Factors that determine whether grazing animals will accept supplements

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Summary

When large groups of grazing livestock which appear, superficially, to come from similar genetic and environmental backgrounds are offered a food supplement, some may not consume it, while others exhibit a wide range of intakes. Such variability in acceptance of supplements creates many practical problems.

An animal usually exhibits neophobia when confronted by a novel food or new surroundings. The baseline level of neophobia is probably innately determined but is modified by an animal's experiences. Continued exposure, particularly with others that eat that supplement (mothers, other adults or conspecifics) increases the naive animal's motivation to sample and thereby learn about the supplement. In this way, nutritional wisdom gained by individuals in herds or flocks may be passed from one generation to the next.

Once ingested, a supplement may elicit positive or negative metabolic **stimuli** that are collated by the central nervous system (CNS) thereby generating conditioned associations between characteristics of the supplement, e.g. flavours or other cues, and its post-ingestive effects on the CNS. Positive post-ingestive effects and suitable food cues generate a high 'hedonic rating' for that food in the animal. This rating is subject to modification whenever the supplement is ingested, as the animal's requirements change in line with its changing physiological state, and as other alternative foods in the pasture become more or less available or nutritious.

Non-acceptance of supplements by individual animals is apparently partly genetically determined by innate baseline neophobia and avoidance of certain food cues. Non-acceptance or lower intakes of a previously ingested supplement may result from alterations in the animal's own energy or nutrient requirements with changing physiological state, or the presence of newly available foods that can be selected by the animal to give an alternative diet which better optimises the 'cost—

benefit' relationship. Reductions in supplement intake may also be due to food aversions formed via nonspecific negative stimuli that inadvertently become associated with food ingestion (e.g. created by disease),

Introduction

During dry periods, availability of forages and their digestible energy and nutrient contents decline and production by grazing animals is reduced. At these times, graziers often decide to provide food supplements for their livestock and may report that animals seem unwilling to consume these. Moreover, they may find that the supplement is readily eaten by the next-door neighbour's animals and yet is not accepted by their own stock. Even within groups of animals that ingest supplements, intakes may be unpredictable and highly variable.

The amount of supplement offered is usually decided on a simple 'intake per animal' basis but, in practice, intakes of supplement by individual animals are extremely variable. For example, in a study of the intake of a liquid urea-molasses supplement by 200 grazing, adult wethers in winter on the New England tablelands, 97 wethers did not ingest any supplement, and among the other 103 wethers, estimated intake varied from 5 to 550 ml/d. This variability occurred even though the wethers had initially been confined in a small area (4 ha) around the feeding dispenser for one week to allow them to become accustomed to the supplement and the surroundings, after which they were given a further 3 weeks to become familiar with the supplement and the feeding site before their supplement intakes were estimated over a 5-day period (Nolan et al. 1975).

This is not an isolated case. There are now numerous studies in which intakes of supplements by individual animals in herds or flocks have been estimated

using food or supplement markers (such as tritiated water, lithium chloride, chromic oxide and ytterbium). The results show that, in most instances, some individuals do not ingest any supplement and those that do ingest supplement exhibit a wide range of intakes (e.g. grazing heifers offered meatmeal (Llewelyn et al. 1978); grazing sheep offered oats, hay or **urea-molasses** blocks (Lobarto and Pearce, 1978); grazing cattle offered soybean-meatmeal supplement (Williams et al. 198 1); pregnant grazing ewes offered grain (Hinch et al. 199). This variability in intake will not be obvious when only mean intakes are recorded and may not be taken into account when supplement-response relationships are evaluated. Further, there is the unanswered question: when supplements promote improved production of herds or flocks, would the group responses have been greater if all animals had eaten about the same amount of supplement?

In this paper, we have summarised current information related to food intake and food preference which may help to explain the variation in the extent of acceptance or avoidance of supplements in field situations.

Animals can make appropriate food selections-in certain circumstances

In the knowledge that individual animals may not ingest a supplement when it is offered, or individuals may ingest very different amounts of supplement, it is appropriate to consider the question of whether **farm** livestock are capable of choosing a balanced diet when they have sufficient amounts of suitable foods. Can their selection among these foods be directed in a way that means that they obtain the necessary amounts of energy and nutrients while, at the same time, avoiding excesses or toxicoses?

In 19 15, Eward in Cornell determined the intake of energy and nutrients by pigs when they were offered unlimited access to a smogasbord of foods that made it possible' for them to meet all of their requirements for maintenance and growth. Once accustomed to the foods, some of these 'choice-fed' pigs grew faster than their conventionally fed counterparts at the same research station. Moreover, their intakes of dietary components seem appropriate in the light of modem feeding standards. These pigs, in accord with current concepts, also reduced their intake of protein as they aged in line with their reducing protein requirements relative to energy intake. There is now overwhelming evidence that laboratory and farm animals, when given an adequate choice of foods, can choose balanced diets to meet their current needs for maintenance, growth and production (Forbes, 1995; Kyriazakis and Oldham, 1993). The further question is then: why do animals sometimes choose not to ingest supplements that we know (or assume) will be of benefit to them? Forbes and

Kyriazakis (1995) have provided some answers to this question. To shed more light on this question, it may be helpful to review the underlying theory of food recognition and animal responses to known and unknown foods.

The importance of food-recognition cues and associated post-ingestive events

To make the directed selections of which they are capable, animals must have the ability to identify and differentiate between foods. This ability depends on the physical or chemical characteristics of the food as detected by the senses of odour and taste (flavour), sight (colour, form) and texture. They must also have innate or learned information about the food.

Apparently, animals exhibit either preference for, or avoidance of, any food depending on innate responses (exploration, and attraction or timidity) or on their previous experience of the consequences for their internal environment of ingesting that food. Learning about foods involves an animal associating the sensory properties of each food it ingests with its beneficial or detrimental post-ingestive effects. Responses by the animal to foods are probably breed dependent and modified throughout life. (Arnold *et al.* 198 1).

Certain herbivores ingest a narrow range of foods and recognition of those foods seems to be innate (e.g. koalas seem to recognise leaves of certain eucalypts) whereas some of the omnivores, which includes farm animals, rely on a much wider range of possibilities. Some innate food preferences may have evolved because their effects confer competitive advantages. Thus, through natural selection some species may have acquired an inborn preference for sweet foods (usually sugar and therefore energy-rich) and avoidance of bitter foods (often bitter because they contain potentially detrimental chemicals such as alkaloids or acids). It also seems appropriate that an animal would instinctively avoid foods that are contaminated with faeces (Forbes and Dougherty, 1984)-perhaps because this reduces the likelihood of their consuming internal parasite larvae-and that sheep, for example, would avoid eating foods that have the odour of faeces of the dog-one of the sheep's natural predators (Tien et al. this proceedings). These inborn preferences or avoidances of food flavours would be most important for inexperienced animals. However, because learning about foods begins early in life, possibly in utero or via flavours or other cues present in milk the extent to which recognition of particular foods is inborn, as opposed to learned, is not clear.

Most farm livestock are inquisitive in that they continually explore and test potential food sources in their environment. Changes in an animal's internal state, resulting from a deficiency of energy or of a particular nutrient, may increase motivation in the animal to engage

in this exploration. At the same time, as noted already, animals are apprehensive (neophobic) about new foods and about new surroundings-as most graziers will have observed when offering their stock supplementary food for the first time. Both exploratory and neophobic behaviour are probably, at least in part, genetically determined. If there is innate variability between animals within a flock in their neophobic or exploratory behaviour, we would expect similar variability in intakes to occur when a new food supplement is offered to the group, and this has been consistently reported. There appear to be very few studies of the variation in neophobia within animal populations but studies by Lynch et al. (1989) showed large variation in 'fearfulness' of Merino and Border Leicester x Merino cross ewe flocks. Torres-Henandez and Hohenboken (1979) suggested that fearfulness is heritable and that there are large between-breed differences. There also appear to be differences between animals within breeds.

It appears that the greater the experience an animal has of a food, and of the food container and nearby surroundings, the less intense will be the neophobia and the shorter the time required for an animal to sample and learn about a novel food (Lynch *et al.* 1983).

Social and inter-generational transmission of food recognition

Social transmission of information from mother or other animals can be markedly affected by an animal's food recognition and subsequent feeding behaviour (Bergerud and Nolan, 1970), as has been demonstrated with ewes and lambs (Lynch et al. 1983; Provenza et al. 1993). This can be viewed as the 'getting of wisdom' from others. However, observation of another's eating a food is not enough to condition a food preference; the young animal must itself ingest the food to acquire a preference (Thorhallsdottir et al. 1990). For a young animal, the sight of mother or other animals eating a food may shorten the time between its first exposure to, and when it will sample, a new food. However, conditioned responses to that food will only develop from the food's post-ingestive effects: notably, if the effects are negative, the young animal will subsequently avoid the food even though it can observe mother continuing to eat the food (Provenza et al. 1993). The interval between when a new food is first offered and first eaten can be greatly reduced by the presence of other animals eating the food. The presence, in a novel food, of a familiar flavour derived from an animal's preferred foods can also shorten the time to first ingestion and also increase the rate of buildup in intake of a novel supplement by grazing sheep (Tien et al. 1997). The role of different cues such as odour, taste or flavour (odour and taste together) in determining association between food and its post-ingestive consequences has been widely studied in rats but is not well understood in farm animals.

'Trial and error' learning

Leaving aside an animal's innate or socially acquired preference/avoidance of foods, the development of an individual's responses to foods depends on personal experience obtained by 'trial and error'. Stephens and Krebs (1986) have argued that it is reasonable to expect that an animal should be able, if necessary, to override innate preferences or aversions, by learning that some foods with an innately 'attractive' appearance or flavour are nutritionally inappropriate or even toxic whereas some innately unattractive foods are nutritious and non-toxic. Similarly, they should be able to modify learned responses as circumstances change. To achieve the best outcome, they should choose predominantly from foods that they have learned are appropriate for their current needs, but they should also sample small amounts of other foods in order to discover whether nutritious foods have become newly available and to adjust and optimise their food combinations accordingly.

Conditioned responses to food uses

Once an animal has sampled a food it can form an association between cues that identify the food and its potential effects on the animal's internal environment. In general, the post-ingestive response to the provision of useful energy, amino acids, minerals, vitamins or, alternatively, unwanted energy or nutrients or toxins will depend on the animal's physiological state and hence its current demand for particular food constituents. The direction and strength of the CNS response can be expected to alter the nature of the 'food-consequence' association that leads to the memory of a particular food and the animals conditional response when subsequently confronted with the same food cues.

A conditioned response to a food is developed from a neural integration of food-specific environmental stimuli (visual, odour, taste or texture cues) with stimuli generated from within the body (Garcia et al. 1989). The internal stimuli may arise in the gut (e.g. peptide hormone release), liver (rate of oxidation of substrates) or brain (body temperature) and may be transferred by nerves, hormones or other chemical messengers. Nerves in the buccal region and in the viscera join in the brain stem which is linked to the **limbic** system and thence to the brain cortex (Glenn and Erickson 1976). Severing the neural connections between the liver and brain has been shown to alter food preferences (Anil and Forbes, 1980). Information could reach the CNS via the peripheral nerves, or the endocrine or immunological system or combinations of these. The food-consequence association probably involves cognitive processes (Provenza et al. 1994) but the development of conditioned responses in deeply anaesthesised animals suggests that associations can be formed noncognitively (Provenza et al. 1993).

The nature of the response to a food providing a certain nutrient (e.g. amino acid) is likely to depend on whether the nutrient is essential or not, and if it is essential, whether or not the animal's potential growth or development is currently being limited by insufficiency of that nutrient. The current requirement of the animal for energy or nutrients will be determined by factors such as age and maturity and whether the animal is pregnant, lactating or parasitised. A food providing needed digestible energy or a deficient nutrient could be expected to elicit a strong positive stimulus to the CNS, and to increase the preference for that food in the future. If, on the other hand, the nutrient were provided by a food in amounts sufficient to elicit toxicosis, then a negative stimulus to the CNS could produce a conditioned aversion to that feed. Another food that provides non-toxic amounts of the nutrient when it is not currently required, may have little effect on the animal's future preference for that food.

In practice, foods seldom provide a single nutrient, and the post-ingestive stimuli elicited by ingestion of a food may be more complex than that has just been suggested. Stimuli may be positive with respect to some components and indeterminate or negative with respect to other components. The situation faced by the animal can be likened to that of a person formulating leastcost, maximum benefit diet. A database containing a **number** of edible foods is used in conjunction with a desirable diet specification (which has upper and lower limits for energy density and essential nutrients, and upper limits on certain potentially toxic ingredients). Formulations are determined by linear programming or other methods to give unique solutions which represent different combinations of ingredients that fall within specifications. Each of the formulations may then be further evaluated to determine which of these diets gives the maximum-benefit at least-cost.

Hedonic rating

An explanation for the variability in intakes of foods in general and supplements in particular, is afforded by introducing the idea that animals effectively rate foods using a hedonistic scale that ranges **from** 'pleasurable' to 'repugnant' depending on the strength of the food cues and post-ingestive events. An animal's response to a particular food may **shift** along this scale over time according to the strength of the association between most recent experience of a food and its post-ingestive response. This process is seen as being iterative: modifications of a particular food's hedonic value may occur whenever that food is ingested; the '**shift** distance' will depend on the previous rating, but will move further away from any initial setting with repeated reinforcement of the same association.

The initial hedonic rating for any food may be set innately and then modified by social experiences and personal learning. Thus, individual animals may start life with a different hedonic settings with respect to the same food. These settings may then change continually but to different degrees throughout life in response to changes in physiological state of the animal and the other foods it encounters. Herds or flocks may differ markedly in their responses to pasture and supplementary food availability depending on their innate, species-specific hedonic food ratings. Hedonic food ratings within groups may be altered by differences in inter-generational social transmission of information about foods, or by differences in the learning opportunities of the animals because of different experiences with foods in different geographical locations. Individuals within such groups will be subject to some common learning experiences but may exhibit further variation arising from factors such as their dominance rankings in the flock and the priorities they give to competing behaviour traits (e.g. predator avoidance-which determines their likelihood of testing spatially dispersed foods.

The process by which animals experience and learn about food is represented in general terms in Figure 1. The strength of the conditioned response probably depends on the strength of the stimuli evoked by the food cues and of the net effect of the positive or negative stimuli arising **from** the post-ingestive effects on the animal's internal state, as well as on the extent of reinforcement of the association by repeated bouts of exposure to the same stimuli.

The nature of the response to ingestion of a particular food may even be further modified by **non**-nutritional consequences of ingestion. The food may elicit a lower hedonic rating, for example, if it is found in a rather inaccessible site, or is far from the watering point, or is in an area that increases the likelihood of the animal's being subject to predation.

Supplementation-increasing the choices of available foods

Within groups of animals that accept supplements, what is the basis for the considerable between-animal variation in intake? In the tradition of this symposium, we offer some speculative answers to this question.

Variation in intakes of supplements by individuals may be a function of the variety and amounts of foods available to animals. If an animal had, say, 6 familiar pasture plant species and a familiar supplement available to it, it would have the opportunity to choose a balanced diet **from** among 7 familiar feeds. That animal could perhaps satisfy energy, protein and other requirements from combinations of only 3 or 4 different foods. In some instances, the combinations might include more or less of the supplement, or even exclude it altogether.

The foods selected will depend on the physiological state of the animal (which will determine the current dietary requirements), the ability of each food to meet those demands as judged by their current hedonic rating, and, in addition, other factors that will be different for different animals such as the number of

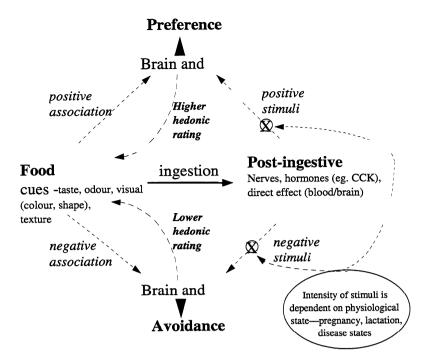


Figure 1 Sensory stimuli associated with ingestion of food and the stimuli (neural, hormonal or immunological) resulting from subsequent metabolic effects during digestion and metabolism of food constituents are integrated by the CNS. A learned association is made between the food cues and the metabolic response which leads to subsequent acceptance or avoidance of the food. The food cue alone can subsequently elicit the acceptance and ingestion or avoidance and non-ingestion of the food, and the hedonic rating of the food is continually updated in response to testing.

familiar foods available to each animal. We have often obtained results that are in accord with this suggestion using tritiated water labelled foods or, more recently, LiCl-labelled supplements. Again, we would also predict that the choice-feeding combinations will be affected by the animals' individual demands for energy and nutrients as determined by physiological state—growth, lactation, pregnancy load (single foetus, multiple foetus) or by the presence of disease or parasitism.

The situation is more complicated if the supplement is unfamiliar, as the animals may have less incentive to test an unfamiliar supplement if combinations of familiar foods with a pleasurable hedonic rating can provide an adequate and balanced diet. Even if, as often appears to be the case, the animals do test small amounts of the supplement, they may not obtain positive postingestive consequences if the other dietary choices are already providing an adequate and balanced diet. In this case no positive hedonic shift for the supplement is to be expected. In this situation, it is possible that a temporary hedonistic shift might be artificially induced by using the cues from another food which was previously associated with intensely positive post ingestive consequences. Strong evidence for this possibility is given by Tien et al. (1997).

Factors that determine whether grazing animals will accept supplements

Having proposed a theoretical **framework**, we will now look at three examples of supplementary food intake patterns to see if practical observations support the theory outlined above. Based on our model, the ideal conditions for maximum acceptance of a supplementary food would be:

- an animal in a physiological state promoting the motivation to test available foods;
- as sources of energy or a deficient nutrient;
- a highly inquisitive animal with relatively with low levels of neophobia;
- an animal receptive to social influences;
- a rapid and positive post-ingestive response when the supplement provides the necessary metabolites, and few if any negative effects or toxicoses; and
- a limited number of contrasting food sources from which to choose.

The pregnant ewe fits some, but not all, of the above criteria. The pregnant state is such that motivation

good acceptance of supplements by most animals.

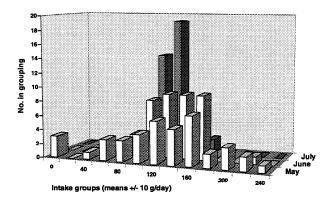


Figure 2 Intake of a sunflower meal supplement by grazing Merino weaner ewes estimated in late May, mid June and late July on the tablelands in northern NSW. The results show the large variability in intakes of the sheep in the late autumn, and the much reduced variability later in the winter.

to locate and eat foods that provide both energy and protein should be high, and the post-ingestive consequences of ingestion of a protein and energy rich food would be expected to be highly positive. In contrast to weaners, adult ewes would already have had a wide diversity of experience of alternative foods.

In a study of crossbred ewes in late pregnancy, Resksupaphon (1995) made estimated simultaneously the intakes of pelleted protein supplements and of pasture. She found considerable variation in the intakes of supplements over the last 3 weeks of pregnancy. In general, supplement intake was higher (P<0.01) for twinbearing ewes than for those with single foetuses (Table 1) although less so in the period closer to lambing. This decline in group intake was primarily due to a large increase in the number of twin-bearing ewes that did not eat supplement, which corresponded with a decline in their intake of supplement relative to forage from the pasture. These fmdings indicate that physiological differences can influence supplement intake considerably: in this case, the supplement which had earlier been eaten was rejected by a large proportion of the ewes carrying twins. The reasons are not clear, but the reduced ingestion of supplement could be due to the reduced mobility of these animals, or a reduced willingness to congregate near the feeders, rather than to changes in the hedonic rating of the supplement based on changes in post-ingestive consequences.

The third paradigm, which meets few of the criteria likely to promote acceptance of a supplement, is one in which animals are mature and require nutrients only at maintenance levels. Such animals would be unlikely to have rapid or positive post-ingestive responses after testing a supplement. Moreover, they would be likely to have a broad experience of a wide range of foods, the supplement being simply one new food to be tested in a situation where there would be less opportunity of social learning to occur. An experiment of Tj iposumirat (1994) fits these specifications.

A cottonseed based supplement was offered to 101 mature Merino ewes (6-9 years old) grazing on an apparently low quality improved pasture -but a pasture on which the animals had been maintained for most of their lives. The supplement which was unfamiliar to these

Table 1 Mean intake of pasture and supplements by twin- and single-foetus bearing ewes in the last 3 weeks of pregnancy.

Time prepartum	Litter size	Pasture intake (g)	Supplement intake (g)	Supplement/ pasture intake %	Non-eaters of supplement %
3 weeks	Single	1961ª	36.9ª	1.9ª	33
	Twin	1555⁵	81.1°	5.2°	0
2 weeks	Single	1900ª	50.1 ^b	2.7ª	13
	Twin	1782ª	62.1 ^b	3.6 ^b	0
1 week	Single	1681ª	35.9 ^a	2.0ª	27
	Twin	1714ª	36.7ª	2.3ª	58

ewes was given at a rate of 250g/head per d. In this study (Table 2) 33% of ewes did not eat the supplement on the second day of exposure and, 3 weeks later, 17 % were still not eating the supplement even though the group as a whole was losing weight. Several subgroups could be categorised within the flock, viz.:

- **the neophobic group** (17%): the non-eaters that never ingested supplement and were probably at the end of the fear **continuum**:
- the **improver group** (52%): animals that increased their intake of supplement over the 3 weeks (either non-eaters that overcame neophobia and started to eat, or small-eaters that increased their hedonic rating of the supplement during the 3 weeks; and
- the regressive group (32%): ewes whose intake declined over the 3 weeks. This latter group included the potential explorers group (6%)—ewes whose intake was greater than 300g/d at the first test but subsequently declined (these ewes did not show normal neophobic behaviour and so may be considered to be at the inquisitive end of the 'fear continuum' and to be the 'teachers').

It would seem that the regressive group obtained little positive post-ingestional CNS feedback after eating the supplement or had alternative pasture foods that they could include in order to optimise their diets. Alternatively,' it is possible that they were unwilling to compete for the limited food resource at the supplementation site, but studies of animal aggressiveness and supplement intake, if anything, suggest a negative correlation (Juwarini et al. 198 1).

The flock means given at the bottom of Table 2 provide a picture that is similar to that from many supplementation studies. Mean intakes of supplement increased while animals were exposed to the supplement, and weight loss was less in eaters than non-eaters. However, the overall correlation between weight change and supplement intake was 0.204 and not significant. The correlations within groups were also low (<0.25) and non-significant.

More importantly, however, the results within the notional categories indicate responses to supplements in grazing flocks are generally more complex than suggested by whole-flock averages. Despite their declining supplement intake, the regressive subgroup had the lowest mean weight loss among the 3 groups, indicating that they were better nourished (P<0, 10) than those in the learning group with their higher supplement intake, or in the neophobic group which refused supplement throughout the experiment. The indications are that animals in the regressive group sampled the supplement in the context of all the familiar foods available to them. They then choose to eat the supplement only to the extent that it was fitting in an overall process of diet optimisation, or they ingested small amounts in order continually re-assess the hedonic rating for the supplement.

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Table 2 Intakes of supplement and liveweight changes of three subgroups within a flock of 101 mature grazing ewes, categorised according to whether they were non-eaters (Neophobic group) or increased (Improver group) or decreased (Regressive group) their supplement intakes during a **3-week** period of provision of with cottonseed meal pellets

Intake sub-group	Initial liveweight (kg)	Weight loss (kg)	Initial Intake (g)	Final Intake (g)
Neophobic (n=6)	40.5	0.91	0.	0
Improvers (n=52)	38.6	0.51	51	144
Regressive (n=32)	37.6	0.38	230	82
Mean	38.7	0.55	158	234

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