

Food preferences in farm animals: why don't they always choose wisely?

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INTRODUCTION: SUCCESSFUL AND UNSUCCESSFUL DIET SELECTION

While people can express their preferences in abstract form, animals can only demonstrate which food they prefer by which food they eat, or the ratio of intakes of each food, when given a choice. Thus, the food preferences of animals are monitored by their diet selection and there is now a very substantial amount of evidence to support the concept that farm animals, like laboratory animals, are capable of choosing a balanced diet from two (or more) foods, one of which has more, the other less, of an essential nutrient than is required for optimum metabolism. This is to be expected, as an excessive intake of a nutrient incurs penalties arising from its excretion–metabolism which may be as disadvantageous as a mild deficiency of a nutrient. The general background to diet selection is provided by Emmans (1991) and a catalogue of successes is reported by Illius & Gordon (1993) and Forbes (1995).

Against this background there are numerous examples of animals that appear not to be making appropriate choices (from the standpoint of the human observer), implying that their food preferences are governed by factors other than, or additional to, nutritional wisdom (ability to combine the foods selected to provide the correct balance of nutrients). Given the general agreement that animals are capable of choosing a balanced diet when given the opportunity, it seems now to be more fruitful to examine cases where food selection appears not to have been optimal, thereby learning more about the limits to diet selection as a strategy for animals and a tool for human keepers of animals. The rest of the present paper explores the possible reasons for these 'failures' in order to assess whether such cases can be explained by inappropriate experimental design or whether there are some genuine failures to select adequately. Failure to select optimally could be due to constraints imposed by the animal, by the environment (more particularly the nutritional environment) or to interactions between the two, and we address these in turn.

CONSTRAINTS IMPOSED BY THE ANIMAL

Learning: the importance of sensory differentiation between foods

An animal must be able to differentiate between the foods on offer by sensory means otherwise no selection would be possible, no matter how different their nutritional value. Given that there are these sensory differences, the animal might have an innate preference for one food, e.g. because of its sweet taste (Ashley, 1985). However, nutritional value is not always closely correlated with sweetness so that the associations the animal learns, between sensory properties and nutritive value, are much more

valuable to it than innate preferences. Thus, a bitter flavour imparted to food will cause initial rejection but if the nutritional value remains balanced then normal intakes are resumed within a few days. A good example of this is the lack of effect of inclusion of Bitrex, the most bitter substance known to man, on the long-term intake of food by pigs (Blair & FitzSimons, 1970). Thus, there is no need to be concerned about the exact nature of the flavours used to differentiate between two foods as animals soon learn to associate them with the nutrient yields of the foods in which the flavours are incorporated and to eat for nutrients rather than just for taste.

A clear example of the need for sensory differentiation and learning is provided by work with young broiler chicks (Kutlu & Forbes, 1993), in which mild heat stress increases the requirements for ascorbic acid (vitamin C), offered a choice between a normal food with no supplementary ascorbic acid and an exactly similar food containing 200 mg protected ascorbic acid/kg. When neither food was coloured the birds did not differentiate between them and ate at random. When each food was given a different colour (red or green), however, and the birds were trained to associate each colour with the nutritive value of the food by giving them separately in half-day periods for 6 d, they subsequently selected significantly more unsupplemented food when in the thermo-neutral environment and significantly more supplemented food when in the hot environment. A sudden change in environmental temperature was followed by a gradual change in the proportions of the two foods eaten as the birds learned that the red (or green) food was no longer the one that made them feel metabolically most comfortable.

The principle of a training period, in which foods are offered singly in turn to allow the animal to learn to associate a particular set of sensory properties with certain metabolic 'feelings', was introduced by Kyriazakis *et al.* (1990) and this protocol has been adopted by other groups working in the field (Bradford & Gous, 1991; Shariatmadari & Forbes, 1993). Without this enforced training period some animals learn quickly while others eat one food only, or both at random, for many days before suddenly 'discovering' the other food and subsequently selecting an apparently balanced diet (Fig. 1; Dalby *et al.* 1994a). The implication is that the food with the lower protein content is adequate for growth as there was no consistent difference in growth rate between pigs.

Exposure of broiler chickens to whole grains at an early age appears to confer benefits at the later stages of growth, in terms of ability to select foods to meet nutrient requirements (Mastika & Cumming, 1987).

It should be noted that mammals have evolved to make associations particularly strongly with the flavour and/or smell of foods, while for poultry the visual appearance of food is a good cue (Wilcoxon *et al.* 1971). Food position, i.e. left or right, is not a powerful cue, as in most cases there is little or no association between the exact position of a food item and its nutritive value, whereas the smell, taste or appearance of food can be closely correlated with nutritive value. However, birds can use position if no other sensory cues are available, as demonstrated by the results of Steinruck *et al.* (1990). Methionine-deficient birds were either given high- and low-methionine foods in the same position every day for 36 d, or the positions of the foods were reversed every 9, 6 or 3 d. Where the positions were unchanged there was a 68% choice of the high-methionine food, which was sufficient to give a balanced diet. However, as the changes became more rapid, so selection was less appropriate, being 65, 62 and 58% for the 9, 6 and 3 d change-over birds respectively. Methionine is colourless and has little taste so birds could only learn the difference between the two foods by their positions in the cage; moving the

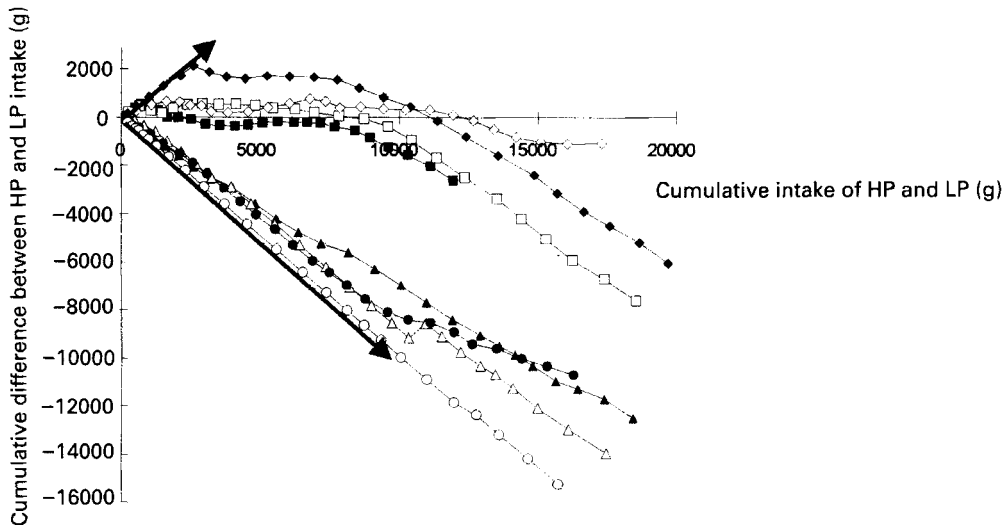


Fig. 1. Selection paths for eight growing pigs offered a choice of high- (HP; 292 g crude protein ($N \times 6.25$; CP)/kg) and low-protein (LP; 155 g CP/kg) foods, shown as the cumulative total intake of both HP and LP *v.* the cumulative difference between the intake of HP and LP. \blacktriangleright , Intake entirely from HP (upper) or LP (lower) food. Four pigs ate mostly LP all the time while three others ate half-and-half (random?) at first but then mostly LP. One animal (\blacklozenge) initially took all HP but after a few days ate approximately equal proportions of the two foods (the line becomes horizontal) and eventually changes to eating almost all LP.

position confused them and necessitated their relearning the relationship between position and methionine content. The detailed results presented by Steinruck *et al.* (1990) clearly demonstrate this relearning process, a decrease in the proportion of the high-methionine food eaten following each change-over. It is not helpful to deliberately confuse animals by swapping the position of the two foods daily, a point apparently missed by Owen *et al.* (1994) who explain that the reason they did not exchange foods daily was that this would not be feasible in commercial practice.

In summary, farm animals can select a diet appropriate to their metabolic needs as long as the foods offered are clearly differentiated by flavour or colour and the animals have the opportunity to learn the nutritional difference between the foods.

Learning and memory retention

Once learned, for how long is the memory of the nutritive value of a food retained? Growing broilers seem to forget the aversive properties of a coloured food paired with an intraperitoneal injection of cholecystokinin within a few days (Covasa & Forbes, 1994), but lambs apparently retain the memory of a flavour they experienced in their mother's milk or even *in utero* for many months (Nolte & Provenza, 1992) and of wheat grains for many years (Green *et al.* 1984). In the latter case the memory is specific to the one type of grain, as Mottershead *et al.* (1985) have shown that sheep trained to one type of grain behave naïvely when offered another. When LiCl was put in food for lambs or ewes, they recognized these foods after 2 months without exposure (Thorhallsdottir *et al.* 1987). Sheep approached the LiCl-paired foods very cautiously but always ate a little, although sometimes intake increased once they realized it was no longer harmful. However, it

should be noted that the aversions that were developed towards a LiCl-paired food constitute a very strong food aversion paradigm.

If a food is very toxic then it makes sense to retain a memory of its associated sensory properties for a lifetime, and most experiments using LiCl fall into this category. If, however, a food or a mixture of foods is preferred because it contains an appropriate mixture of nutrients, then it might be counter-productive if a memory is retained for too long since the nutrient requirements of animals change with time. In the case of selection for protein by growing pigs, for example, soon after weaning a diet containing 230 g crude protein ($N \times 6.25$; CP)/kg is most preferred, while the same animal, 3 months later, prefers a diet containing only 150 g CP/kg (Kyriazakis *et al.* 1990, 1993). This change in diet selection was achieved by a progressive increase in the proportion of the low-protein food selected in the diet.

We can conclude, therefore, that a sensory property of a food which has become associated with an overtly toxic effect of eating the food will evoke long-lasting memories and persistent avoidance but that differences in the sensory properties of foods with milder metabolic effects are retained for short periods to allow relearning appropriate to changes in the requirements of the animal or changes in the nutritive value of the food. It cannot be assumed, therefore, that just because an animal has experienced a food in the past, it necessarily retains the memory of that food. It is necessary, therefore, to offer pairs of foods for several days before assessing the animals' preference to allow time for conditioned associations to develop, even if they have had previous experience of one food, or both. Preference tests which offer each pair of food for a few hours only are only monitoring innate preferences and are not likely to demonstrate nutritional wisdom.

Social influences on diet selection (social facilitation)

Can the social environment influence diet selection? In a 'good' experiment the animals are individually penned in a controlled environment so that individual intakes can be monitored. However, we know that the behaviour of animals in groups can differ markedly from that of individuals and there is strong evidence of nutritional wisdom being passed between individuals (e.g. mother to offspring, older to younger animals; Provenza & Balph, 1987) and even naïve birds learn to eat whole wheat more quickly when paired rather than caged singly even when neither bird is experienced (Covasa & Forbes, 1995). Animals living together in a group tend to copy from each other and there is usually a leader (a successful individual) which guides the others to the desired food (Dove, 1939).

Individually-penned animals show widely different patterns of diet selection, even when the mean appears to be nutritionally appropriate (Kyriazakis *et al.* 1990), but this variability was greatly reduced by pairing (Covasa & Forbes, 1995), even though individually-caged birds could see each other through the wire-mesh walls of the cages. The social environment can also affect the retention of food-related memories, as heifers conditioned to avoid eating larkspur (*Delphinium ajacis*) by adulteration with LiCl lost this conditioning more quickly when kept with unconditioned heifers than when not kept with such untrained animals (Ralphs & Olsen, 1990).

Keeping animals in groups might shorten the learning period but might also lead to competition for trough space and result in inappropriate food choice by some of the less-dominant individuals.

A serious study should be made of the effect of single-penning and the social environment on diet selection and particularly on the variation in selection between individuals. If the potential to use diet-selection methodology to study the optimum nutrition of farm animals is to be realized then practical problems such as optimum group size and the need for a training period need to be resolved.

Identifying 'nutrient requirements' of animals (the need of adequate control)

In few choice-feeding experiments have the nutrient requirements of the animals been defined independently, such that the diet selection of the choice-fed animals can be interpreted, and it would be easy to make unwarranted assumptions. For example, it is generally considered that chicks do not require supplementary ascorbic acid in their diet and the fact that they choose a significant proportion of a supplemented food (see p. 430) might be taken as evidence for unwise selection had it not been demonstrated that, under the conditions of the experiments, dietary ascorbic acid was beneficial to growth and food intake, especially at high environmental temperatures.

The principles of diet selection have been clearly stated by Emmans (1991): the expectation of what animals should eat is only realistic if we know the requirements of the animal(s) in question. Although standard textbooks or tables of nutrient requirements can be consulted, it is preferable to conduct dose-response experiments with a series of single foods with a range of compositions (made as mixtures of the foods) to be given as a choice against which to compare the adequacy of the diet chosen by animals selecting from two or more foods. If the animals' requirements change with time and this change is reflected in appropriate adjustments to the proportions of different foods chosen, then this strengthens conclusions that animals are selecting foods with a nutritional purpose. The change with time could be naturally occurring due to growth, or an imposed change, such as that due to temperature.

Emmans (1991) also proposed that various combinations of foods, made as described previously, should be offered in pair choices, to test the proposition that the animals are making a directed decision to eat certain proportions of the two foods. If animals are eating for protein then it would be predicted that the higher the protein content of the high-protein food, the less of it should be eaten and this has been shown to be the case for growing broiler chickens (Shariatmadari & Forbes, 1993), growing pigs (Kyriazakis *et al.* 1990) and growing sheep (Kyriazakis & Oldham, 1993). It is surprising how few other experiments have included such comparisons, and conclusions about specific appetites are thereby not as strong as would otherwise be the case.

Just because two foods offered in a choice situation differ in their content of a nutrient, e.g. protein (according to some calculation or limited analysis) this does not necessarily restrict animals to selecting only on the basis of that nutrient. Bradford & Gous (1991) found that pigs grew well and efficiently when given choices between pairs of foods containing 220, 180; 220, 140; 220, 100; 180, 100 g CP/kg. However, they observed that the isoleucine content chosen was almost exactly what would be predicted for optimal growth and suggested that the pigs might have been selecting in order to obtain the correct amount of the most limiting amino acid.

Where diets selected by choice-fed animals are compared with 'control' diets care must be taken not to draw unwarranted conclusions. For example, broiler chicks given free access to foods containing 456 and 86 g protein/kg selected proportions which gave the

same growth as controls (Kaufman *et al.* 1978). As they grew the proportion of the high-protein food taken in the diet fell to give a decline in the protein content of the selected diet from 250 to 140 g/kg. The authors pointed out that this was a lower protein content than the single food given to controls, but as that contained an excessive amount of protein (265 g/kg) this was not surprising.

Previous nutritional history must be taken into account when deciding whether animals have selected wisely. Pigs made fat through feeding a low-protein food subsequently selected a much higher protein content when choice-fed (233 g CP/kg) than those previously given a high-protein food (175 g CP/kg); this diet selection enabled the former pigs to deposit fat at a slower rate and protein at a faster rate than the latter animals, and return their body composition to a 'desired' one (Kyriazakis & Emmans, 1991). It must also be borne in mind that gender influences growth potential and that male pigs chose a diet higher in protein than female pigs chose (228 v. 181 g CP/kg).

As the nutrient requirements of animals vary with stage of growth, gender, breed and nutritional history so diet selection should not be expected to be static or uniform across animals. Great care is needed, therefore, in deciding which is more 'correct', the choices made by the selecting animal or the expectations of the human observer, when interpreting the results of diet selection studies.

CONSTRAINTS IMPOSED BY THE ENVIRONMENT, INCLUDING THE NUTRITIONAL ENVIRONMENT

In order for animals to make a directed choice there must be some combinations of foods on offer that are nutritionally imbalanced, otherwise there is no benefit to be had in choosing. Many experiments have offered a choice between two foods, neither of which is demonstrably imbalanced. For example, there have been several experiments on amino acid appetite in growing pigs in which it was either shown that pigs could grow perfectly well on either diet when given alone, or in which it can be deduced that this was the case (Fairley *et al.* 1993; Henry, 1993; Dalby *et al.* 1994b). Therefore, individual animals adopted different choices and overall no significant selection was apparent.

Paradox of two foods with low protein contents

It is clear that the two foods offered to the animal must differ in at least one nutritional dimension if an appropriate diet selection is to be achieved. However, there are instances where animals have been given a choice between two foods neither of which fulfil their requirements, either due to miscalculation of their requirements or intentionally (since this could be an experiment that reflects choice situations in nature). The expectation is that the animal will consume the less-limiting food (e.g. the food with slightly inadequate protein) and avoid the more limiting very-low-protein food. Such choices have been given to laying hens (Holcombe *et al.* 1976), broiler chickens (Shariatmadari & Forbes, 1993), growing pigs (Kyriazakis *et al.* 1990) and sheep (Cooper & Kyriazakis, 1993). In these instances, however, animals appear to consume appreciable amounts of the more-limiting food and in some cases approached a random choice (care is needed in interpreting the work of Holcombe *et al.* 1976, however, as the position of the foods was changed daily). Kyriazakis *et al.* (1990) suggested that this behaviour consisted of an amplified sampling behaviour, where substantial selection of the less-limiting food (that

did not satisfy the requirements of the animals) was followed by a consumption of the more-limiting one, since animals needed to be aware of any changes in their nutritional environment as neither food satisfied their requirements.

Do animals have to work for one food?

Ashley (1985) has reviewed work with rats trained to work for foods in operant conditioning situations. He concluded that laboratory animals are prepared to work harder for some nutrients (such as protein and minerals) than others (such as carbohydrates and fats). Farm animals are also easy to train in operant conditioning situations in which they have to 'work' for a food by pressing a coloured panel (sheep, Hou *et al.* 1991; pigs, Baldwin & Meese, 1979; poultry, Savory, 1989). If the animal has to work harder to obtain one food than the other, then this is likely to bias selection in favour of the food that is obtained with less effort.

Another situation in which animals have to 'work' to obtain food is when they are part of a group in which a social hierarchy has developed. An animal low in the pecking order might not be able to gain equal access to both foods while a dominant animal might feel obliged to maintain its position by eating more of the 'better' food. This situation could be accentuated when the space at the trough is not sufficient for all animals in the group, such that free and continuous access to both foods can be achieved by all animals simultaneously.

Grazing animals are constrained from free selection of the better parts of pasture if these areas are close to faeces of their own or other species (Marten & Donker, 1964). This appears to be a way of avoiding consumption of infective parasitic larvae. As a consequence of the avoidance behaviour, the swards grazed by sheep and particularly cattle show a bimodal distribution of herbage mass and height, with ungrazed patches of tall herbage around faeces and short, frequently grazed herbage over most of the field.

The situation in which the animals are given a choice between a faeces-contaminated but highly-nutritious herbage and an uncontaminated one with low nutritional value is dealt with in a later section.

ANIMAL-ENVIRONMENT INTERACTIONS: SHORT-TERM DIET SELECTION AS
PART OF A LONG-TERM FEEDING STRATEGY

In this section we will describe cases in which animals appear to be unsuccessful in selecting a diet that meets their requirements in the short term, but where their selection makes sense when viewed as part of an overall feeding strategy.

Where one food contains a toxin

If two foods on offer could be combined to produce a balanced diet, but one of them contains a 'toxin' (anything which causes a disturbance in metabolism), then the animal could be expected to select less of the toxin-containing food even if this means suffering a deficiency or excess of an essential nutrient. For example, rapeseed meal is an economically attractive source of protein but even modern rape genotypes (with low levels of glucosinolates) contain toxins, so the taste of rapeseed could be used as a cue to aversion. Growing pigs given choices between high- and low-protein foods containing

zero or high levels of rapeseed meal found both rape-containing foods to be aversive, leading to over- or underconsumption of protein (Kyriazakis & Emmans, 1992). Without rapeseed meal, pigs chose mixtures of the foods to give overall protein contents very close to their requirements; when rapeseed meal was included in the high-protein food the diet selected was significantly lower in protein, while when it was in the low-protein food they chose the reverse diet (with a significantly higher protein content than required). However, pigs given access to a single rape-containing food grew as quickly and efficiently as those fed on fishmeal-containing foods, or those offered choices, so the toxins in rape must be fairly innocuous. When both high- and low-protein foods contained rapeseed meal, selection between them was such that their requirements could be met and the overall protein content of the diet selected declined (as expected) in a systematic manner as the pigs grew.

Perhaps the effect of a toxin depends on whether it has an immediate or a long-term effect on metabolism. Rapeseed meals with low to moderate levels of glucosinolates are goitrogenic and cause depressed levels of circulating thyroxine and a degree of compensatory thyroid hypertrophy. The hypothyroid state does not have an effect in the short term on the performance of pigs as measured by their growth rate (Christison & Laarveld, 1981). The thyroid status of the pigs in the experiment of Kyriazakis & Emmans (1992) was not assessed and it is possible that they were suffering from a degree of hypothyroidism, although their growth was not affected. Similarly, food intake was not affected, since perhaps eating as much as possible, or as much as needed, of such food and growing as fast as possible might be seen as a strategy to overcome, or dilute, the adverse effects of the glucosinolates in the food.

Ruminants need roughage

The ruminant animal is faced with the dilemma of, on the one hand, choosing a nutrient-dense food which allows it to grow and reach puberty as quickly as possible while, on the other, supporting a stable and healthy rumen environment. However, part of the ruminant animal's objective of achieving satisfactory energy intake under natural circumstances depends greatly on maintaining the rumen as a functioning organ. Highly digestible concentrate foods are fermented rapidly and consequently each meal is followed by a rise in the rumen concentration of volatile fatty acids and other products of fermentation that could lead to a disruption of the rumen environment. Given a choice between a concentrate food and a forage, such as hay, sheep eat considerable quantities of the latter, even though it is less nutrient dense and takes more time and effort to harvest, chew and digest than the concentrate. For example, even though dairy cows ate more dry matter and produced more milk when given finely-chopped silage, compared with medium- or long-chopped silage made from the same grass (Castle *et al.* 1979), when given a choice of all three they ate significant amounts of the latter two foods. Similarly, growing lambs (Cropper, 1987; Cooper & Kyriazakis, 1993), lactating goats (J. M. Forbes, unpublished results) and growing heifers (J. H. M. Metz, personal communication) took about 20% of their DM intake as long forage (or a food of low nutrient density) when they also had free access to a more concentrated food.

Rapidly fermentable nitrogenous compounds also upset the rumen balance (by imposing a surplus metabolic load of NH_3 ; Nolan *et al.* 1993) and sheep avoid urea where possible (Kyriazakis & Oldham, 1993) even though this is a good source of N for the

rumen microflora. When two foods with protein contents above requirements were offered, the sheep consistently ate more of the food with the lower protein content. However, when the choice was between a high-protein food and one supplemented with urea to the same total N content, the high-protein food was preferred, giving an overall protein content of the diet that was greater than required. The sheep preferred to eat an excess of undegradable protein than an excess of urea, presumably because of the more toxic effects of an excess of the latter. Goatcher & Church (1970) observed almost total rejection of a urea-containing food, but this was not surprising since the concentration of urea was high enough to cause illness and even death.

The grazing behaviour of sheep on a ryegrass (*Lolium perenne*)–clover (*Trifolium repens*) pasture also seems to be similarly constrained in order to prevent an excess intake of rapidly-fermentable carbohydrate and protein (Newman *et al.* 1992; Parsons *et al.* 1994), i.e. their diet does not consist entirely of clover, even though this would give a greater quantity of nutrients per unit of harvesting effort. These tactics may be viewed as part of the animal's overall feeding strategy, which enable it to obtain adequate nutrient intakes and maintain healthy rumen function, and thereby achieve its long-term goals.

Faecal contamination at pasture

It is often observed that grazing animals avoid parasite-infested patches of herbage, possibly using the smell of faeces as a cue (see p. 435). While it is not yet clear whether or not sheep will avoid parasite-infested patches by means other than faecal contamination, it is certain that infection by parasites affects diet selection in housed sheep, increasing the protein intake relative to energy (Kyriazakis *et al.* 1994). This has been assumed to reflect the changes in nutrient requirements imposed by the parasites.

However, the grazing animal is presented with a paradox, since in addition to herbage associated with faeces possibly being contaminated with infective larvae, the nutritional content in this herbage (in terms of N content and digestibility levels) tends to be higher than that available elsewhere, because of the fertilizing effect as the faeces decompose. The higher nutritive value of herbage around faecal patches should, therefore, offer the opportunity for nutrient-limited animals to improve their nutritional status (an even greater need would exist for animals that are already parasitized, since their nutrient requirements are even further increased). This situation poses a classical trade-off in which the diet selection (or foraging behaviour) of the animal has to be made with the opposing needs of meeting its nutritional requirements on the one hand, and avoiding intake of infective larvae on the other. The way the foraging animal solves this question in terms of diet selection has only recently been addressed by the experiments of I. J. Gordon (personal communication).

CONCLUSIONS

The food preferences of animals, as expressed by the proportions eaten when a choice is given, are generally directed towards providing a balanced diet, i.e. one in which the quantity of each essential nutrient is closely matched to the quantity required for optimal metabolism. However, there are many situations which are likely to either interfere with animals' ability to select diets appropriate to their needs or in which the diets actually selected differ from the human observer's expectations for 'nutritional wisdom'. We have

not highlighted these with the intention of casting doubt on the usefulness of the method or practice of diet selection, either to the animal in meeting its nutrient requirements or to the agricultural scientist in trying to understand more fully what makes animals feel most comfortable metabolically, but rather to help us to design more appropriate experiments in future and to interpret their results with more insight than has often been the case hitherto.

We have shown that the animal needs to be aware of the nutritional differences between two foods which differ in taste, colour or some other sensory discriminating factor and we have outlined the influences that social interactions between animals can have on food selection. In addition, the foods on offer must be capable of providing a balanced diet when taken in appropriate proportions, i.e. selection cannot match requirements if both foods contain more (or less) than the required concentration of the nutrient in question. Further complications arise in the grazing situation, through faecal contamination, and where ruminants need a minimum amount of roughage to ensure normal rumen function, even though this may imbalance the diet in other respects. The presence of a toxin in one food can markedly reduce the animal's preference for that food and it can be concluded that preferred foods, or the preferred ratio of two or more foods, are tuned to provide a diet which promotes maximum metabolic comfort.

We believe that, given the appropriate conditions, diet-selection methodology provides a very powerful tool for nutritional and behavioural scientists and has great commercial potential. However, we have concentrated in the present review on some factors which must be taken into account when designing experiments and practical feeding systems, and when interpreting the outcome of such exercises.

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