

RESEARCH ON FORAGING BEHAVIOUR: PROGRESS AND PRIORITIES

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ABSTRACT

Recent developments in research on aspects of foraging behaviour in grazing ungulates are reviewed, with particular reference to the understanding of the mechanics of the grazing process, the factors influencing selective grazing activity, and the interactive nature of ingestive and digestive constraints to forage consumption. The implications of vegetation heterogeneity to the interpretation of experimental evidence, and its relevance in intensive and extensive pastoral systems, are discussed. It is concluded that there is a need for more effective integration of research activities at the interface between studies on grazing ecology and digestive ecology. Also, there is much to gain from a commitment to coordinate programmes of controlled research and field studies, across the range of vegetation heterogeneity reflecting variations in climate, soil and management. Recent developments in mathematical models of foraging strategy and its components provide the basis for such integration, but rigidities in research funding procedures can inhibit effective development of inter-disciplinary research.

KEYWORDS

Foraging strategy; ingestive behaviour; ingestive and digestive constraints; heterogeneity.

INTRODUCTION

At the corresponding session of the 17th Congress, Gordon and Lascano (1993) described the suite of decision-making processes defined as foraging strategy, and reviewed evidence on the influence of vegetation characteristics on the strategies of animals grazing intensively managed grasslands in both temperate and tropical conditions. The authors emphasised the important contribution of controlled experimentation carried out under these relatively simple conditions to an understanding of the processes mediating forage consumption and discriminatory grazing behaviour. Taylor (1993), however, argued that the substantial spatial and temporal heterogeneity implicit in extensive grassland systems limited the extrapolation of this evidence to such systems. Illius and Hodgson (1996), though suggesting the need for similar studies in more heterogeneous conditions, argue that the principles established in one set of conditions should be relevant to others. These authors comment further on the difficulty of deriving functional or mechanistic explanations of behavioural strategies from the essentially descriptive information which is characteristic of heterogeneous environments, and on the advantages to be gained from the pooling of information from natural and agricultural ecosystems.

In this review our objective is to evaluate recent evidence on the behaviour of grazing herbivores, and its implications to theories of foraging strategy, in four main areas:

- the mechanics of the grazing process
- selective grazing behaviour
- the balance between ingestive and digestive constraints to forage consumption
- the impact of vegetation heterogeneity

We will be particularly concerned to focus on the implications of variations in the spatial scale and the magnitude of vegetation contrasts to the interpretation of experimental results, and their

relevance to aspects of grazing management in both intensive and extensive systems.

GRAZING MECHANICS

Functional response. There is now an extensive literature on the influence of vegetation and animal characteristics upon the determination of bite dimensions, bite mass and the short-term rate of forage consumption. The evidence was reviewed at the 17th Congress (Gordon and Lascano, 1993) and more recently (Hodgson et al., 1994; Demment et al., 1995; Ungar, 1996) and will not be repeated here. However, it might be summarised as follows:

1. Bite mass is influenced primarily by the sensitivity of bite depth to variation in sward height, and there is often a close proportional relationship between these two variables across a remarkably wide range of variation in sward height (Burlison et al., 1991; Gong et al., 1996; see Fig. 1). Variations in herbage bulk density may contribute independently to variation in intake per bite (Black and Kenney, 1984; Mitchell et al., 1993).
2. Bite area, though clearly not a constant simply reflecting limiting mouth dimensions, is nevertheless substantially less sensitive than bite depth to variation in sward conditions (Laca et al., 1992; Edwards et al., 1995; Ungar, 1996).
3. Bite rate is in general negatively related to bite mass, reflecting the increasing importance of manipulative movements (prehension and chewing) as bite mass increases (Spalinger and Hobbs, 1992; Laca et al., 1994; Ungar, 1996).
4. Despite the generally negative association between bite mass and bite rate, the short-term (instantaneous) rate of intake still tends to increase progressively though as an asymptotic function of bite mass (Spalinger and Hobbs, 1992; Demment et al., 1995; Ungar, 1996).

Much of the evidence summarised above comes from studies on temperate pastures, or pasture analogues, with domesticated animals. Specific evidence from range conditions or range and browse plants, and involving a selection of grazing and browsing animal species, fits within the same generalisations (Short, 1985; Koerth and Stuth, 1991; Spalinger and Hobbs, 1992; Ginnett and Demment, 1995; O'Reagain and Grau, 1995). However, there are indications that variations in leaf density and leaf/stem ratio have more impact in tropical than in temperate swards, reflecting their generally lower values in the former case (Stobbs, 1973a,b).

The value of small-scale controlled studies to an understanding of the mechanics of the grazing process, and the importance of this understanding to the definition of relevant plant and plant community characteristics and management strategies (Ungar, 1996), should not be discounted. Nevertheless, the importance of grazing time as the link between short-term intake rate and daily forage intake is self-evident (Gordon and Lascano, 1993; Demment et al., 1995; Ungar, 1996; Illius and Hodgson, 1996) and should now be seriously addressed. Woodward (1997a), for example, has argued that grazing time may be to some extent constrained by the needs for ruminating time, dictated primarily by diet characteristics, and for idling time,

reflecting animal factors including nutritional status. Although there are some limitations to this approach, it does offer an improvement over those assuming a fixed grazing time or a fixed number of jaw movements (see also Illius, 1997).

Causation. Resolution of some of the major functional relationships outlined above leaves unanswered some teasing questions about causation. We focus here on two of these issues, relating respectively to the determination of proportionality of bite depth to sward canopy height, and the determination of bite area.

Optimality arguments suggest that animals should bite as deeply as possible into the sward because deeper bites result in greater bite mass, consequently greater instantaneous intake rate, and therefore greater daily intake. Furthermore, while bite benefits (bite mass) increase linearly, at least in artificial swards (Laca et al., 1992; Mitchell et al., 1993), Woodward (1997b) argues that bite costs (force or energy) increase only sub-linearly with bite depth, so cost-benefit arguments alone seem incapable of explaining partial consumption, even if variations in herbage quality with depth are considered. Bite depth may be constrained if animals reach their physical limit of bite energy (or force). The results of Hughes et al. (1991) however showed that animals typically do not graze to the limit of peak bite force (and hence bite energy) when grazing grass swards, and more recent work by Illius et al. (1995) confirms this. A second constraint would be if deep bites resulted in grazing into undesirable layers of the sward or a pseudostem barrier, as suggested by Barthram and Grant (1984). Although Barthram and Grant's hypothesis seems reasonable, measured bite depths are often too shallow to be explained by the presence of such a barrier. However, Laca et al. (1993a) point out that bite depth is not constant over the area of the bite (see also Fig. 2). Mean bite depth is then often an underestimate of the maximum depth to which an animal bites, and it may be this maximum depth which is limited by old pseudostem or stem material in established swards (Barthram and Grant, 1984; Mitchell, 1995; Woodward, 1997b).

Demment et al. (1995) and Ungar (1996), in reviewing evidence on bite dimensions, comment on the lack of explanation for the constancy of the proportional link between sward surface height and bite depth. A tenable explanation was suggested recently by Mitchell (1995), who showed that the potential area of herbage encompassed at a bite, including leaves laterally displaced within the jaws, increased substantially as bite depth increased to 30-50% of sward height, but that further gains in potential bite area with deeper penetration within the sward canopy were relatively small (Fig. 3). This simple model of declining incremental gain with progressive penetration appears to be applicable across a range of sward heights, and to reflect the balance between initial leaf capture and subsequent escape from incisor grip during biting (Mitchell, 1995). However, it is based on information from simple seedling swards. Its application to swards with normal variation in the vertical distribution and maturity of leaf and stem (Hodgson, 1985) will depend upon the balance between vertical changes in bulk density and in structural strength of the constituent tissues and their impacts on the cost/benefit balance of deeper biting (Illius et al., 1995; Illius, 1997).

While it has been shown that bite area is weakly and negatively correlated with sward bulk density (Laca et al., 1992; Mitchell et al., 1993), this relationship cannot be fully explained by proposing limitations to bite force and biting energy. However, uncertainty over the control of bite area may be resolved if this is viewed as a three-stage process. Bite area on short swards is a reflection of sward height and the ability of the lips and teeth to capture individual tillers for

excision (Laca et al., 1993a; see Fig. 2). On longer swards it may be limited by the effects of leaf bulk density or structural strength on biting effort, though these effects may be small (Hughes et al., 1991; Laca et al., 1992). Ultimately, bite area will be limited by maximum jaw or tongue sweep, a limitation which may apply for low strength pastures (Woodward, 1997b). In this complex but nevertheless plausible scenario it is not surprising that no clear consensus of interpretation has yet developed (see also Illius, 1997).

SELECTIVE GRAZING

The conceptual basis for investigation of selective grazing behaviour is now well established. It involves the influence of visual, olfactory or gustatory cues used by animals to identify preferred components within the vegetation canopy, and the effects of variations in the relative frequency and physical distribution of these components on the outcome of selective behaviour (Gordon and Lascano, 1993). A clearer appreciation is also emerging of the ability of animals to adjust diet composition in response to previous experience (Mirza and Provenza, 1990) and current nutrient demand (Kyriazakis and Oldham, 1993), and of the potential influence of post-ingestive feedbacks on diet selection (Provenza, 1995; Launchbaugh, 1996). These latter issues are dealt with by Provenza (1997) and will not be elaborated here. Nevertheless, Illius and Hodgson (1996) comment that understanding of the cues which determine discriminatory responses is still rudimentary, and there is virtually no basis for predicting the trade-off decisions likely to be made by animals grazing in multi-dimensional choice environments. This is unfortunate because it is clear that, in such heterogeneous conditions, animals must regularly make choices between alternative combinations of plant characters in determining where and when to take bites. At this level there is urgent need for coordination of interests in observational work in complex natural environments and manipulative work in controlled environments. The two approaches should be regarded as complementary.

Cues and Choices. In research to date, emphasis in controlled grazing experiments has concentrated upon either physical plant characteristics (height, bulk density, structural strength) or biochemical characteristics (whether defining nutritional or antiquality factors), and few authors have attempted to combine the two sets of variables (but see Bazely, 1990). There have in fact been relatively few clear-cut demonstrations of the quantitative effects of specific chemical entities on dietary preferences in grazing studies (e.g. Marten et al., 1973), though there is now increasing awareness of the important influence of biochemical cues on selective behaviour (Launchbaugh, 1996).

Kenney and Black (1984) and Edwards et al. (1996a) studied interactive questions in principle, using artificial foods or feeding procedures, but there have been few such studies under grazing conditions. This may be because thinking in the grazing context has concentrated on the influence of physical plant characteristics on rate of intake as a primary determinant of choice, with little reference to the potential importance of biochemical cues as moderating factors (Illius and Hodgson, 1996). The issue here is primarily one of research methodology, because definition of trade-off choices requires a multi-choice context within which to work, and a relatively sophisticated interpretation of grazing behaviour. Investigations of trade-off decisions involving independent variations in sward height and bulk density (Demment et al., 1993), or sward height and maturity (Griffiths et al., 1997), are examples of what is possible.

Canopy structure. Investigation of selective grazing strategy has generally been restricted by the complexity of the vegetation base,

and the confounding influences of variations in plant preference and accessibility, even in the relatively simple context of intensively managed, monospecific swards. The conventional sigmoidal form of the distribution of tissue bulk density through the canopy profile (e.g. Hodgson, 1985; see Fig. 2) is generally derived from the cumulative data from a series of point or quadrat samples. Provided the sward surface height is relatively uniform, such distributions may also be valid for the purposes of describing conditions at any particular bite location. The frequently cut swards of Illius et al. (1995), for example, exhibit a similar sigmoidal density profile for small sward patches. However, description of variation in vegetation characteristics at the patch or bite levels assumes increasing importance in heterogeneous conditions, and in those circumstances the aggregation of sample data can produce misleading results (e.g. Gibb and Ridout, 1988). The importance of a comprehensive description of sward canopy structure, taking into account both vertical and horizontal heterogeneity, is now well recognised (Gordon and Lascano, 1993; Dove, 1996; Schwinning and Parsons, 1996). Definition of elements of either vertical or horizontal heterogeneity has been a feature of several studies (e.g. Milne et al., 1982; Clark and Harris, 1985) but the technical procedures for measuring and describing variability in three dimensions are not readily available. The quantity of information required to comprehensively describe canopy structure in these terms would be challenging. Perhaps the most practical way forward would be to quantify canopy structure along random transects (e.g. Rook, 1995; Edwards et al., 1996b) and to relate these statistics to observations of searching behaviour and patch selection (e.g. Focardi et al., 1996). Definition of vegetation structure should take into account concepts of scale of variation for both plants and animals (Dove, 1996; Edwards et al., 1996b; Illius and Hodgson, 1996) and is probably best viewed, at the finest level of "grain", in terms of bite-sized units.

Partial preference. Recent studies on patterns of discrimination between grass and legume components of pastures, with emphasis on monospecific patches or plots as the basis for choice, have demonstrated clearly the importance of partial preference in influencing dietary balance (Newman et al., 1992; Parsons et al., 1994), but have not established rationale for the balances observed. The effects on diet composition of time of day, previous experience, and variations in the relative proportions of constituent monospecific swards on offer (Parsons et al., 1994), indicate intriguing dimensions for further studies on selective behaviour.

When offered choices of monospecific perennial ryegrass and white clover pastures, sheep demonstrate preference for a mixed diet containing 50%-70% clover (Parsons et al., 1994), though there is evidence of a continuing nutritional advantage to diets of up to 100% clover (Gibb and Treacher, 1984; Beever et al., 1986). Furthermore, sheep, cattle and goats all appear to demonstrate preference for a similar dietary balance in these conditions (Parsons et al., 1994; Orr et al., 1995; Penning et al., 1995a,b; Cosgrove et al., 1996), despite differences between species in rumen function and digestive efficiency (Domingue et al., 1991; Van Soest, 1992). These observations provide further food for thought about the potential importance of balancing decisions influencing selective behaviour. They also draw attention again to the issue of "selection for rarity" across a range of sward combinations (Newman et al., 1992; Parsons et al., 1994; Poli et al., 1997), as identified earlier by Milne et al. (1982) and Clark and Harris (1985).

The results of Illius et al. (1992) in which sheep preferred to graze from sward trays of mixed grass/clover vegetation of intermediate clover content (50-60% by DM) rather than from trays with either

higher or lower clover content (Fig. 4), demonstrate alternative evidence for partial preference. This effect was interpreted in terms of observed differences between trays in rate of intake. However, in this context there is need for a clearer resolution of the conundrum of association between potential rate of intake and "preference". Which is chicken and which egg? In many circumstances it is not easy to distinguish cause and effect but, in future, objective appraisal will require an explanation of causation as well as a definition of association.

Foraging strategy. Selective behaviour has normally been considered in the context of bite or patch selection, and manipulative studies have seldom involved larger scales of activity. However, the impacts of variations in topography, predation and cover and the siting of water points on spatial and diurnal patterns of movement and search are clear (Coughenour, 1991; Stuth, 1991; Murray and Illius, 1996; Stafford Smith, 1996). Though discrimination may be essentially a bite-by-bite phenomenon against a heterogeneous vegetation background, there is recent evidence for a "near-far" foraging strategy in insects which may be optimal where perfect knowledge of feeding opportunities is not available (Motro and Schmida, 1995). The extent to which this strategy may be applicable to grazing ungulates is not clear. There are conflicting views of the spatial recall and memory retention of grazing animals (Edwards, 1994; Laca and Demment, 1996), and several authors have discussed the potential importance of sampling behaviour in retaining an information base for foraging (Illius and Gordon, 1990; Parsons et al., 1994; Wilmshurst et al., 1995).

Finally, in the context of this section, there is some inconsistency in the limited experimental evidence on the applicability of optimal foraging theory (OFT) to the selective behaviour of grazing animals (Focardi et al., 1996). In the case of patch selection and residence time, OFT implies awareness of conditions over a set of adjacent patches and the ability to make trade-off decisions to maximise rate of energy intake across them (Langvatn and Hanley, 1993; Demment et al., 1995; Wilmshurst et al., 1995). Laca et al. (1993b) suggested that their animals adjusted the use of a series of patches in checkerboard designs to maximise instantaneous intake rate in a manner consistent with OFT, whereas Griffiths et al. (1997), in studies with linear sequences of patches, found no evidence that use of individual patches was influenced by conditions on adjacent patches.

FORAGE INTAKE: INGESTIVE AND DIGESTIVE ECOLOGY

Studies on the voluntary food intake of animals under indoor feeding and grazing conditions have run in parallel for many years, focusing respectively on the importance of digestive (e.g. Mertens, 1994) and ingestive (e.g. Hodgson et al., 1994; Ungar, 1996) limitations. The two approaches have often involved working with a common suite of plant variables, though the conceptual and mathematical models within which these variables are used may be quite different. Thus, estimates of plant digestibility may be used as an indicator of nutrient concentration and potentially of primary intake limitation for both cut and grazed forages through its influence on digesta load (Weston, 1996), but may also be used as an indicator of structural strength and resistance to defoliation in grazed swards. Similarly, estimates of plant fibre content in indoor studies are likely to relate primarily to the ability of cellular tissue to resist crushing and shearing during chewing, and hence the rate of breakdown for digestion or passage from the rumen (Inoué et al., 1994), but in grazing studies emphasis is more likely to be placed on measures of tensile strength and resistance to breakage as factors influencing biting effort and bite dimensions (Illius et al., 1995). Though these characteristics may be

linked in a qualitative sense, the physics of plant fibre structure and breakdown (Wright and Vincent, 1996) dictates that the relationship is not simple (Henry et al., 1996).

Despite these similarities in approach to understanding the control of forage intake in housed and free-grazing animals, there has been little attempt to combine the two approaches in either field experimentation or, until recently, in modelling. This is no doubt due in part to the difficulty of achieving independent control of the quantitative and qualitative sward variables associated with increasing maturity (Wilmshurst et al., 1995) or of alternative parameters of nutritive value (Langvatn and Hanley, 1993) in field studies. These difficulties have often been compounded in studies where the effects of changes in ingestive and digestive constraints were confounded as swards were progressively defoliated by grazing animals.

The major distinction between forage feeding and grazing conditions, of course, relates to the influence of the horizontal and vertical distribution of plant components (vegetation canopy structure and heterogeneity) on the foraging strategy and ingestive behaviour of grazing animals. These factors collectively increase the time and effort involved in finding and ingesting forage, and may constrain forage consumption through their effects on the rate of forage intake. At the same time they increase the opportunity to improve the nutrient status of ingested forage by selective grazing (Demment et al., 1995), though the balance between the effects of these two conflicting factors on nutrient intake is not always clear (see Hodgson et al., 1991).

Voluntary food intake by housed animals may be predicted effectively from separate constraints on either the fill of the digestive tract or the concentrations of circulating metabolites, subject to specific limitations associated with nutrient imbalance or low fibre intake (Poppi et al., 1994; Forbes, 1995). Similar conceptual models have been used in the investigation of intake control under grazing conditions, with the additional constraint of limits to the rate of ingestion of grazed forage (Demment et al., 1995). However, conventional theory based on alternative constraints (e.g. Mertens, 1994) may be inadequate in these circumstances, where limitations in intake rate and rate of digestion may frequently reinforce one another. For grazing conditions the conceptual model of a balance between the effects of stimulatory and inhibitory factors first proposed by McClymont (1967) may be more appropriate. The principle of energy deficit and its stimulatory effect on appetite (McClymont, 1967) is implicit in the Forage Consumption Constraint (FCC) of Weston (1996). Further, the relationship between the organic matter digestibility of the diet (OMD) and the discrepancy between FCC and forage intake (both expressed as units of organic matter per unit of metabolic body weight) illustrates one possible element of interactive tension between energy demand and digestive limitation (Weston, 1996). However, the suggested incorporation of a grazing time limit, reflecting muscular fatigue, as an additional constraint for grazing animals represents a return to less satisfactory concepts of sequential constraints (see also Illius, 1997).

Recent theoretical models (e.g. Illius and Gordon, 1990; Spalinger and Hobbs, 1992; Demment et al., 1995) incorporate concepts of both digestion-limited and behaviour-limited intake, though the two sets of constraints are still handled essentially in a sequential rather than an interactive sense. Laca and Demment (1996) comment that ingestive and digestive constraints are interdependent. However, there is little hard experimental evidence on which to base models of interactive intake control in grazing conditions. It is time for a more determined investigation of the common ground occupied by

practitioners in grazing ecology and digestive ecology (see Dove, 1995; 1996) in order to define more rigorously the interactions between the factors influencing forage ingestion by grazing animals, and their relative importance, in defined conditions. Evidence of this kind will be important to an understanding of foraging strategy and its consequences at all levels of vegetation heterogeneity. The work will not be easy, because it will demand complementary monitoring of ingestive and digestive behaviour over time scales ranging from minutes to weeks, and the simultaneous manipulation of metabolic status and/or digestive feed-backs. However, appropriate methodology is available for the achievement of these objectives (Penning et al., 1984; Beever et al., 1986), and the conceptual basis for linking the effects of these essentially internal and external factors on forage intake through their impacts on meal size and frequency is also available (Forbes, 1995). Developments in this area should be an immediate priority for research on foraging strategy.

IMPACT OF HETEROGENEITY

The objective in this section is to examine the extent to which variations in the spatial scale and magnitude of vegetation contrasts may modify the functional responses discussed in previous sections. This implies consideration of the commonality of responses across intensive and extensive pastoral systems (*sensu* Taylor, 1993).

The variance and range of environmental variables may tend to increase with the scale of observations in natural (and, by inference, extensive) plant communities (Demment et al., 1995). However, there should be no automatic assumption that within-enclosure contrasts are necessarily different in the two situations, particularly in relative terms. The spatial scale of foraging decisions may range from the individual bite, through grazing patch and feeding station, to the level of plant community, home range and, ultimately, landscape (Stuth, 1991). Probably only the first three are relevant to intensive conditions, though we suggest that, in principle, decision-making processes from the bite to the feeding station level should be similar across the range of grazing conditions, and influenced primarily by the same set of pasture characteristics.

Spalinger and Hobbs (1992) define three grazing conditions in which rate of intake of forage is limited, respectively, by searching for food items which are not readily apparent (Process 1), by travelling between food items which are apparent (Process 2), or by the rate of consumption of food items (Process 3). Process 3 may be regarded as most representative of intensive pastures, whereas Processes 1 and 2 relate most appropriately to extensive grazing conditions and selective grazing behaviour. However, the three processes reflect an inter-related set of derivations from the same conceptual information base (Spalinger and Hobbs, 1992; Farnsworth and Illius, 1996).

Optimal foraging theory dictates that behaviour at a particular bite site will be influenced by grazing opportunities at alternative sites (Demment et al., 1995). However, for any given animal species it is logical to assume that, once a potential bite is identified and a decision made to take it, the mechanisms of prehension and severance and their effects on bite dimensions and the characteristics of herbage in the bite will be determined solely by the nature of the vegetation at that point. The basis for behavioural contrasts between animals in intensive and extensive pastoral systems therefore lies primarily in the opportunity for mobility in the use of alternative forage resources, and the extent to which this is exploited. However, even in extensive systems freedom of movement may be restricted by the pressures of home-range behaviour (Hunter, 1962), and rangeland animal populations are characterised by sedentary as well as migratory species (Murray and Illius, 1996). This is the context in which

management decisions on enclosure size and position relative to plant community distribution, and the positioning of water points and salting/feeding stations, can have important effects on the stability of plant and animal communities (Stafford Smith, 1996).

Against this background, it seems logical to argue that the basic parameters of foraging strategy are essentially the same across a range of grazing conditions. In principle, therefore, understanding developed in one context should be entirely appropriate to application in another, and indeed this appears to be the case (cf Koerth and Stuth, 1991; Spalinger and Hobbs, 1992; Ginnett and Demment, 1995; O'Reagain and Grau, 1995; Ungar, 1996). The behavioural factors likely to assume more importance in extensive than in intensive systems are those associated with searching activity and grazing time, and with the separation of selective, ingestive and chewing behaviour as components of the ingestive process. It is noteworthy that understanding of the time relations of the components of ingestive behaviour is a very recent attainment (Spalinger and Hobbs, 1992; Laca et al., 1994; Newman et al., 1994), and understanding of the factors controlling grazing and searching time is still a major priority, for both intensive and extensive systems (Laca and Demment, 1996; Illius and Hodgson, 1996).

It is tempting, though probably simplistic, to draw a contrast between intensive and extensive systems in terms of the relative importance of ingestive and digestive constraints to forage intake. The generally higher fibre content and lower nutritive value of forage in extensive grazing conditions would imply a greater expectation of digestive limits resulting from reduced rate of digestion and increased bulk in the digestive tract, against the background of a higher processing demand to meet specified nutrient requirements (Spalinger and Hobbs, 1992). However, increasing emphasis on selective behaviour in animals grazing lower-quality forages is likely to introduce its own constraints to rate of forage intake (Laca and Demment, 1996). There is limited information on the effects of alternative selective strategies on the ability of animals to maintain nutrient intake across a range of vegetation conditions (Gordon and Illius, 1989; Hodgson et al., 1991). In contrast, there are clearly close links between aspects of digestive and ingestive strategy across animal species, with particular reference to the question of niche separation within guilds of sympatric herbivores in areas like the Serengeti grasslands (Murray and Illius, 1996).

This all leads to the conclusion that the major contrast between intensive and extensive grasslands lies more in the behavioural principles of vegetation response to herbivory against an unstable climatic background (Coughenour, 1991; Stafford Smith, 1996), than in the behavioural principles governing vegetation use by the herbivores themselves. It is noteworthy that discussion of foraging strategy at the XVII Congress concluded with an appeal for better information on plant responses to foraging, as well as on the links between foraging strategy and animal performance (Taylor, 1993).

CONCLUSIONS

Foraging science is developing rapidly on a range of fronts, and much progress is being made in specific areas. However, our ability to integrate information across these areas is less well developed. For example, we have hardly started to quantify the combined effects of variations in the physical and biochemical characteristics of plants on the selective behaviour of grazing animals. At a different level, our understanding of ingestive and digestive processes is far in advance of our ability to describe the interactions between them, and hence to be able to predict bite selection or forage intake. This points to the need for a comprehensive conceptual framework for

foraging behaviour which encompasses all of the relevant areas.

The perceived imbalance in understanding may reflect lack of clarity in defining the goals of foraging science. The proposal of implicit goals, such as the ability to predict an animal's daily herbage intake, quickly highlights areas requiring further work since such goals cannot be adequately attained until the full range of underlying processes has been addressed. Some of the important interface areas have been identified in this review.

Simulation modelling provides the discipline to organise information in a modular fashion, and to define protocols for investigating interface issues in an objective manner. In this way it is possible to identify variables which define the boundaries between adjacent discipline areas, and the links between them. For example, bite mass and composition are outputs from ingestive studies but inputs to digestive studies; grazing time is affected by nutritional status but is itself a component of ingestive behaviour; and intake from a feeding station sits at the intersection of interest between intensive and extensive systems. This analysis identifies the question of coordination of information between intensive and extensive systems as but one of a series of interfacing questions which require solution.

A particular area of weakness is the definition of spatial heterogeneity and the description of searching strategies linked to it, but there are broader issues than this in the prediction of forage intake by grazing ungulates. Progress is now being made in relating the principles of optimal foraging theory to grazing conditions (Farnsworth and Illius, 1996; Illius and Hodgson, 1996). Further advances in these difficult conceptual areas will be dependent upon continuation of the stimulating symbiotic relationships between interests in natural ecology and in the ecology of managed agricultural systems. It will also be greatly aided by a more imaginative attitude amongst national and international funding agencies to inter-disciplinary research. These problems are not insurmountable, but their solution will require sustained effort to ensure recognition of foraging science as a relevant entity, and the outcomes of research in foraging science as a legitimate contribution to the management of grazing systems.

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Figure 1

The relationships between sward surface height (SSH) and bite depth (BD) in sheep and goats grazing a series of grass species at vegetative and reproductive stages of growth (from Gong, 1994). These relationships are derived from the pooled results of a series of measurements made on turves cut from swards of 5 different graminaceous species, each at 2 stages of maturity, and offered individually to penned sheep and goats under controlled conditions (see Gong et al., 1996). Appropriate regression equations were:

Sheep: vegetative swards	$BD = -0.55 + 0.51 (\pm 0.067) H$	$R^2 = 0.67^{***}$
Goats: vegetative swards	$BD = -6.96 + 0.61 (\pm 0.070) H$	$R^2 = 0.76^{***}$
Sheep: reproductive swards	$BD = -13.52 + 0.82 (\pm 0.074) H$	$R^2 = 0.84^{***}$
Goats: reproductive swards	$BD = -22.10 + 0.94 (\pm 0.102) H$	$R^2 = 0.78^{***}$

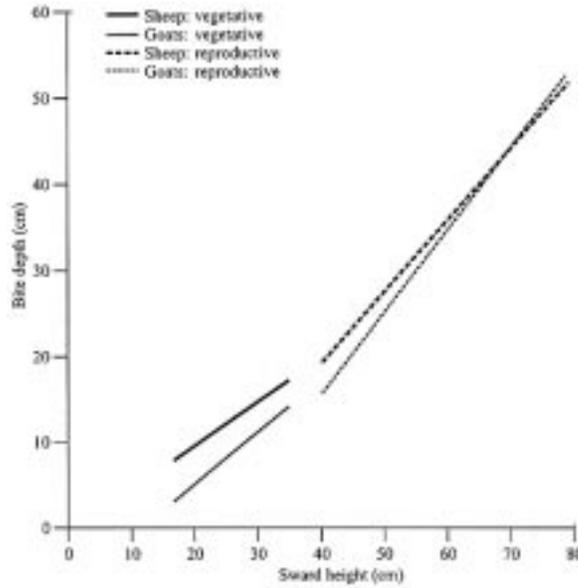


Figure 2

Hypothetical vertical profiles of cross-sectional area of the bite and canopy bulk density at the bite site (from Woodward, 1997b).

$A(h)$ = cross-sectional area of bite

$B(h)$ = canopy bulk density at bite site

SSH = sward surface height

Z = bite insertion height

Then: Bite mass $W(g) = \int_z^{SSH} A(h) B(h) dh$

and Average bite depth $\bar{D} = \left(\int_z^{SSH} (SSH - h) A'(h) dh \right) \div (A(SSH))$

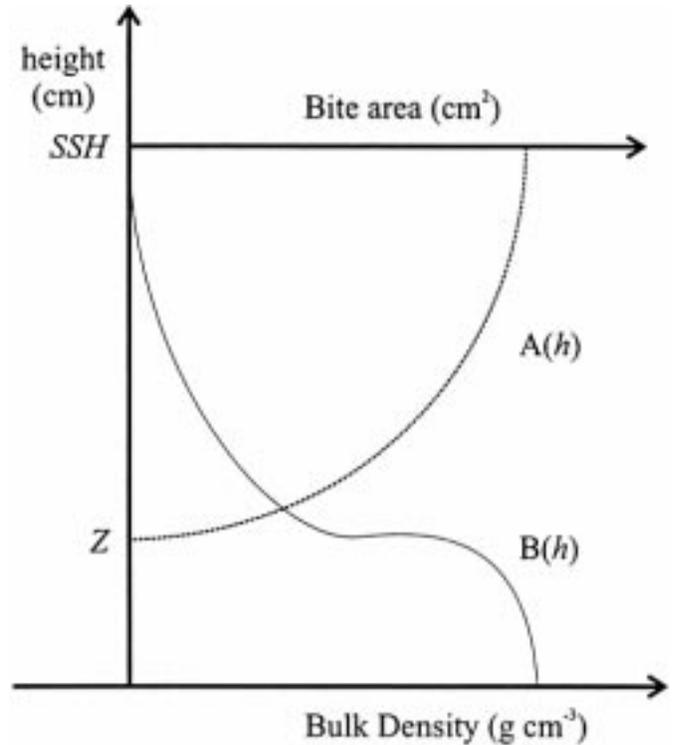


Figure 3

The influence of sward height and bite depth upon potential horizontal displacement of foliage during grazing, and on bite area (from Mitchell, 1995). This figure illustrates the influence of bite depth (expressed as a proportion of sward height) upon the opportunity for horizontal displacement of individual leaves or tillers for successful gripping between incisor teeth and dental pad in grazing sheep or deer. The incremental gain in potential bite area ($2 \times \text{displacement} \times \text{incisor arcade width}$) is substantially greater for the first 25% increment in bite depth (2a) than for further increments (2b and 2c). The results relate to seedling swards with uniform vertical distribution of herbage (see Mitchell et al., 1993); effects in normal swards will depend upon the balance between the effects of vertical changes in bulk density and structural strength.

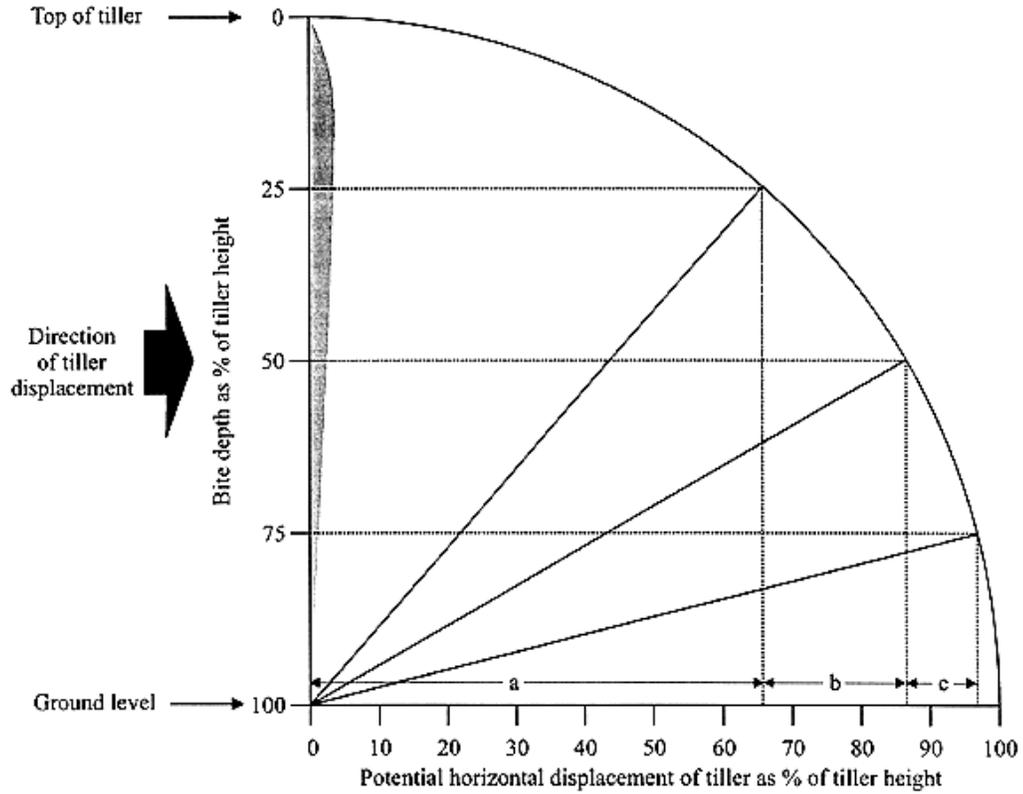


Figure 4

Proportions of bites (PB) from pairs of sward trays (1 and 2) varying in clover content (CLO) (from Illius et al., 1992). This figure summarises the grazing preferences exhibited by penned sheep offered a series of pairs of sward trays providing contrasts in clover content but of the same height in short-term feeding trials. There were 25 paired combinations of clover content varying between 0% and 100% by dry weight, and between-pair contrasts (sward 1 minus sward 2, or vice versa) ranged from zero to 80%. The appropriate regression equation was:

$$PB(1) = 0.52 + 0.064 CLO(1) - 0.000081 CLO(1)^2 - 0.0055 CLO(2) + 0.000056 CLO(2)^2$$

$R^2 = 0.45; n = 128$

