. Another example: The intake of a small, fat animal is likely to be reduced more by high environmental temperatures than that of a large lean animal of the same body weight.

Whereas prediction of intake by regression analysis is very suitable when the situation for which prediction is

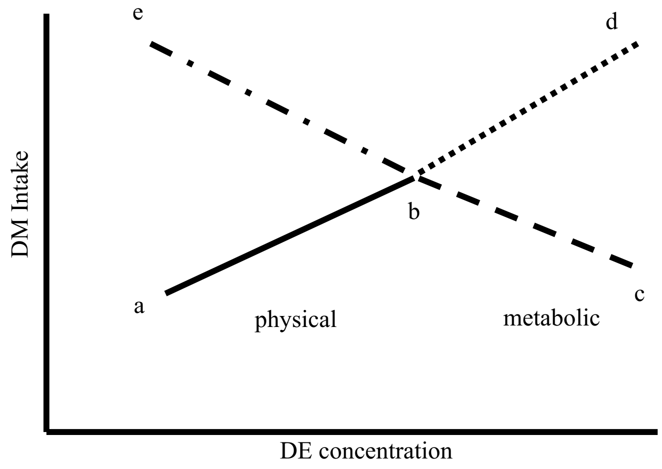

Figure 2. Notional relationship between food intake and diet digestible energy (DE) concentration (see text for explanation).

required is within the range of observations used in the equations, it can give misleading results outside this range. Therefore, these equations are of limited use in exploring underlying features of intake control and predicting intake in novel situations (e.g., intake of novel genetically modified [**GM**] food by an novel GM animal).

Teleological Approach

Teleology is defined as "the doctrine of adaptation to purpose" (Webster, 1915). In this case, the "purpose" is survival and the transmission of genes to the next generation. For the purposes of this paper, the concept is emphasized rather than the mechanism.

Simple "rules" can be proposed, such as "animals eat for calories," but whereas this approximates in some situations for simple-stomached animals, it is not valid if we wish to encompass forage-based diets for ruminants. The next step is to propose that "animals eat to satisfy nutrient (energy) requirements unless prevented by a limiting factor," and examples of this approach can be found (Conrad et al., 1964; Forbes, 1977; 1980). A more sophisticated example was proposed by Poppi et al. (1994), who used six limiting factors, intake being predicted as that resulting from the application of the most limiting factor.

However, it seems most unlikely that the animal ignores one limiting factor just because another factor is even more limiting. For example, consider an animal being fed a series of diets with ever increasing DE concentration (Figure 2). As DE increases (*a* to *b*) from a low level, intake increases as rate and extent of digestion increase and release rumen capacity more quickly. Eventually, there comes a point at which the animal is eating sufficiently to meet its requirements for energy, and from that point upwards (*b* to *c*), intake decreases. It is difficult to imagine that below the threshold, there is no input to the intake-controlling systems of the body from sensors sensitive to energy-related signals (*b* to *e*). Equally, can we envisage that once above the threshold, there is no input whatever from stretch receptors in the rumen wall and elsewhere (*b* to *d*)? The convergence of pathways carrying signals from the periphery to the CNS (Forbes, 1996) seems to deny the possibility that intake is limited solely by whichever factor happens to be most limiting at a particular time.

An alternative concept is required, therefore, that more readily acknowledges the multifactorial nature of feed intake control. The following is an outline of such an approach (Forbes, 1999; Forbes and Provenza, 2000), which is offered as a stimulus to further thought and experimentation.

There is feedback from many sensors providing the CNS with information on such factors as energy status of the liver, extent of repletion of adipocytes (leptin), degree of stretch of various viscera, and external factors, such as weather and the behavior of other animals, both fellow-herbivores and predators. It is proposed that the strength of the signal from each of these sensors to the CNS is proportional to the deviation from optimal (e.g., if the optimal intake of ME by a beef steer is 150 MJ/d, and it is eating 10 kg of feed with an ME concentration of 12 MJ/kg, then the absolute deviation is 150 − 120 = 30 MJ and the proportional deviation is 30/150 = 0.20.

The word "discomfort" is proposed to describe this deviation because animals will expend effort in order to reduce it. Discomfort increases with an excess or deficiency of a nutrient, with physical distension of stomach or intestines, above a certain daily grazing time, with social pressures, and with numerous other things. Some factors only cause discomfort when above a threshold (gut fill, eating time), whereas others do so when provided in greater or lesser amounts than are optimal. The optimal intake of a nutrient is that which, in the absence of other constraints, allows the animal to achieve its potential to grow, fatten, lactate, etc. It is not always something that can be measured, but estimates usually can be made from observations of responses to controlled changes in nutrient supply. The argument is always likely to be circular, however, as maximal rate of production can only be achieved with animals fed ad libitum.

It is further proposed that discomfort increases in a nonlinear manner, with increases in deviation giving ever-increasing effects on discomfort. Evidence on which to base the shape of the response curve to different degrees of stimulation of abdominal receptors is surprisingly sparse. Increasing the volume of a balloon in the reticulum of goats from 800 to 1,200 mL resulted in a greater increase in the number of impulses per second in the afferent nerve fibers than did the increase from 400 to 800 mL, whereas a further increase from 1,200 to 1,400 mL gave an even steeper increase (Iggo, 1955); this type of dose-response information is, however, lacking for chemical stimulants and the small number of "doses" used prevents a proper description of the shape of the dose-response curve. It would be circular to base the implementation of this concept on intake responses to different doses of stimulus, hence the difficulty of providing sufficient evidence on which to base a fully quantitative model based on the concept.

For simplicity, squaring has been chosen to provide the exaggeration of greater deviations, but could easily be replaced by an exponential or sigmoid response curve; an advantage of squaring is that it converts negative deviations into positive signals. However, this symmetry of the response curve is not based on data and again is illustrative rather than definitive. Again, there are few data to provide the basis for a more sophisticated treatment of this feature of the concept.

Weighting factors were used in previous expositions of the concept. These are not justified, however, with our current level of knowledge and have been omitted from the present description. One of the intentions of this concept is to allow various discomforts to be expressed in a common currency; weighting would be an admission that this is not possible, but it must be accepted that considerable experimentation will be required to provide data on which to base differential weighting of the various discomforts.

Once the discomforts have been calculated, they are added together to provide a signal of total discomfort; treatments imposed experimentally have additive effects (Forbes, 1996). According to our definition of discomfort, animals seek to minimize the total by adjusting their intake and/or choice, continuing in the direction that results in a reduction in discomfort, and learning as they go.

The next consideration is the properties of the food and environment that should be included in a semi-quantitative model based on the concept of minimal total discomfort. Whereas a large number of factors could be included, many of them are of little importance in many situations, especially where the food(s) on offer provide adequate amounts of such components as minerals and vitamins. Clearly, the supply of energy, the content of fiber, and the availability of protein in the diet are of central interest in most cases and can be described by the concentrations of ME, NDF, and CP in the food. Whereas this is a considerable simplification of reality (it ignores the ratio of VFA, the degradability of fiber, RDP, rumen-undegradable protein, and individual amino acids, to mention a few), it provides a starting point from which to develop a more comprehensive treatment. There is little point in including the time per day beyond which the animal would prefer not to eat, for example, if it is clear from the outset that this limit will not be reached. The decision as to which factors to include depends on the situation and the interests of the individual. Any attempt to proscribe the factors to be included would imply greater confidence in the concept than is currently warranted.

Interactions between the effects of different controlling factors are not explicitly included in the present discussion. However, in response to such a question as: "Is there really a 'protein optimum' that is independent of energy intake?" the answer is that there is a combination of energy and protein that is optimal, and it is this which the animal is trying to achieve. Failure to achieve it means that, although the animal might have achieved minimal total discomfort for the present circumstances, this is not zero discomfort.

In biology, it is generally assumed that the behavioral programs that can be observed in animals today evolved because they contributed to animals' fitness (survival and reproduction). Is minimization of discomfort identical to fitness maximization? If not, how could such programs have been selected in the evolutionary process? There is a difference between long-term, selectable traits and short-term responses by individual animals to the current situation. It's possible to envisage how animals evolved to cope with fibrous forages, for example, by developing the capacity to store digesta long enough for microbial action to yield nutrients. Having been provided with that anatomy and physiology, the individual then has to live in the real world and be flexible in dealing with different food conditions, including ones in which fiber digestion is not the primary limiting factor to intake. What is selected for is not just a single solution for a specific ecological niche, but an adaptable framework for responding to a changing environment, both in space and time.

A Simple Example

In this simple example, animals' requirements are, for illustrative purposes: ME, 150 MJ/d; CP, 1.00 kg/d; NDF, 6.0 kg/d (no discomfort is generated by a "deficiency" of NDF); and the feed has a composition of 11.0 MJ of ME/kg; 0.14 kg of CP/kg; and 0.70 kg of NDF/kg. An approximate intake is proposed, and the deviation of actual supplies of nutrients resulting from this intake from that "required" are squared and added. Intake is changed up or down and the calculations repeated, iterating until the intake that produces minimal total discomfort is reached. Figure 3 shows the discomfort associated with ME, CP, and NDF at different levels of intake. Total discomfort is also shown, and this is minimized, for this combination of animal requirements and feed composition, at 8.7 kg DM/d.

In its present form, the model is a semi-quantitative working hypothesis. If it is to have potential for prediction, there are a number of questions to be addressed, not least the weightings to be applied to each discomfort and which factors to include for any particular practical situation. However, an advantage of the approach is that it can incorporate almost any factor that influences feed intake (e.g., rate of grazing of sparse pasture via a discomfort generated by time spent grazing above a threshold; Forbes, 2001). Although there is no opportunity in this paper to discuss the use of the minimal total discomfort theory in relation to diet selection, it should be noted that prediction of the animal's behavior towards a single food is a special case of the more general situation of choice feeding, which the model can easily be extended to deal with, as is supplementation with a fixed daily amount of another feed.

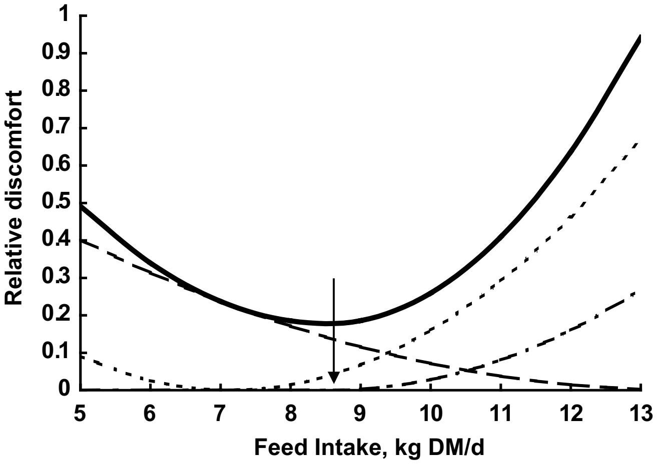

Figure 3. Postulated relative discomfort due to ME (—), CP (···), NDF (– • –), and total discomfort (▬), generated in a beef animal by different daily rates of food intake. Assumed animal "requirements" were: 150 MJ of ME/d, 1.00 kg of CP/d, 6.0 kg of NDF/d. Food composition: 11.0 MJ of ME/kg, 0.14 kg of CP/kg, and 0.70 kg of NDF/kg. The vertical arrow indicates the intake at which total discomfort is calculated to be minimal.

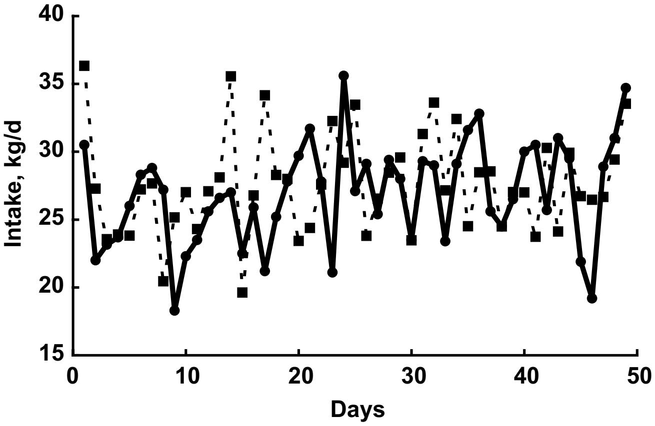

Figure 4. Daily intakes of grass silage by a beef animal. Solid line = observed intakes (R. Kirkwood, unpublished data); dashed line = random numbers with the same mean and SD as the observed intakes.

Day-to-Day Variation in Intake

An animal can only know whether it should be eating more (or less) than at present in order to minimize its discomfort if intake varies from time to time. Even when it has arrived at the optimal state, it can only know whether it should maintain the same level of intake if it tries out the effects of different rates of intake. The concept that animals find an optimal intake by "experimenting" with a range of intakes, which implies that learning is involved, is supported by clear demonstrations that ruminants, like other animals, learn to associate the sensory properties of the food with the consequences of eating that food (Forbes and Provenza, 2000).

Examination of the weights eaten by individual animals on a series of consecutive days confirms the experience of anyone who has studied food intake, that there are considerable daily fluctuations. Examples have been given elsewhere for dairy cows (Forbes, 2001; Forbes and Provenza, 2000) and sheep (Forbes and Provenza, 2000), and Figure 4 shows daily intakes of grass silage by a growing beef animal also given 3 kg of concentrate feed per day (R. Kirkwood, unpublished results). Examination of the records for many more individuals shows similar fluctuations, and these are only partly related to variation in the mean intake of the group of animals of which the individuals are members. Although an optimist might see patterns in such data, plotting randomly generated data with the same means and SD as the observed intakes produces similar fluctuations and pseudo-patterns (Figure 4). However, autocorrelation of the observed data gives positive correlations approaching statistical significance between intakes on consecutive days, and negative correlations, significant in some cases, between intakes separated by 3 or 4 d, whereas randomly generated data do not show such correlations. This suggests that intake might be organized over periods of 3 to 4 d, and further analysis is warranted.

Any suggestion that these fluctuations are animals' responses to changing DM concentration of the silage in order to maintain a constant DMI is refuted by the fact that daily DMI is positively related to DM concentration, whereas there is no significant relationship between the intake of fresh matter and DM concentration (A. Jolaosha, personal communication). Therefore, until we have further evidence, we must conclude that the daily fluctuations in intake by individual animals are only weakly organized in relation to time. They could, nevertheless, still allow the animal to average its intake over several days in order to minimize total discomfort.

This leads us to the hypothesis that these beef cattle fed on grass silage are controlling their forage intake over a period of several days; a high intake one day is followed by lower intakes subsequently to give a more constant level of intake over periods longer than a few days. Yeates et al. (2002) analyzed the patterns of meals taken by dairy cows offered a free choice of two feeds with different protein contents and concluded that they did not balance their protein and energy intakes over a sequence of meals, up to a whole day, even though there was considerable evidence of balancing of diet over periods of many days or weeks. Kyriazakis et al. (1999) stated: "There is little evidence that animals modify their diet selection in response to short-term systemic fluctuations of their internal environment. On the other hand, long-term changes in the internal state of the animal lead to consequent long-term changes in diet selection." They proposed that the extent to which the animal's internal state deviates from optimal is a more important determinant of diet selection than "what time period matters to the animal," and what applies to diet selection should also apply to feed intake.

Conclusion

Approaches used to predict food intake or to describe intake control mechanisms depend on the needs of the user. On the one hand, those who seek to manipulate feeding pharmacologically require information on a limited part of the complex network of physiological processes underlying many of the activities of the animal's body. It is likely to be a very long time before a model to predict feed intake can be developed in which all of the factors controlling appetite are accurately accounted for in feedlot situations. On the other hand, prediction of intake based on observations made under similar conditions offers an empirical solution, but one that will not allow such questions as how to best feed (GM?) animals with novel requirements and physiology, kept in a novel environment, with (GM?) plant materials of novel composition and structure.

This paper has therefore concentrated on a concept in which it is argued that animals experiment in order to learn to minimize total discomfort. Such a framework is hypothetical, but it takes into account sound principles, such as responses to discomfort, integration of feedbacks, learning, and day-to-day variation in intake. It is unlikely that such a hypothesis can be proved or disproved by any single experiment. Rather, its acceptance will depend on whether more credible hypotheses arise and whether it is judged to have potential to be developed into a tool of practical use and/or improved understanding.

Implications

Beef cattle do not control their feed intake in order to achieve a constant intake of a single resource (energy, protein, fiber). This implies that a more sophisticated approach must be developed for formulation of optimal diets and feeding programs than those based on a few independent factors. However, attempts to invoke detailed physiological pathways immediately come up against lack of quantitative relationships and lack of understanding of how numerous hormonal and neural pathways interact. Therefore, the approach adopted here, in which factors of importance in the situation being considered are incorporated into models of total discomfort, may provide a conceptual framework for future developments that account for more of the variation in factors that control intake.

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