Habitat selection according to the ability of animals to eat, digest and detoxify foods

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Large herbivores play a major role in shaping vegetation community dynamics through selective consumption of particular plants and plant communities. An understanding of the factors influencing diet selection at the level of individual bites ('bite scale') is important for prediction of the impact of herbivores on vegetation at the habitat scale. Bite-scale diet selection represents an integration of the twin goals of maximizing nutrient intake and minimizing toxin intake. Recent research with ruminants in pen-fed situations has shown that animals are able to make choices between artificial foods that maximize growth and other production variables. The role of post-ingestive feedback as an important mechanism for allowing animals to assess the nutritional quality of particular foods, and so select optimal diets, has been recognized in a number of recent experiments. Our understanding of the role of toxin intake minimization in diet selection decisions is more rudimentary. An important advance in the last decade has been the acknowledgement of the role of post-ingestive feedback and learning as a mechanism for avoidance of dietary toxicity. Further research is required to assess the importance of these processes in relation to free-grazing animals. The extent to which an understanding of bite-scale diet selection can be used to predict habitat utilization is not well understood. At the habitat scale additional factors such as predator avoidance, social constraints, avoidance of parasitism and microclimatic effects have an important influence on foraging decisions. Future research needs to focus on developing a quantitative understanding of such decisions at the habitat scale.

Diet selection: Habitat selection: Herbivore: Post-ingestive feedback

Large herbivores are major drivers of ecosystem function and dynamics in many terrestrial biomes. Through grazing, trampling, defecation and urination they affect nutrient flows, vegetation community dynamics and the responses of associated fauna. In turn, ecosystem characteristics such as composition, productivity and distribution of resources determine the nutrition of individual herbivores and the dynamics of herbivore populations. Consequently, knowledge of the foraging behaviour and habitat use of herbivores is of primary importance in determining the relationships between individual animal and population performance, and between herbivorous animals and their vegetation resources. Only through the development of this understanding can objective guidance for the sustainable management of natural resources be given.

Herbivores foraging in heterogeneous environments focus their foraging pressure on particular plant communities. Thus, their impact on the vegetation is distributed across the foraging environment in a non-uniform way. A range of factors can influence the choice of habitats by large herbivores, and it is important to understand these influences in order to arrive at a predictive means of assessing how herbivores will distribute their foraging effort within a given environment.

The pattern of habitat selection varies according to factors such as season and species. For example, sheep show marked seasonal patterns of plant community selection (Hunter, 1962). Similarly, different herbivore species utilize different plant communities to different extents. For example, in a recent comparative study (Fraser & Gordon, 1997), utilization of different plant communities by goats (*Capra hircus*), red deer (*Cervus elaphus*) and the South American camelid, the guanaco (*Guanaco guanaco*) was studied. Differences in patterns of utilization of different plant species within habitats were apparent with, for example, red deer showing higher utilization of *Calluna vulgaris* than either goats or camelids. Thus, whilst it is possible to describe the pattern of habitat utilization that we observe in

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particular circumstances, in order to move towards a predictive understanding of foraging patterns, an understanding of the mechanisms which underlie the observed pattern of utilization is needed.

In seeking to understand habitat selection, issues of scale are important. Foraging decisions are made at a range of scales from the bite-scale scale to the regional scale. A number of different systems for describing the hierarchy of scales at which foraging behaviour can be viewed have been described (Senft *et al*. 1987; Stuth, 1991; Bailey *et al*. 1996). As pointed out in these reviews, patterns of foraging at the level of landscape represent, to a certain extent, an integration of decisions made at smaller scales. To understand the patterns of resource use at larger scales (habitat selection), there is a need, therefore, to consider influences on small-scale foraging decisions, i.e. diet selection. To set the discussion in the present paper in context, 'habitat' is defined as being equivalent to 'feeding site' (Bailey *et al*. 1996), being a collection of patches in a contiguous spatial area that animals graze during a foraging bout. 'Diet selection', on the other hand, would be at the spatial level of 'bite' or 'feeding station' as outlined by Bailey *et al*. (1996).

Factors influencing diet selection have been extensively studied, and are the subject of recent reviews (Milne, 1991; Hanley, 1997). From simple observation it is clear that free-ranging herbivores select a diet which is richer in nutrients and which contains lower concentrations of plant secondary compounds than the average available plant material (Murden & Risenhoover, 1993). In crude terms diet selection can be viewed as the process by which herbivores balance the twin goals of nutrient maximization and toxin minimization. Our understanding of the physiological basis of diet selection decisions has been advanced, particularly in the last decade, by research with pen-fed agricultural animals. Some of this work will be reviewed here, and the extent to which conclusions from these studies are relevant to free-ranging herbivores will be considered.

Diet selection: nutrient maximization

Optimal foraging models predict that foraging animals should aim to maximize their rate of intake of the nutrient most limiting to growth and/or reproduction. Intake rate maximization is constrained by both the nutritional quality of available food items and by their abundance. This trade-off between quality and quantity is, therefore, a key factor in determining the diet which different herbivores ultimately select, and is responsible, in particular, for the variation in optimal diet selection solutions for different sizes of herbivores (Gordon, 1989; Illius & Gordon, 1992).

Trade-offs between quality and quantity of available herbage may lead herbivores to select diets of intermediate quality in order to maximize their overall rate of nutrient assimilation (Wilmshurst *et al*. 1995). However, in circumstances where quantity is not a constraint, herbivores should aim to select food items with maximal concentrations of the nutrients most limiting to growth and/or reproduction. There has been some debate as to which the key nutrient for maximization is in different circumstances. Candidates include N (or protein; Mattson, 1980; Kronberg & Malechek, 1997), carbohydrates (or energy; Belovsky,

1984, Murray, 1991; Stuth, 1991; Wallis de Vries & Schippers, 1994) and minerals (Belovsky, 1978). Some studies in the ecological literature are naive in their consideration of protein and energy as being discrete nutrients for ruminant herbivores. There has been a failure to recognize that in nutrient-poor systems, carbohydrate digestion is dependent on an adequate supply of N to the rumen microbial population to allow optimal microbial growth.

Recently, there has been a marked increase in interest in diet selection within the agricultural and nutritional disciplines, bringing with it a notable increase in the nutritional sophistication of research on diet selection. Work with rats and pigs has shown that these species select a diet which matches their nutritional requirements (Rozin, 1976; Kyriazakis & Emmans, 1991). The idea that animals display 'nutritional wisdom' has been extended into ruminant research; for example, in one experiment sheep given a choice between foods differing in crude protein ($N \times 6.25$) content selected a diet which led to maximal growth rates (Kyriazakis & Oldham, 1993). Recent work with dairy cows has also shown that animals are capable of making long-term diet choices which maximize milk yield (Tolkamp *et al*. 1998). Experiments by the same authors also indicate that dairy cows select diets which avoid excessive rumen-degradable N. The area of nutritional wisdom is complicated in ruminants by the interaction between energy and N metabolism in the rumen. Thus, selection of a high-protein diet for protein-limited animals is not necessarily the best solution if there is inadequate carbohydrate as an energy source for rumen micro-organisms. This situation has led to the interesting hypothesis that ruminants select a diet which favours optimal conditions for rumen fermentation. This hypothesis has been tested by manipulating rumen pH through acid and alkali infusion, but with inconclusive results (Cooper *et al*. 1995).

This recent work on nutritional wisdom in pen-fed situations has been useful in bringing an understanding of ruminant nutrition to the question of diet selection. In some studies, however, the diet selected by experimental animals has not supported the nutritional wisdom hypothesis (Forbes & Kyriazakis, 1995). This finding may be due, in part, to the fact that agricultural animals have not been selected for their ability to select an optimal diet from pelleted alternatives. This situation leads to the question of how nutritional wisdom is achieved. The assumption in the earlier work was that ruminants learn about the nutritional properties of their foods through post-ingestive feedback. The experiments described previously involved a period of training during which animals were given the opportunity to experience each food item in isolation for feeding bouts of 1 or 2 d before being offered choices. The idea that ruminants learn to select appropriate diets by learning to associate sensory cues with post-ingestive consequences has gained credence through a number of recent infusion experiments. It has been shown, for example, that sheep offered flavoured diets while simultaneously being intraruminally infused with urea or casein will subsequently show a preference for the food paired with the infusate (Villalba & Provenza, 1997). A similar phenomenon has been demonstrated for energy sources where preferences for flavoured feeds have been enhanced following previous pairing with sugar (Ralphs

et al. 1995) or volatile fatty acid infusions (Villalba & Provenza, 1996). However, some caution is required in invoking positive post-ingestive feedback as the basis for diet learning in free-grazing systems; indoor feeding experiments on nutritional wisdom and positive post-ingestive feedback involve simple food choices where the animal is given individual foods for feeding bouts lasting 1 d or more. This situation does not mimic the free-grazing situation, where there is little evidence that animals restrict their diet to individual food items for any length of time.

The assumption in much of the ecological literature is that food choices are made not on the basis of learned responses to the physiological consequences of consuming particular food items, but on the basis of simple sensory cues which provide immediate information about the nutritional properties of different plants (Bazely, 1990; Edwards *et al.* 1997). There is some evidence that previous experience can influence the diet selected by sheep (Langlands, 1969), but this finding may be as much to do with experience of harvesting particular plants than with experience of their nutritional properties.

There have been few rigorous tests of nutritional wisdom in free-grazing situations. In one experiment with sheep grazing *Calluna vulgaris* (Duncan *et al.* 1994*a*) the N demand of the experimental animals was manipulated by offering them isoenergetic supplements differing in crude protein content. The hypothesis was that animals with inadequate supplies of N in the rumen (barley supplement) would seek out a more N-rich diet than those with adequate N supplementation (soyabean supplement). The sheep were allowed to graze a *Calluna vulgaris* moorland where N-rich patches had been created by fertilizing with NH_4NO_3. Sheep showed a dramatic preference for N-enriched patches despite no discernible difference in the morphology of fertilized and unfertilized patches. However, the supplementation regimen had no impact on diet selection. Measurement of rumen NH_3 concentrations suggested that even barley-supplemented animals had reasonably high concentrations of N in their rumens, possibly due to more efficient urea recycling. The experiment clearly demonstrated that ruminants show a strong preference for nutrient-rich food patches. The question of how, and whether, they match their diet selection to their requirements remains unclear. It may be that in most natural scenarios there is no need to limit the quality of the diet selected, since food plants with excessive concentrations of nutrients are never encountered. There is a need for further studies on nutritional wisdom in relation to free-grazing animals.

Diet selection: toxin minimization

As well as maximizing nutrient intake, herbivores need to minimize their ingestion of the wide range of toxins found in food plants. Quantitative understanding of this process is more rudimentary than that in the area of nutrient maximization. Indeed, the influence of secondary compounds on diet selection is routinely employed as an explanation for the variation in diet selection that cannot be accounted for on the basis of nutrient maximization (Belovsky, 1981; Angerbjorn & Pehrson, 1987). The crude

state of our understanding of the role of secondary compounds in food choice is partly related to the fact that the range of chemical compounds to be considered is diverse, with numerous different groups of secondary plant compounds existing in nature. In addition, the effects of secondary compounds on fitness are unpredictable and difficult to measure. Furthermore, nutritive value and secondary compound concentrations often show an inverse relationship in plants, making it difficult to distinguish between their relative effects on food choice. A number of different experimental approaches have been employed to investigate the role of secondary plant compounds in diet selection. One approach is to incorporate the isolated toxin into artificial feeds and to investigate the impact on food choice (Elliot & Loudon, 1987). This approach has the disadvantage that isolating secondary compounds from their natural location within the plant may radically alter their physiological effects. At the other extreme, observational approaches have been adopted where natural variation in concentrations of secondary compounds in natural foraging environments has been related to utilization of food plants by free-grazing animals (Cooper *et al.* 1988; Owen-Smith, 1994). The problem here is one of attributing cause and effect with concentrations of a large range of chemical compounds varying simultaneously, making it difficult to attribute observed preferences to particular compounds. Experiments using intact food plants in controlled circumstances have provided some convincing demonstrations of the impact of individual secondary compounds on food selection (Hjalten & Palo, 1992; Duncan *et al.* 1994*b*; Rangen *et al.* 1994; Tixier *et al.* 1997) and further studies of this nature would be helpful.

In common with research on diet selection in the area of nutrient maximization, there has been much recent interest in the idea that ruminants learn to avoid plant secondary compounds through learning to associate their post-ingestive consequences with sensory cues. Research on conditioned food aversions in ruminants follows similar work with rats, which are particularly adept at avoiding toxic foods (Rozin, 1976; Zahorik & Houpt, 1981). The majority of these experiments have employed artificial aversive stimuli, such as LiCl and apomorphine, which induce nausea. The general protocol for these experiments typically involves feeding novel foods to animals while simultaneously applying the aversive stimulus. These experiments have demonstrated the development of strong aversions to foods paired with aversive stimuli (Ralphs, 1992), and have shown that the strength of the aversion is related to the magnitude of the aversive stimulus (du Toit *et al.* 1991). More recently, it has been shown that herbivores can develop mild conditioned food aversions to aversive stimuli which they would naturally encounter in food plants (Kyriazakis *et al.* 1997). The original context for much of the work on conditioned food aversions was as a management tool to train livestock to avoid toxic plants (Ralphs, 1992). More recently there has been some speculation that conditioned food aversions represent an important mechanism by which ruminants avoid toxicity in free-grazing situations (Provenza *et al.* 1992; Provenza, 1995). Experiments to date have predominantly been conducted in artificial conditions in which animals are given simple

choices between artificial feeds following a period of conditioning to artificial aversive stimuli. There is a substantial gulf between this scenario and the free-grazing situation where animals select a wide range of plants within a single feeding bout and where the aversive stimuli do not necessarily stimulate the emetic system. Thus, further experimentation is required before invoking conditioned food aversions as an important influence on toxin avoidance in the field.

One of the difficulties in attributing diet selection decisions to the presence of secondary compounds in food plants is that physiological responses of herbivores to secondary compounds are highly variable. This variability arises because herbivores have efficient mechanisms for minimizing the toxic effects of secondary compounds through their detoxification and elimination in a benign form. Detoxification can occur at a number of stages following ingestion. First, there has been some speculation that tannins in particular can lose their biological activity in the mouth by forming complexes with salivary tannin-binding proteins. Such proteins have been identified in rats (Mehansho *et al.* 1987), although evidence for their importance in ruminants is less convincing (Austin *et al.* 1989). There is some evidence that different herbivore species have tannin-binding proteins with particular affinity for the tannins they are likely to encounter in their food plants (Hagerman & Robbins, 1993). Following ingestion, the rumen represents an important site for biotransformation under the action of rumen microbes (Jones, 1981; Dickinson *et al.* 1988; Anderson *et al.* 1993). Following absorption there is further potential for detoxification in the tissues under the action of phase I and phase II xenobiotic-metabolizing enzymes (Watkins & Klaassen, 1986). Both rumen metabolism and tissue level detoxification are highly plastic processes, responding to the presence of substrates with substantial changes in levels of activity. There is thus much potential for inter-animal variability in susceptibility to plant secondary compounds, depending on the degree of physiological adaptation to particular compounds. There may also be inherent differences between species in metabolic detoxification pathways, and these differences may lead to inter-species variation in susceptibility to secondary compounds (Wachenheim *et al.* 1992). Species variation in the tannin-binding efficiency of salivary tannin-binding proteins to different classes of tannins may partially explain the different susceptibilities of herbivore species to the effects of tannins from different sources (Hagerman & Robbins, 1993). Despite the considerable animal variation in susceptibility to secondary compounds, there has been little research on its possible influence on diet selection. Kronberg & Walker (1993) showed species differences in the metabolism of the toxic principle in leafy spurge (*Euphorbia esula*) and suggested that this finding might account for variation in preference for the plant by sheep and goats. In recent work it has been shown that the rate of degradation of oxalic acid in the rumen of goats influences the proportion of oxalic acid-containing plants that goats consume as part of their diet (Duncan *et al.* 1998).

Habitat selection

Factors influencing food selection by herbivores at the bite scale have been described earlier. It has been argued that diet selection decisions can be interpreted as outcomes of the twin goals of nutrient maximization and toxin minimization. The extent to which understanding of foraging decisions made at the bite scale can be amplified in order to predict foraging patterns at the higher habitat scale must now be considered. To what extent can habitat selection be viewed as an integration of numerous bite-scale decisions? As pointed out by Senft *et al.* (1987), the closeness of the relationship between resource productivity and herbivore distribution diminishes with increasing scale. This situation is due to the increasing influence of factors other than purely nutritional considerations in determining foraging patterns. In the real world the herbivore is faced with a series of trade-offs about which habitat to choose. Some habitats may offer more in the way of food for the animal, but at the same time they may present more in the way of risk. For example, the degree of exposure to the weather or predators may be greater.

There has been much work on the relationship between habitat choice and food benefits and predation risk in small mammals and birds (Lima & Dill, 1990). However, little work has been done on the way in which predation risk can influence where a herbivore chooses to feed (Cowlishaw, 1997). One of the factors influencing sexual segregation in habitat use in ruminants is thought to be differences in the susceptibility to predation in males as compared with females and their young (Main *et al.* 1996). If males are less prone to predation, their distribution is more closely related to the distribution of food in the environment, whereas the distribution of females is related to the availability of habitats which offer cover or escape terrain. Whilst this behaviour is frequently observed in wild species, there is now some evidence for the possible influence of predation on the feeding behaviour of sheep. Sheep penned in paddocks in group sizes of less than four had lower intake rates than those in large group sizes (Penning *et al.* 1993). The authors attributed this finding to the possibility that the sheep in smaller group sizes were more vigilant as they viewed the potential predation risk as being greater. Thus far there has been no explicit test of the effects of perceived predation risk on the foraging behaviour of domestic species, although this work has been done in other groups of mammals and birds (Lima & Dill, 1990).

On the other hand, there is increasing evidence from studies on domestic species that avoidance of parasitism can impinge on the foraging behaviour of herbivores. For example, sheep avoided utilizing patches of vegetation which had higher faecal burdens than uncontaminated patches (Cooper, 1997). Parasitic helminth larvae were applied to pastures either in isolation or together with faecal material. The results showed that sheep avoided infected patches when larvae were applied together with their faeces matrix. This finding may have been due simply to avoidance of faeces *per se* as can be seen by the fact that the sheep avoided the faeces from parasitized and non-parasitized animals to the

same extent. Interestingly, infected and non-infected animals avoided infected pasture to different degrees, with non-infected animals showing less avoidance behaviour than infected animals. In nutrient-poor systems this behaviour may result in herbivores trading off the costs of ingesting infective parasite larvae with the benefit of consuming the nutritious grass which is associated with nutrients leached from faeces. Further studies have shown that sheep will avoid the consumption of grass infected with larvae, even though it may offer them higher intake rates (Hutchings *et al*. 1999). This is particularly the case for animals which are naive to parasites. Furthermore, animals that are hungry are more likely to opt for intake rate at the expense of larval ingestion. Whilst these studies are in their infancy, they demonstrate that domestic animals, at least, assess the costs as well as the benefits of their foraging decisions.

Although there have been studies on the dispersion of groups of herbivores and the interactions that take place between individuals (Arnold & Maller, 1985), there is a lack of information about how social behaviour may affect foraging strategy, particularly in heterogeneous ecosystems. Social interactions may limit the efficiency with which herbivores satisfy their appetite drive, either through competitive interactions or the need to maintain cohesive social groups. Competitive interactions may also influence utilization of scarce resources. For example, in an experiment with sheep, different age classes of Scottish Blackface sheep utilized feed blocks to markedly different extents (Lawrence & Wood-Gush, 1988). This finding was attributed to the formation of cohesive social groups by juvenile animals which were uninfluenced by movements of mature ewes to feed blocks. Within groups the position in the social hierarchy can also affect the rate of food ingestion. In red deer subordinates had lower feeding rates than did dominants when in close proximity (Thouless & Guinness, 1986). This finding was attributed to the possibility that subordinates were alert to movement of the dominants, and continuously moved out of their way to avoid conflict. As yet there is no published study which demonstrates that position in the social hierarchy affects an individual's access to food patches or habitats of different quality.

Herbivores may also be influenced in their choice of habitat by the microclimate offered by various habitats (Senft *et al*. 1985). The extent to which animals are influenced by microclimate is likely to depend on their susceptibility to extreme conditions. Thus, sheep that are relatively well insulated and are able to stand severe conditions without energetic cost (Blaxter, 1977) do not appear to be unduly influenced by the need to seek shelter unless they have juveniles at foot (Alexander *et al*. 1979). Deer, on the other hand, appear to respond to topography and adjust their choice of foraging locations accordingly (Staines, 1976). In hot climates, on the other hand, the insulatory capacity of wool for sheep may increase heat stress and lead to their seeking out habitats which offer shelter at the expense of time they could spend in food-rich habitats (Stafford Smith *et al*. 1985)

One of the ultimate goals of the research on intake and diet selection of herbivores in extensive systems is the development of a predictive understanding of habitat utilization to help land managers assess the consequences of their management decisions on animal production and the impact on the vegetation resource. Research on diet selection at the bite scale has progressed sufficiently to allow good predictions of diet choice to be made. The focus in future research needs to translate understanding of the bite-scale decision-making process to higher scales, and to further develop our understanding of the additional factors which influence foraging decisions at the habitat scale. This process has already begun with the development of decision support tools which incorporate quantitative and qualitative rules and relationships derived from foraging experiments, along with expert knowledge, to provide comprehensive computer-based programmes relevant to land managers (Buckland *et al*. 1998). Further developments of this type will help to integrate our current knowledge of foraging behaviour into useful frameworks for land managers.

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