Feeding Behaviour and Nutrient Intake in Ruminants

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Animal production is heavily dependent on energy and nutrient supply which is a function of what and how much an animal eats: the latter depends on its feeding behaviour. Pigs, poultry and ruminants all appear to be able to learn how to choose, from a range of suitable foods, a diet that is close to optimal for their current needs (for protein or amino acids, or minerals or vitamins) as defined by genotype and physiological state. It appears that animals achieve this by learning from mother, and by a 'trial-and-error' learning process that depends on their sensing the metabolic consequences of eating particular foods, e.g. they make associations between 'fingerprint' attributes (taste, odour, texture, position) of certain foods and any negative post-ingestive stimuli (malaise) resulting from their ingestion, and form aversions such that they subsequently reduce their intake of, or totally avoid, those foods. This aversion model has been tested in animals by creating aversions to foods (either novel or familiar) by administering lithium chloride to produce post-ingestive malaise. Preference for a particular food, on the other hand, may result from the food's being associated with a feeling of well-being (reduced malaise) after the food is ingested.

Introduction

Production in farm livestock is heavily dependent on nutrition. What and how much animals eat depends on their feeding behaviour (Provenza, 1991). This statement may seem obvious but it seems that, as nutritionists in search of maximum production, we often forget that the foods (plants, or supplements) which we believe are good for animals are not always eaten by them. We need to understand the reasons why animals find some foods 'palatable' or acceptable, and others not so.

In I9 16, Kempster found that hens given a choice of foods selected an appropriate diet and had higher egg production than those given a single food. At about the same time, Evvard (19 15) characterised the intake of energy and nutrients by pigs when offered unlimited access to a smorgasbord of foods capable of providing a well-balanced diet. Notably, the diets chosen by the pigs show a close resemblance to current feeding recommendations. After becoming accustomed to the foods (a learning period), some of the choice-fed pigs grew faster than had been previously reported for conventionally fed pigs at that research station. The choice-fed pigs reduced their intake of protein-rich foods (and the **protein:energy** ratio in their diet) as they aged. Since then, much more evidence has been produced to show that laboratory and farm animals can make 'appropriate' food choices (see papers by Cumming and colleagues in earlier volumes of "Recent Advances"). Despite this evidence, the question of whether animals, when given the opportunity to select freely from a variety of foods, can choose 'wisely' has been, over the years, a contentious one (for discussion, see Forbes and Kyriazakis, 1995). This situation has probably arisen because animals, when given food choice, do not always appear to take full advantage of the array of foods and nutrients available to them. However, the current consensus is that animals do exhibit 'nutritional wisdom', though only in the (non-cognitive) sense that they learn to make appropriate choices between alternative foods such that their current nutrient needs are met, as far as is feasible, whilst at the same time they avoid toxicity.

There are numerous demonstrations that various animals - e.g. chickens (Mastika and Cumming, 1987; Shariamadari and Forbes, 1990), sheep (Kyriazakis and Oldham, 1993) and even children (Birch and Deysher 1990) - when offered a choice of foods that differ only in concentration of a single nutrient, can, after a period of exposure to those foods, select among them so as to meet their current requirements as closely as possible. At the same time, they will minimize their intake of substances that would have led to non-specific nutrient imbalances, or excesses/toxicities. Pigs, for example, given a choice of two foods differing mainly in crude protein content formulated their own diet in line with their decreasing requirement for protein relative to fat as they matured (Kyriazakis, Emmans and Whittemore, 1991). In a

similar way, sheep choose foods with a different protein content so that their mixed diet matches their current protein requirements whilst also avoiding an excess intake of a rapidly degradable dietary protein source (Kyriazakis and Oldham, 1993) or a urea-supplying feed (Nolan *et al.* 1993, and below) that might have predisposed them to ammonia intoxication. This latter experiment provided a demonstration that reductions in intake were commensurate with the 'dose', or type, of substance leading to the aversion (and so, presumably, to the degree of resulting internal malaise).

Emmans and Oldham (1988) have proposed that what animals choose to eat from the foods on offer at any time is indicative of their striving to meet their current nutritional demands (determined primarily by their genotype, which is a 'blueprint' for their optimal or desired growth and development, but modified by their current physiological state, ambient conditions, parasitism, disease etc.). An important rider can be added to this theory: animals choose mainly from the foods known to them (they are apprehensive about unfamiliar foods and surroundings or, in other words, they exhibit *neophobia).* The consequence is that they must 'test' unknown foods and surroundings, in order to learn whether these can be classified subsequently as 'familiar-safe'. Foods which are not in this category may not be consumed in significant quantities, even though they could potentially make an important contribution to balancing the animal's diet - for example, with grazing animals, supplements may fall into this category.

Aversion and learning

Unpleasant experiences (e.g. malaise, nausea) occurring around the time a food is eaten will normally cause that food to become aversive. Learned feed aversions are common in sheep, pigs and poultry, and appear to be acquired when excesses of nutrients or toxins stimulate the emetic system. This involves interactions between areas in the brain stem including the area postrema and the chemoreceptor trigger zone (see Provenza, 1995). Administration of anti-emetic drugs attenuated the development of Li-induced aversions in sheep (Provenza *et al.* 1994). The strength of the aversion appears to be correlated with the concentration of the aversive substance (e.g. LiCl, morphine; Skinner & Martin 1992), the time between the ingestion of the food and the onset of malaise, and the animal's previous experience with the toxic food (Provenza, 1995). Rogers and Egan (1975) demonstrated that lambs became averse to foods eaten when they were undergoing amino acid imbalance. How a response to this imbalance is mediated is not clear; however, the brain stem, central nervous system and the neurotransmitter, serotonin, appear to be involved (see Provenza, 1995), and in some instances heat load may also be a factor (see below).

It appears that animals quickly learn about foods from their mother and other more experienced animals, and especially by a 'trial-and-error' process that depends on their sensing the metabolic consequences of eating particular foods (Provenza, Lynch and Nolan, 1993). For example, they make associations between sensory attributes (taste, odour, texture, position) of certain foods and any negative post-ingestive stimuli (malaise) resulting from their ingestion, and form aversions such that they subsequently reduce their intake of, or totally avoid, those foods - in general these associations appear to be clearest in natural situations with complex decisions being less clear in 'artificial' situations. That these processes are non-cognitive (i.e. 'hard-wired') is clear from experiments in which conditioned aversions to familiar foods have been produced by LiCl in anaesthetized rats (Roll and Smith, 1972) and sheep (Provenza, Lynch and Nolan, 1993).

Malaise leading to conditioned aversion

It is interesting to speculate about the factors that might lead to aversion-producing malaise. One reason may be that the animal is directly affected by toxins (e.g. alkaloids; Olson and Ralphs, 1986; glucosi-nolates, Duncan and Milne, 1992) which are rapidly absorbed. All animals have mechanisms for detoxifying and excreting unwanted metabolites, but the processes take time - so the rate of ingestion of nutritious foods containing toxic materials may need to be restricted until the rate of absorption and removal are approximately equal. Sheep given nutritious diets containing different LiCl toxicities, reduce intake as toxicity increases, apparently to limit their intake of Li to a 'tolerable' level of 40-60 mg/kg liveweight (duToit *et al.* 1991). If the toxicity limit is reached for one food before the requirement for a particular nutrient is satisfied, it seems likely that the animal will then choose an alternative source of food containing the wanted nutrient. This may lead an animal to choose smaller amounts of a wide variety of plants (Provenza, 1995).

Aversions to foods can also be caused by nutrients that would not normally be considered to be toxic, e.g. an excess supply of propionate into the portal blood is aversive (Ralphs *et al.* 1995) probably because it affects the flux of metabolites through the citric acid cycle in liver cells and promotes metabolic acidosis. Similarly, excess ammonia absorption causes toxicity by altering the biochemical balance in brain cells (Felipo *et al.* 1993). Thus, although high-energy diets enable ruminants to obtain nutrients rapidly, (which is perhaps why they show a preference for grain-based diets), they nevertheless appear at times to restrict intake of grain diets, and choose alternative foods. This is probably because the absorption of volatile fatty acids or lactate arising from rapid microbial fermentation of starch in the rumen is causing toxicosis (Provenza, 1995). In a similar way, an excess of protein in the diet leading to an unwanted

level of amino acid absorption will require the liver or other tissues to deaminate large amounts of these substances to a-keto acids (e.g. a-ketoglutarate, a citric acid cycle intermediate) and ammonia. The ammonia is removed via the urea cycle at a considerable energy cost (2 ATP/mole urea synthesised). The surplus keto acids can be oxidised with the generation of ATP, and if ATP is not required, used in the synthesis of fat.

The need to detoxify or remove energy or protein in excess of requirements may create a further metabolic burden - heat production - which is known to have important consequences for food intake and production, especially in hot/humid environments. It would be interesting to test whether a high heat load is itself an aversive stimulus. Ruminants on low digestibility, low nitrogen diets absorb excess VFAs relative to amino acids. Their sub-optimal food intake may be a notable consequence of the detrimental effects of excess heat production on intake (Leng, 1992). It may therefore be particularly important for animals in tropical areas to be offered, or to have the opportunity to choose, diets that closely match their requirements for all nutrients, as this will minimize their heat load. On the other hand, an excess intake of protein (especially if amino acids are imbalanced) might also be detrimental because heat load increases when the excess amino acids are deaminated and metabolised. On a mass basis, the removal of excess protein leads to the highest heat production - excess carbohydrate (or VFAs) is next, and excess fatty acids (which tend to be deposited in the body) give rise to the lowest heat production. Because animals require less energy to maintain deep body temperature in hot environments, they tend to eat less than animals in cooler environments and so may require a higher ratio of protein (and other nutrients) relative to energy: however, additional protein must provide an appropriate balance of amino acids (and other nutrients) for protein deposition and tissue growth. Otherwise, the heat cost associated with the removal of unwanted amino acids may cause further reductions in feed intake and production. This protein 'dilemma' may be the reason for the apparently contradictory effects on animal production that have been obtained when animals in hot environments are offered additional protein.

Selection for specific nutrients

Chickens requiring a source of thiamine to overcome an induced deficiency of this vitamin, learnt to make an appropriate choice between a thiamine-containing, control diet and an otherwise identical alternative, thiamine-deficient diet (Hughes and Wood-Gush, 197 1). One explanation for these findings is that the intake of nutrient-deficient foods is reduced because animals develop acquired aversions to those foods which can be expected to produce a metabolic imbalance/ malaise (Rogers and Egan, 1975; Provenza, 1995). An alternative explanation is that, in thiamine-deficient animals, ingestion of the thiamine-supplying

food is reinforced by a post-ingestive feeling of well-being (Forbes, 1995). The mechanisms by which the aversive response is developed and mediated are currently being actively studied but remain to be clearly defined.

There have been numerous demonstrations that animals can exhibit 'wisdom' in selection of nutrients where a single nutrients is supplied in excess of current requirements. For example, in an experiment designed to determine if sheep could identify and select from two pelleted diets of differing protein:energy ratio (Armstrong 1992), we noted that animals offered the 'high quality' diet ingested about one-third of that ingested by those on the 'low quality diet', and therefore received less than a maintenance ration. Subsequent examination of the diets revealed an unexpectedly high Cu:Mo ratio in the 'high quality diet'. It appeared that the copper present was reducing the intake of this diet, possibly to a 'balance' point where the benefit gained from the diet (supply of energy and nutrients) was just outweighed by the negative effect of excess copper ingestion. This kind of effect may also have been the explanation for the reduced intake of poplar when it was associated with urea/ammonia as compared with NaCl administration (Nolan et al. 1993).

When animals make appropriate food choices, it appears that, at times, both cognitive and affective processes are involved (see Provenza, 1995). The latter involve conditioned responses dependent on animals making an association between the taste (and smell) of the food eaten and some body-receptor-mediated response to metabolic changes that follow ingestion, digestion and absorption of nutrients into the body, i.e. the animal optimizes its metabolic environment by selecting foods whose positive attributes (provision of energy and essential nutrients) outweigh their negative attributes (energy cost of prehension, digestion and metabolism; provision of unwanted or toxic substances) so that, on balance, there is a move towards the optimum supply of energy and nutrients to enable the animal to develop according to its genetic potential. Recent studies at Utah State University (Provenza, Scott, Phy and Lynch, pers. comm.) show that sheep given a choice between three feeds composed of the same ingredients but in different proportions could quickly identify the feed with highest digestibility (highest metabolisable energy concentration) even though the differences were very small (8.1-13.8% CP, 9.2-1 1.3 MJ/kg). These feeds were also linked with flavours (onion and oregano) thought possibly to assist discrimination or enhance preference. However, flavour did not play a major role in identification of the 'best quality' feed - lambs apparently selected feeds solely on the basis of nutrients. It was also noted that animals sampled at least a small amount of all feeds on all occasions.

The tendency of animals to choose a small amount of a range of available foods--even when one alone is ideally formulated and some of the others are consid-

ered by the researcher to be of little nutritional value -has been put forward as an argument against the animal's 'nutritional wisdom'. However, eating a variety of foods in general gives a greater likelihood of a balanced diet, and a reduced chance of over-consumption of particular toxins. There may also be a further benefit - that the animal is in this way continually testing its feeding environment and becoming familiar with the post-ingestive consequences of ingesting foods potentially available to it.

Experimental confirmation

Confirmation of the impact of post-ingestive feedback on feed choices is well illustrated in two experiments recently conducted at UNE. In the first (Waters 1994), we asked whether ewes could become adverse to lucerne (*Medicago sativa*), a normally highly acceptable feed, if the ingestion of lucerne was associated with malaise caused by lithium chloride.

In this experiment, 30 mature ewes, which had previously been exposed to lucerne, were tested to determine their willingness to eat lucerne. This was done by recording the number of bites taken in two minutes from freshly cut lucerne presented vertically (clamped upright in a wooden base). All ewes readily ingested lucerne in these initial tests. On 23 March, within one hour of consuming the lucerne, half of the ewes were dosed with LiCl (225mg/kgW). The remainder were dosed with NaCl. This procedure was repeated the following day. All animals were subsequently pen-tested to determine if they would eat lucerne. Subsequently (3 days after LiCl treatment) their choice of plant species was recorded when they were first released into a lucerne paddock. The averse sheep were then left in the lucerne paddock with the non-averse sheep to maximize the opportunity for the averse animals to learn that the lucerne was eaten by non-averse sheep. Testing continued for another 20 days to monitor the extinguishing of their aversion to lucerne.

The results of this experiment demonstrated a complete aversion to lucerne in the LiCl-treated animals on the third day post-treatment (Figure 1). This was a remarkable finding - sheep had become averse to a food that is normally considered to be 'highly palatable'! This aversion was slowly extinguished over the next 20 days, by which time 84% of the ewes were eating some lucerne in pen tests, but still at a slower rate than the control animals. Observations of the ewes when first released into the paddock on 29 March showed that some of the 'averse' ewes (6/13) did taste lucerne plants. The novelty and intensity of taste cues have been shown to be important in acquiring and retaining aversions (Nachman and Ash, 1973; Burrit & Provenza, 1991). Moreover, age is an important component of the 'memory of aversion' with younger animals being more likely to more quickly extinguish (or 'overcome') conditioned food aversions (Ralphs and Cheney, 1992).

Figure 1 The intake of lucerne by sheep before (23-24 March) and after dosing with LiCl solution (averse group) or NaCl solution (control group). On 25 March, the averse group totally avoided ingesting lucerne. The aversion was thereafter slowly extinguished.

Disappearance of Li-induced Aversion to Lucerne
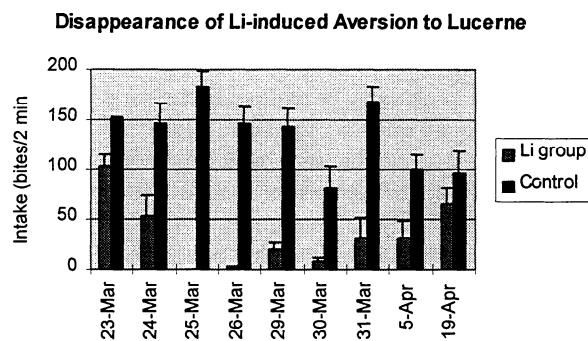
The fact that these animals did not eat in the pen tests, yet tasted lucerne in the paddock, raises the possibility that aversions to foods may not only be associated with the food's sensory properties, but also with the context in which the food is found. It seems that, as well as the sensory properties of the lucerne, the environment of the test site may have been also associated with the nausea resulting from the LiCl treatments. Ralphs & Olsen (1990) and Ralphs (1992) reported that an aversion to larkspur *(Delphinium sp.)* established in penned cattle was extinguished when the animals were released into the field, but the aversive response returned when the animals returned to the training environment. Given these observations and the neophobic nature of sheep, a contextual memory seems likely.

In a second study, we trained sheep to ingest a novel food, poplar leaves, and subsequently determined the effects of intra-ruminal doses of NaCl, LiCl and urea, given soon after the sheep had ingested poplar, on their subsequent daily patterns of poplar ingestion. Eighteen sheep were randomly allocated to each of 3 equal groups, i.e. NaCl, LiCl and urea. The sheep grazed each day and were trained to eat freshly cut poplar branches in yards after an overnight fast. The number of bites by each sheep was recorded during a 5-minute test for 3 days before, and at intervals after drenching. The sheep were given LiCl (10 g in 50 ml water) after having eaten poplar on day 3, subsequently exhibited a decreased intake of poplar (Figure 2, from Nolan *et al.* 1993). In contrast, control sheep given NaCl showed no change in intake of poplar. The poplar intake of sheep drenched with 5g of urea on day 3 tended to be lower than the intake measured on the previous day, and when 10 g urea was given to these sheep on day 4, intake of poplar was subsequently much lower than for those sheep which were drenched with NaCl.

Figure 2 The intake of poplar by sheep before and after drenching with NaCl solution (control group), urea solution or LiCl solution. Aversion to poplar by sheep was apparent in the latter two groups (significantly lower intakes relative to control sheep).

Intake of Novel Food (poplar leaves)
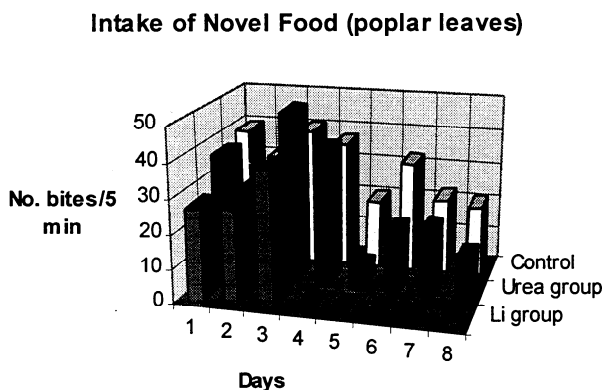
Urea is rapidly degraded in the rumen to ammonia - a potential toxin, but also a substance well-known to sheep; poplar, when associated with urea intake, was not totally avoided, as it was after LiCl administration. Sub-clinical ammonia intoxication may have occurred in this group after urea administration producing malaise and aversive conditioning. It seems likely that mild conditioning may operate in the same way when sheep graze on high-nitrogen pasture, and this may affect their subsequent selections of pasture species.

These experiments demonstrate how aversive conditioning can enable animals to exhibit 'nutritional wisdom'. Recently, Provenza and colleagues (pers. comm.) have extended this concept by suggesting that satiety with respect to a food just eaten can cause malaise and aversion. Thus, they suggest food preferences and aversions reside along a continuum, with animals becoming mildly averse to nutritious foods eaten to satiety.

Supplementation of existing diets

Grazing animals face the challenge of meeting their energy and nutrient requirements from an array of plant species, sometimes augmented by feed supplements. By and large, they appear to manage this challenge well. However, there are occasions when they do not appear to take full advantage of the array of plants, supplements and nutrients available to them. One grazier may report that her animals eat a particular supplement during the winter months and perform well, whereas a grazier next door reports that his animals will not eat the same supplement. What is behind these reports?

At this conference in 1985, J. J. Lynch discussed the factors influencing acceptance of supplements by sheep and highlighted two points: that very

little was known about the factors influencing dietary preferences in ruminants and that most of our understanding of dietary preferences was based on rat or human models.

Has this situation changed in the last decade? Certainly the work of Lynch and colleagues has clarified the role of familiarity of foods and surroundings, and the sensitive stages of life for learning about new foods (reviewed by Chapple & Lynch, 1986). Neophobia (fear of novel items) has also been recognised as a major inhibitory factor in the initial acceptance of unfamiliar foods by sheep. But how much do we really understand of the mechanisms by which ruminants, or other livestock for that matter, make choices when there is more than one food on offer (in a mixed pasture, for example)? And how do these mechanisms influence total voluntary intake and the balance of nutrients provided to the animal?

In 1975, a marker method for estimating the intake of supplements by individual animals was described and used to estimate the intake of a urea-molasses supplement by sheep during the winter in the New England region of northern NSW (Nolan *et al.* 1975). Of 200 sheep offered the supplement, 97 did not ingest it and, among the remaining 103, intakes varied from 5 to 550 g/day. Many similar studies have been made with sheep, cattle and other species since then, and all provide a similar picture. The variation tends to be greatest when the supplement is first put out (e.g. at the start of winter) and to decrease with time. The results in Fig. 3 are typical: they show the mean intakes of a protein-rich supplement ("Nor-pro") by 40 ewes on native pasture during May and June at a site near Armidale.

Figure 3 The intakes of protein-meal supplement by individuals in a group of 40 grazing sheep during early Winter. Three sheep did not ingest any supplement. The intakes of the remaining individuals varied widely.
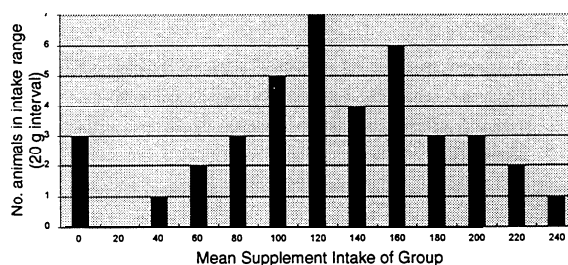
When examined again in late June, the intakes of the ewes showed much less variation, suggesting that the ewes had become more familiar with the supplement and the feeding site, or that their preference for this feed had increased as a consequence of a greater demand for supplementary amino acids.

Concluding comment

The term 'palatability' is frequently used to explain why a food is more readily or less readily ingested. It is our contention that this term has little meaning and minimal value. It does not define a property of the food. Foods may be rejected because they contain toxins. However, non-toxic, nutritious foods may also be rejected because the animal is apprehensive about the feeding environment or the food is novel/unfamiliar. (This is a common occurrence with winter supplementation). The same food may be accepted on another occasion, or in another context, because the animal is familiar with the food and the feeding environment, and it has, at the same time, a requirement for the energy or nutrients provided by the food. But what about the taste - doesn't that determine palatability? This may be partly true, at least in the short term. Sweetness is often associated with high energy, high protein foods: bitterness with toxic substances such as alkaloids, tannins etc. Animals generalise across groups of similar materials. As already mentioned, they also tend to test small amounts of a variety of substances, and to eat more of these if they provide necessary nutrients without producing malaise. They generalise, but they also learn to discriminate. When pigs were given food with a high content of Bitrix -'the bitterest substance known to man'- its inclusion had no effect on their long-term food intake (Blair and FitzSimmons, 1970). When animals avoid foods or supplements, we should avoid calling the foods 'unpalatable' and instead concentrate on the (probably) sound behavioural reasons why the animals are not eating the foods we nutritionists consider are 'good for them'.

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