Pasture Ecology Meeting
Plant-Herbivore Relationships

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Conference organized by

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Foreword

The Pasture Ecology meeting was organized in Clermont-Ferrand/Theix on 31 May and 1st June as a satellite meeting of the 19th congress of the European Grassland Federation held in La Rochelle (France) in May 2002. Eighty-eight scientists from seventeen countries joined this meeting and had deep and stimulating scientific exchanges on vegetation dynamics, plant-herbivore interactions and management in grassland ecosystems. We are pleased to publish here the three main papers that were given in the session focussed on plant-herbivore relationships.

Grazing is one of the major processes that affect grassland ecosystem dynamics. Grasslands are no longer seen only as a feeding resource for domestic herbivores, but also as an environmental resource through its contribution to biodiversity, biogeochemical cycles and landscapes. Thus, there is a considerable need to improve scientific knowledge by including a comprehensive view of how grazing can contribute to the multi-functionality of grasslands. Grazing results from complex interactions between animals and vegetation. These interactions occur at different spatio-temporal scales from the smallest that is the prehension of bites to the largest at the plot level. On all of these scales, animals create and respond to heterogeneity of the vegetation. The creation and maintenance of heterogeneity at different scales can be analysed in terms of constraints or benefits for grazing animals' diets and for grassland management for environmental purposes, biodiversity for example. The three papers gathered here bring an overview of recent scientific advances in the comprehension of the grazing process from small to large scales and give some prospects in the development of grazing management for a multi-purpose use of grasslands.

R. Baumont
Guest Editor
Review article

Sward structural resistance and biting effort in grazing ruminants

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Abstract — Grazing ruminants face complex decisions in searching for and harvesting adequate forage to meet their requirements in the face of heterogeneity in the abundance, nutritive value and distribution of resources. Some of the major decisions which affect the bite mass and therefore, forage intake adjustments in bite depth, bite area and exerted bite force, are made in relation to heterogeneity in sward structure. A number of relationships have been established linking the adjustment of bite mechanics in response to variations in sward height and bulk density on temperate forages for animals of a range of body sizes. However, there is less consistency in the response of the bite mechanics to the greater variations in structural resistance that arise from the vertical and horizontal arrangements of the plant morphological organs of leaf, pseudostem and stem. Furthermore, only limited progress has been made in quantifying the biting forces involved in grazing, the linkages between the plant morphological organs and their effect on bite force and, the interaction with body mass. In this paper, we discuss the different hypotheses that have been proposed to explain the regulation of bite depth and provide evidence for their acceptance or rejection. We comment on the knowledge gap in understanding biting force mechanisms across animal species of contrasting body mass, and stress the need for differentiation between the concepts of biting force and biting effort.

bite / effort / force / ruminants / structure

Résumé — Résistance de structure du couvert végétal et effort de prélèvement des bouchées chez les ruminants au pâturage. Face à l’hétérogénéité de la ressource en abondance, en valeur nutritive et en répartition, les ruminants au pâturage doivent prendre des décisions complexes pour rechercher et récolter les fourrages nécessaires à leurs besoins. Certaines de ces décisions affectent la masse de la bouchée et donc, l’ajustement de l’ingestion en terme de profondeur et de surface de la bouchée, ainsi que de force de prélèvement. Ces décisions sont prises en relation avec l’hétérogénéité de la structure du couvert végétal. Nombre de relations ont été mises en évidence liant l’adaptation de la mécanique de la bouchée aux variations de la hauteur et de la densité du couvert végétal de fourrages tempérés pour des animaux de différentes tailles corporelles. En revanche, les grandes variations

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1. INTRODUCTION

The harvesting of forage is a particularly time-consuming exercise for ruminants; a large number of bites, of a relatively small bite mass, are required to meet the nutrient intake requirements for maintenance, growth and reproduction. A number of reviews have discussed the mechanisms of foraging behaviour [7, 9, 45, 50, 59, 60], including the considerable advances that have been made in understanding the influence of the independent effects of sward height and sward bulk density on the components (e.g. bite mass and bite rate) of daily herbage intake [19, 30, 38, 59]. However, despite the comprehensive information available, researchers are still unable to predict the intake responses of grazing animals to changes in the vegetation structure and morphology of more complex swards. Illius and Hodgson [41] suggested that this lack of predictive power emphasised the abundance of descriptive studies, and called for studies to actively seek a mechanistic explanation of sward-bite interactions. Descriptive and mechanistic approaches are, however, essentially intertwined due to the difficulty of clarifying the many confounding, and indeed complex sward-bite interactions.

Our aim is to focus attention on the importance of the interaction between the morphological plant organs encompassed within the bite, and biting effort, an area that has received considerably less attention, even though the effects of the distribution of plant morphological organs on the feeding strategy in ruminant species has recently been stressed [59]. The principles should have direct relevance to ruminants foraging in both temperate and tropical ecosystems.

In this paper we define sward structure and the terminology associated with the study of bite mechanics, describe the anatomy of the grass leaf with respect to severance, and highlight the potential contrasts in severance action across animals of different body mass. The inconsistency in terminology, the methodologies and their suitability for assessing bite force are identified. Evidence of the hypothesised linkage between bite depth, bite area and bite force is discussed, and lastly the idea of assessing biting effort is introduced.

2. SWARD STRUCTURE AND BITING FORCE TERMINOLOGY

Studies investigating the linkages between the structural organs and food comminution in the mouth have been reviewed [56], but there is comparatively less information on the linkages between sward structure and biting effort. Further progress
within this field calls for a review of the definitions of the terminology used in this area. Morphological changes that occur with plant maturation lead to different proportions, and relative age, of leaf, pseudostem, stem, and inflorescence in the vertical dimension of the sward [13]. The architecture of these organs within the sward canopy is termed sward structure. Sward bulk density; the weight of herbage per unit volume, increases with increasing sward depth. This pattern is more pronounced for tropical pastures than for temperate pastures [28, 67], and the slope of the relationship can also vary markedly across swards of different structure within temperate pastures [see 25]. The volume of a bite is the major contributor of intake rate, and comprises bite depth, which is the vertical distance that animals insert their muzzle into the sward, and measured as the difference between sward surface height and the residual height post-grazing, and bite area, which is the horizontal area of herbage encompassed within a single bite [38, 48]. Evidence from temperate swards shows that bite area exhibits less sensitivity to sward variation than does bite depth [12, 48, 53], although Wade and Carvalho [74] suggest that bite area is the primary parameter that animals adjust to increase bite mass.

In linking the disciplines of plant mechanics with foraging behaviour we define five plant-based terms: (i) fracture force in tension, which is a measure of herbage strength and is estimated from the maximum force that produces fracture of the plant organ/s [80]; (ii) tensile strength, which is the fracture force in tension per unit cross-sectional area of the plant specimen [80, 81]; (iii) maximum force in shear, also a measure of herbage strength and is the maximum force required to fracture the plant organ/s, and is determined from the height of the highest peak on the force displacement curve (N.B.: it does not represent the force to fracture the whole plant organ) [80]; (iv) specific work to fracture, equally known as toughness as it is measured by the energy required to shear the test specimen per unit cross-sectional area of the plant specimen [18, 80] and (v) resistance, which is the theoretical, accumulated force required for severing all of the plant organs encompassed within a bite. Two important animal-based terms are: (i) bite force, which represents the three-dimensional force applied in severing a bite (N.B.: this term does not represent the force exerted during chewing as given by Pérez-Barbería and Gordon [57]) and (ii) biting effort, which represents the power applied by the animal to sever a bite and includes components of resistance, bite force and head acceleration (N.B.: the importance of the individual components may interact with species body mass and species differences in severance action, see below SEVERANCE ACTION).

3. GRASS LEAF ANATOMY

Plants are the primary producers in most food chains, and animal subsistence and production is dependent upon them. Forages, like all plants, however, have evolved structures that resist ingestion by grazing animals (grazing resistance; [11]), as a means of ensuring their own continued existence within ecosystems.

The grass leaf anatomy responsible for protection against herbivory can be modelled as a three component system [71], consisting of sclerenchyma tissue, vascular bundles and epidermal cells covered by a protective cuticle. These components comprise the ‘fibre’ fraction, along with a matrix consisting of thin-walled parenchyma cells found in the leaf mesophyll. However, these thick-walled cells that are heavily lignified, and hence confer mechanical strength to the plant by way of attachment to chained bundles of vascular tissue only account for a small proportion of leaf cross-sectional area. Despite this, the fibre
component accounts for 90–95% of the longitudinal stiffness of grass leaves [71].

The critical disparity between the leaf anatomy of grasses from the C3 and C4 photosynthetic pathways lies in the greater number of veins, and smaller interveinal distance [62, 78], and a higher proportion of sclerenchyma [1, 78] in C4 species. These structural characteristics strengthen plant tissues [72]. In tropical ecosystems, environmental temperature increases the rate of plant growth, which increases plant strength [72], and also reduces the moisture content between the sclerenchyma fibres [72], which leads to increased herbage strength [34, 36]. Nevertheless, despite possible categorical groupings of plants, plant anatomy will vary between plant groups, genera, species and even lines within a species [77], but while some plants may be stronger in tension, fracture properties will be more dependent on the organisation of the bundles of sclerenchyma which determines brittleness [73].

Wright and Vincent [81], in their review of the mechanics of fracture in plants, discussed the three modes of crack propagation in a leaf; shear, tension and torsion, and it is the modes of shear and tension that have attracted interest from plant and animal scientists alike. Assessment of the mechanical properties of grass leaves is far from new. It has provided information for the design and improvement of the cutting mechanisms in forage harvesting machines [34, 51], and for plant breeding programmes where the primary objective is to increase forage intake [20, 36, 52], through increasing the forage’s feeding value [70]. These studies have focussed primarily on the properties of fracture in shear. The interest in relating the tensile properties of plants to aspects of foraging behaviour, particularly prehension, is of more recent origin [42, 68, 80], and has led to a clearer definition and use of tensile strength to quantify fracture properties in tension and the specific work to fracture (i.e. toughness) in shear for determining properties such as those associated with food comminution in the mouth. Henry et al. [35] contended, however, that there was a lack of evidence to support the partitioning of the fracture mechanics between prehension and chewing.

The sclerenchyma tissue content is often reported in biomechanical studies where the structural and fracture properties of plants have been extensively evaluated [73, 80]. Fracture force in tension is well correlated with the volume-fraction of sclerenchyma tissue [80] when the sclerenchyma tissue is below 15% of the volume-fraction of the leaf, and the fibres are laterally separated [71, 73]. Above 15%, the fibres can be continuous across the leaf, rendering the leaf brittle [81], and thus more susceptible to fracture since the leaf will lose a large proportion of its strength with only a very small applied force [72]. The plant properties that increase mechanical resistance, chiefly the fibre component, are essentially the same as those that reduce plant digestibility [66, 80]. However, to rely on the nutritional indices of Neutral Detergent Fibre (NDF) or Acid Detergent Fibre (ADF) to provide measures of herbage strength and resistance would be inappropriate since fracture force in tension (the maximum force that produces fracture) is poorly correlated with both NDF and ADF [80], whereas, for example, the work to fracture in shear (the area under the displacement curve) is well correlated with both NDF and ADF, as well as the lignin content of the leaf [80].

4. SEVERANCE ACTION

All ruminant species have a common dental structure that consists of four paired incisors set on the lower jaw, with a thick pad of connective tissue, also known as the dental pad, positioned on the upper jaw. The act of severance entails the incisors closing against the dental pad to grip each mouthful of herbage before fracture of
plant tissue occurs, although cattle have been observed to grip herbage against the incisors using the tongue [16].

The structural arrangement of parallel venation in grass leaves, ensures that leaves exhibit little fracture sensitivity, thus the damage at the point of incisor insertion does little to act as a concentrator of stress [72]. Wright and Vincent [81] commented that unlike small herbivores which can avoid the problems of indigestible fibres in plant tissues, by eating around them (e.g. larvae of the gum-leaf skeletoniser moth, *Uraba lugens*) or cutting the lamina with their mandibles or incisors (e.g. rabbits have upper and lower incisors), ruminants must use their strength. If strength scales with body mass [42], then how do small-bodied ruminants cope with the same constraints as large-bodied ruminants? Vincent [72] suggested that sheep (*Ovis aries*), like geese, probably use a strategy that involves creating a crease on the lamina, through pulling the lamina at an angle across the incisors, and thereby reducing the force required to create fracture. There is no known quantitative evidence for this severance action in sheep, and there is the puzzling concern, as Vincent noted, that it is difficult to create creases across multiple lamina. Cattle (*Bos taurus*), sheep and goats (*Capra hircus*) foraging on a range of swards have been observed to insert and/or move their mouth sideways into swards to gather herbage [21, 28, 61]. In these examples it is likely that animals were making use of the shearing cusps on the molars to grip and sever plant tissue [see also 63], thereby obtaining a bite mass above what would otherwise be possible.

5. QUANTIFYING BITE FORCE

The idea of measuring the mechanical resistance of plants is far from new, but the motivation, approach and reporting have varied considerably [5, 18, 22, 32, 35, 51, 52, 73, 80]. One consequence has been the number of different descriptive terms that have surfaced and these are often used interchangeably. ‘Strength’ and ‘toughness’ are both biological terms that have been adopted in quantifying plant mechanical resistance [e.g. 17, 22], possibly since they represent a physical attribute that is easily understood. There is, however, some confusion since toughness commonly implies strength. Correctly defined, toughness is a measure of the energy required to propagate a crack, and not a measure of the force involved in fracturing material [81]. This definition is crucial since it implies that toughness is an important mechanical parameter for the chewing dynamics, but not for the process of severance of plant material.

Other inconsistencies have emerged in the definition of tensile strength and the use of the term shear strength, which has no clear definition in its own right, and, therefore, varies in terms of its units of expression [e.g. 23, 69, 80 for tensile and 20, 43 for shear]. According to Wright and Vincent [81] tensile strength should be reported as the force for crack propagation per unit cross-sectional area of plant material, and consistent expression of tensile strength would greatly facilitate across-study comparisons. However, it is not always a feasible use of resources to conduct laborious estimates of tensile strength within the context of animal-based studies. Fracture force is a measure of the maximum force required to fracture a test specimen [80]. It takes no account of cross-sectional area of the plant material [80], and so has less acceptability for comparison across different plant species with contrasting tiller size-density relationships, and thus potentially contrasting lamina cross-sectional area. Fracture force measurements, however, can be carried out more quickly since they omit the additional laborious cross-sectional area measurement, and thus can provide objective information on herbage.
strength, as long as the above constraints are borne in mind.

When answering questions on the causal relationship between bite force and bite mechanics, an area of concern lies with the estimates on single, whole or separated fractions of plant organs and their relation with clumped plant material encompassed within a bite. For single tests to have direct relevance, one question of particular importance, and that does not appear to have been answered, is the potential error associated with estimates using a constant multiplier [e.g. 42]. In practical terms, it is unlikely that the bite force required for the severance of 10 leaves together will be the summation of the strength of 10 single leaves, unless a correction for the packing effect of leaves encompassed within the bite is applied. The absence of a constant multiplier would have implications for the scaling of bite force with modulations in bite area [e.g. 42, 68]. Other factors worthy of consideration are that the number of leaves able to be creased i.e. running at an angle over the incisors, would be of a magnitude lower than the total number grasped. This is of particular importance for the severance action in small ruminants [see 72]. Furthermore, it is difficult to conceive that integrating the estimates of fracture force in tension from single, separate tests of leaf, pseudostem and stem can model the predicted force for a bite encompassing two or more morphological components, unless measurements are made at a very fine level of precision (i.e. 1 cm strata), forming serious constraints for swards more applicable for testing with large-bodied animals.

Indirect assessments of bite force [42, 68] are derived from estimates of the force required to fracture plant organs in the vertical dimension. Although the contribution from Illius et al. [42] predicted bite forces indirectly from regressions based on a separate set of swards, they amassed their data from three studies, which may not be possible where time is a major constraint. Small-scale apparatus’ that provide direct, quick and reliable estimates from field conditions would aid progress. There has been some recognition of the need for the development of portable field operated devices that measure fracture force in tension [68] and tensile strength [76] in situ, providing an estimate of the magnitude of the contrast in resistance, for a given bite volume. Progress has nonetheless been slow and fraught with difficulties; Westfall et al. [76] in a short communication described a portable tensilometer with hand-operated modified pliers and an electronic recording system, and Tharmaraj [68] discussed a portable lever operated clamping apparatus mounted on a tripod frame, which expressed the peak fracture force reading (Fig. 1). However, for neither apparatus was it clear how the rate of acceleration during fracture was controlled.

Furthermore, an indirect estimate of bite force from fracturing plant organs in tension does not fully mimic the mode of the characteristic jerk action in the horizontal plane during severance. By comparison, direct quantification of the forces involved in severing herbage in grazing animals yields potentially more valuable information as biomechanical force plates [75], such as those used by Hughes et al. [40] and Laca et al. [47] record three dimensional forces (Figs. 2 and 3). Consequently, some disparity between values obtained from indirect estimates as compared with direct methodology must be expected (Griffiths and Gordon, in preparation). In the foreseeable future, such technical difficulties will become inconsequential if effort is made to partition and present the force according to the Cartesian coordinates. This is also a critical point of evaluation as animal species of contrasting body mass may allocate the force between the Cartesian coordinates differently. It is important to recognise that bite force predicted indirectly from estimates of fracture force and tensile strength, provide only a theoretical framework for
comparative purposes. These predictions also leave many unanswered questions as to the effort exerted, particularly as evidence does not suggest a 1:1 response in bite geometry with plant resistance (see below SUMMIT FORCE HYPOTHESIS).

6. BITE DEPTH AND THE LINKAGE WITH BITE AREA AND BITE FORCE

An increasing number of studies have focussed on the responses of the bite mechanics to the structural complexity and the rigidity of plant organs, but can we draw any consistency between studies and quantitatively relate the response patterns to bite force? Three hypotheses have been proposed for the regulation of bite depth penetration:

- Summit Force (6.1).
- Balancing reward against cost of bite procurement (6.2).
- Marginal Revenue (6.3).

In discussing the available evidence to support or reject the above three hypotheses we pull together studies which have provided supporting data on fracture force in tension, tensile strength and leaf toughness and/or bite force when examining the parameters of bite volume. There are relatively few studies that meet this criterion, and all of these come from the vegetative temperate forages. Only a few studies [e.g. 54, 69] have assessed tensile strength on forages in more extensive grassland environments, but these studies have not provided parallel data on bite volume. There is a need to evaluate the hypotheses for swards displaying greater structural complexity.

Figure 1. Tensile bite fracture force apparatus (from Tharmaraj [68]).
including those present in extensive grassland environments.

6.1. Summit force

The Summit Force hypothesis [37] was originally offered as an explanation for the association between bite depth and pseudostem height [8, see also 2, 3] with the rational response being one of animals being constrained by the effort required to sever pseudostem within the lower stratum. The estimated fracture force of pseudostem was later quantified [80] as approximately three times that measured for a single leaf, and arose from the complex arrangement of concentric sheaths around the immature leaves and growing points. In order to maintain consistency in bite force, the Summit Force hypothesis implied that once the limit in force had been reached, that animals

![Figure 2. Exploded view of a force plate apparatus (adapted from Webb and Clark [75] and Griffiths and Gordon, unpublished).](image-url)
Figure 3. An example of the output from a force plate apparatus for a series of 15 bites (from Griffiths and Gordon, unpublished).
would adjust bite area to maintain a constant bite force in the face of increasing strength or tiller density.

There are comparatively few reports documenting tiller, or leaf and stem strength, and tiller density on bite area. Despite this, there appears to be general consistency across studies in that the rate of reduction in bite area is much lower than the rate of increase in tiller density or tiller strength [39, 48, 53, 68]. This suggests that there is only a partial adjustment in bite area in relation to sward structure, and furthermore, the adjustment has little effect in reducing the energy required to sever a bite [79]. This partial compensation in bite area also explains, at least in part, the absence of significant patterns in sweeping tongue movements in cattle in response to decreased lamina length across swards of different structure [25]. Mitchell [53] demonstrated, using pooled data from sheep and red deer (Cervus elaphus), that bite area was only 35% greater on wheat (Triticum aestivum) swards than ryegrass (Lolium perenne) swards of identical height, despite the ryegrass swards exhibiting 110% stronger tissues (measured by shear). The reduction of bite area in an attempt to maintain the biting force momentum can thus be considered to be a small effect. This inference is supported by the few direct evaluations of biting force. Hughes and colleagues [39, 40], using boxed swards anchored to a force plate, found no supporting evidence for a maximum force that goats or sheep exerted across a range of sward arrangements within immature swards and across sward species. Similarly, cattle grazing from hand-constructed swards mounted on a force plate were not observed to exhibit a maximum force per bite [46]. Furthermore, Illius et al. [42], in a study with goats, found appreciable variation in the indirect estimates of bite force, derived by substituting the grazed heights into polynomial regression equations summarising force-canopy structure relationships, across broad- and fine-leaved plant species. More recently, Tharmaraj [68] indirectly estimated bite forces using a field-operated bite force meter and found no indication of a maximum force that cattle exerted across a range of plant species and tiller densities. The absence of a maximum bite force that animals exert, irrespective of how the bite dimensions are balanced in the face of tiller structural rigidity and bulk density constraints, does not, therefore, lend support to the Summit Force hypothesis. This is also consistent with the fact that not all leaves within the bite are severed simultaneously but rather in close succession (W.M. Griffiths and I.J. Gordon, unpublished data). In practical terms obtaining a measure of the peak bite fracture force is of little importance, and it is the average force applied for a given bite that needs to be assessed. Furthermore, rejection of the Summit Force hypothesis is supported by the consistent findings that, across a wide range of body sizes, animals do not always fully exploit the available depth of regrowth [sheep and guanacos (Lama guanicoe) [6], bison (Bison bison) [10], cattle [27, 33]].

6.2. Balancing reward against cost of bite procurement

A second hypothesis utilising economic principles described an efficient forager as one that forages to maximise, or at the very least, balance the reward against the cost of bite procurement i.e. force per bite [40]. However, as with the Summit Force hypothesis there does not appear to be any constancy in the force per bite. Hughes [39] found that sheep were more willing to increase the force exerted if the force was compensated by a greater reward, while Illius et al. [42] found that the expenditure:reward ratio for goats was not consistent across a range of plant species. More recently, Tharmaraj [68] found a fluctuating
expenditure: reward ratio across short and tall swards, but a constant ratio when swards varied in tiller density only. The calculation that the energy gain from increased penetration will always exceed the energy cost [42], implies that the greatest gain will be achieved from severance of material encompassed within the buccal cavity at the base of the sward, in the absence of uprooting. Why then, do cattle and other species, restrict their grazing depth to some fraction of sward height, even when the sward is composed solely of lamina [48]? Furthermore, goats have been found to be insensitive to the differential costs in penetration depth for broad-leaved and fine-leaved species, with the ratio between pseudostem height and grazed height changing little across the sward species [42]. It, therefore, seems likely that the avoidance of a lower stratum may be unrelated to the greater effort required by the animal to detach plant organs relative to bite reward. Rather, it may reflect the fact that encompassing pseudostem within the bite slows down bite formation, and would require additional jaw movements to chew the more fibrous material. Therefore, the animal strikes a balance between severance and chewing constraints, as discussed in the model of Spalinger and Hobbs [65] and further evaluated by Shipley and Spalinger [63]. The relationship between bite mass and chewing behaviour has also been ascribed to the need to strike a balance in the maintenance of a grazing momentum [49]. However, the importance attached to striking a balance between severance and processing may be over-emphasised since cattle are able to prehend, and manipulate the contents of existing bites, within the same jaw movement [49], effects that were assumed to be mutually exclusive in Spalinger and Hobbs’ model [65]. The overlap between prehension and chewing can be, however, incorporated into models, as shown by Farnsworth and Illius [24].

6.3. Marginal revenue

Delving deeper into the application of economic principles, a study by Illius et al. [42] marked a further attempt to understand the conceptual basis of bite depth. These authors demonstrated, using goats and a group of fine- and broad-leaved grasses, that depth of penetration into a sward could be predicted when account was taken of the marginal revenue i.e. the differential increase in bite force relative to the differential increase in energy intake rate. Despite the variation in the predicted bite forces (by indirect measures) and contrasting grazing depths, the goats grazed to a common marginal revenue, although the value of marginal revenue differed between the fine- and broad-leaved species. This hypothesis is both puzzling and plausible. Among the three fine-leaved species, there was a clear linkage between the mass of material removed and the force involved in severing those bites, but the reason for differing common marginal revenue between the fine- and broad-leaved species remains unclear. It is worth noting that had these authors examined only one plant species from each of the fine- and broad-leaved categories, an approach that would have been reasonable, their conclusion would not have held, emphasising that the marginal revenue hypothesis may not explain penetration responses across swards of greater structural complexity. Critical evaluation of the hypothesis across swards of contrasting structure and animals of different body size awaits.

To summarise, the evidence to support the three current hypotheses is weak and new initiatives are required to shed light on the determinants of bite mechanics.

7. EFFORT VS. FORCE

Increasingly it has become obvious that there is no conclusive evidence to support
any of the three key hypotheses that have been put forward as mechanisms for observed bite depth penetration responses. It may not be that we need to put forward new hypotheses, rather we need to discover new approaches of thinking the problem. Central to our understanding of biting force has been the assumption that the force applied in severance will be proportional to the strength of individual plant components, although Illius et al. [42] argued that the structural arrangement of the plant components has the greater bearing on the force exerted. Nevertheless, the implication is that severance occurs as a result of muscle moving against a fixed anchor of body mass, and the costs of severance for a given force are then lower for species of greater body mass, owing to the allometric scaling of force with body mass \( W^{0.67} \) [58]; \( W^{0.69} \) [42] using the assumption that the force generated by muscle is proportional to muscular cross-sectional area [14]. Leaf tensile strength has been found to be of greater importance in determining plant acceptability for sheep than for cattle [54], a finding that more likely reflects the constraints imposed on the smaller body mass and thus smaller potential muscular effort, rather than the suggested shorter retention time and lower digestive ability of small ruminants [54]. An intra-specific allometric relationship between body mass and grazing depth \( (M^{-0.15}) \) has been reported [31, 42], although the relationship was only present on the tall swards in the study by Gordon et al. [31]. By contrast Canigano et al. [15] did not find evidence for an intra-specific relationship between body mass and grazing depth in cattle, despite a wide contrast in body mass (256–608 kg). Furthermore, there has been consistency in bite depth for inter-species variation in body mass; cattle vs. sheep [55], sheep vs. guanacos \( (Lama guanicoe) \) [6]. Given these inconsistencies in the literature on intra- and inter-specific species depth of penetration responses we are left wondering about the real costs involved in grazing [42]. It might then be helpful to begin by thinking of the act of severing plant material as a two-step process; (i) ‘head’ resistance, which is the force required to accelerate the mass of the head in a steady momentum and (ii) ‘herbage’ resistance, the strength and architectural arrangement of the plant organs in 3D-space, with the summation of these two resistances shaping the biting effort ([53], J. Hodgson personal communication). This provides a clear distinction between biting effort and biting force.

Further, the laws of motion state that for a given force, the rate of acceleration will be greater for a small object than for a large object. Chambers et al. [16] reported the rate of head acceleration as some 65% greater for sheep than for cattle grazing the same sward. There is little quantification of the effort and associated costs incurred in upholding the tension in the muscles of the neck to maintain the head momentum, although Illius et al. [42] comment that it must be considerable. The contribution of the ‘head’ resistance to maintain a cyclic momentum for the applied effort can be predicted to be of some significance. This is despite the relatively small energy cost associated with bite severance as a result of the small displacement, although the displacement will increase with increasing number, and height, of tillers captured within the bite. If tiller length is viewed as a moment arm, the distance and angle perpendicular to the tiller, from the tiller’s rooted position to that at severance will increase with sward height and/or tensile strength, implying that displacement and acceleration are important components of biting effort. In support, Chambers et al. [16] found that the rate of head acceleration of sheep decreased with increasing sward height. However, these authors did not observe a similar pattern for cattle.

The allometric relationship between force and body mass would provide the generality that researchers seek, but as biologists and ecologists we need to recognise
the existence of many exceptions. In the only known evaluation of biting force across species body mass, Hughes [39] showed that goats (23.5 kg W) did not fully utilise their body mass ($W^{0.37}$, estimated from Tab. 5.12 and text from p. 82 [39]) to sever bites from 15 cm perennial ryegrass swards, with bite depth substantially smaller than that recorded for sheep (64 kg W) ($W^{0.64}$, estimated from Tab. 5.12 and text from p. 82 [39]). Other studies have also observed goats to exhibit a shallow penetration depth on vegetative swards [26], suggesting that goats may not exploit the force stored in their muscles for prehension. This suggests that constraints imposed by mandibular length may be a further critical parameter that needs to be corrected for in assessing biting effort. There is ample evidence that incisor breadth scales with body mass [e.g. 29, 31], and that total masseter weight, which reflects masseter tissue size, is correlated with body mass [4]. However, whilst mandibular length does scale with body mass, there appears to be no compensation between mandibular length and masseter muscle mass in ruminants, unlike in some carnivores [44]. By inference a lack of correlation between mandibular length and masseter muscle mass implies a weaker gripping force at the incisors (see also [64]) leading to increased tiller slippage during initial clamping of herbage as well as during the jerking motion of the head. This implies that, irrespective of body mass, animals with longer mandibles are likely to incur substantially reduced bite masses for the applied bite effort with increasing canopy depth. Placing this into perspective, goats have a higher mandibular length:body mass ratio than sheep (F.J. Pérez-Barbería and I.J. Gordon, unpublished data), and this may account for the observed responses by goats in the study by Hughes [39]. These additional animal-based constraints strengthen the argument that it is biting effort rather than biting force that needs to be evaluated, and therefore providing a ‘real’ measure of the constraints in handling forages rather than just a measure of the force required to fracture a given plant organ.

8. CONCLUSION

Given the importance of bite depth as a contributor to bite volume and intake rate, there remains considerable scope for understanding the mechanistic basis for bite depth regulation. Increasing evidence points towards responses in bite depth to the vertical positioning, and maturation, of the morphological organs within the sward canopy. Assessment of biting effort would represent a more holistic approach to understanding the animal’s response to sward structural complexity, and might explain why the adjustments in bite geometry have been of a smaller magnitude than the change in herbage resistance. More explicit arguments have been hampered by the limited available bite force data, much of which has been collected from swards exhibiting relatively limited variation in structural strength, and from comparisons across plant species where other physical and chemical characteristics may also vary [40, 42, 46, 68]. Despite the obvious technological difficulties in quantifying the various components of biting effort that have been described in this paper, progress on this front will remain essential to aid the development of predictive foraging models.

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Abstract — Large-scale spatial patterns, whether in the height, density, or species composition of vegetation, are one of the most demonstrable and widely recognised features of heterogeneity in large herbivore grazing systems. But to understand how their existence relates to grazing processes, and what the implications of the patterns are for plants, animals, and for land users, requires adding spatial concepts, and dynamics to our knowledge of the interactions between plants and animals. Neither approach has been traditional in agricultural research. In this paper, we provide an overview of what we propose are some of the key topics and questions that arise in attempts to understand spatial aspects of the interaction between plant growth (food resources) and animals’ behaviour. Rather than review advances in any one area in detail, we look at some basic principles of the fundamentally different ways in which animals eating from vegetation (with or without selectivity) affect the components of plant regrowth; the variance about these; the way this ‘seeds’ the creation and maintenance of heterogeneity, and most important the outcome (intake) for the animals. Likewise we outline some basic features of animals’ behaviour, given heterogeneous and so spatially distributed food, which includes the expected rates of encounter; learning and memory; and both the benefits and costs of social interactions when foraging as a group. In this way we combine knowledge from several disciplines (plant physiology; animal science; behavioural ecology and not least from practical agriculture) with a goal of providing a basis for the development of simple pragmatic means for manipulating a grazed but multipurpose landscape to balance diversity, heterogeneity and agricultural performance.

cognitive abilities / foraging costs / optimal grazing / rate of encounter / social behaviour
être les éléments clés des interactions spatiales entre les herbivores et les couverts pâturés. Nous déclinons comment différents modes de prélèvement de la végétation (sélectifs ou non) affectent la croissance des repousses, leur variabilité spatiale, les motifs d’hétérogénéité à large échelle, et les performances des animaux qui exploitent ces couverts. Ce faisant, nous soulignons les processus mis en jeu lorsque des herbivores exploitent l’hétérogénéité spatiale des couverts, en particulier le rôle des probabilités de rencontre avec les items alimentaires préférés, les mécanismes comportementaux d’apprentissage et de mémorisation, ainsi que les coûts et les bénéfices de la sociabilité sur les choix individuels. Ceci nous amène à faire appel à des compétences disciplinaires variées, relevant de l’écophysiologie végétale, de la nutrition et du comportement animal, et de l’écologie comportementale, ainsi qu’à des compétences appliquées en agronomie et élevage, afin de proposer des règles de gestion des couverts prairiaux dans un contexte de multifonctionnalité de leurs usages.

aptitudes cognitives / comportement social / coût de sélection / pâturage optimal / probabilité de rencontre

1. INTRODUCTION

There are numerous sources of heterogeneity in vegetation, to the extent it is probably more difficult to explain how vegetation can ever be homogeneous, than it is to accept its spatial complexity [27]. There may, for example, be an intrinsic heterogeneity in the soil or other resources and this may or may not interact with the distribution and propagation of plant species, and the re-distribution of resources by animals [32]. Each of these topics deserves ongoing review. But what we address here are some specific features of the creation and maintenance of heterogeneity – those induced by decisions made by herbivores about where and when to place their bites.

Even within these confines, a study of grazing is unavoidably a study of a complex system. It is spatially heterogeneous as animals both create, and respond to, variations in vegetation state. Most important, it is a dynamic system, as defoliation impacts on the rate of replacement of the vegetation. At least one of the major processes, biting, is discrete (rather than continuous) and stochastic (as there is uncertainty as to where and when animals may place their bites) [44]. There are numerous non-linearities in the biological responses. It is recognized that such features generate spatial and temporal complexity at a number of scales, and that such a system would be expected to exhibit a potentially bewildering array of phenomena, even without the vagaries of animal behaviour [33]. In physical sciences, one approach to understanding such a system would be to develop a body of theory – a framework – for how we would expect the system to behave under a succession of carefully defined circumstances, against which we could overlay the potentially complex phenomena observed in experiments and in practice, in which numerous factors may interact, and so allude to interpretations of how these phenomena arise. This is what we attempt here. In all cases we work with grazing seen as a spatial and dynamic system, but we start with some conceptually simple examples and systematically add in factors, notably those for which information from controlled experiments is available.

Complex phenomena can arise in part from simple rules operating locally and at a fine scale. We look first at what is known about the processes operating at the fine (bite) scale and consider how far we can go in explaining the origin of phenomena at larger scales, without at this stage evoking any larger scale behaviours.
Next, we review evidence for larger scale (e.g. social, flock/herd) foraging behaviours, and then discuss how these may add three major aspects to the overall understanding. First we consider information gathering (sensory knowledge and spatial memory) and discuss its adaptive value according to environment complexity. Second we consider social behaviours and how these may both help and hinder foraging success in individuals. Here we explore the probability that the very ‘rules’ for foraging (notably preference) which are the driving processes for the fine patch scale impacts, may change at different scales as animals are seen to respond to the allocation of space, and/or their proximity to group members. Third, we consider the way animals moving around the resources as an aggregated group, might alter their success in approaching the maximum marginal value for the rate of supply of resources by modifying where and when they distribute their defoliations. We parallel this with accounts derived from different rotational grazing scenarios in agriculture.

While we recognise the continuum of these impacts across the scales, we proceed systematically in an attempt to unravel the complexity of the phenomena that emerge in grazing systems. Our aim is to focus attention on those aspects of heterogeneity that might be manipulated or controlled with a view to increasing the sustainability of grasslands for alternative goals.

2. HOW FAR CAN FINE SCALE INTERACTIONS EXPLAIN THE ORIGIN OF PHENOMENA AT LARGER SCALES?

2.1. Sequential (deterministic) vs. random biting

First we use a previously published model [39, 44] to consider the impact of some fundamentally different ways in which animals might place their bites in space and time. In the first case we consider what would be the outcome if animals were to take bites in a strict sequence such that no bite sized ‘patch’ was revisited before all other patches had been eaten from. Note this would give rise to the situation where animals were at all times eating from the next largest patch in the vegetation. We contrast this with the case where we imagine animals may take bites totally at random. In all cases, we perform a full mechanistic analysis of the constraints to searching for and handling food [37, 46], such that the state of each vegetation patch determines bite mass, and the animals face the time costs of prehending and masticating each bite, which in turn affects the rate at which animals progress through the array of patches. But in these first ‘simplest’ cases, we can consider foraging with the minimal involvement of any costs of searching, as if the next bite were adjacent to the last.

The outcome of even these simple foraging examples (Fig. 1a) is revealing, as it emphasises the importance of the dynamics of vegetation (resource replacement) and the impact of foraging on the components of this. At low stocking rates, intake would be seen to be unaffected by grazing method, as intake is not constrained by vegetation state and each animal eats its ‘fill’. But at high stocking rates, animals (each and all) would appear to do better grazing spatially and temporally at random. The explanation is that stochasticity gives the vegetation a chance. Where the animals graze patches in strict sequence, each patch suffers the same defoliation (which becomes severe at high stocking rates as animals progressively reduce the overall vegetation state), and each patch is defoliated at the same (frequent) deterministic interval [38]. There is spatial heterogeneity in vegetation state, simply because animals can only bite from a small proportion of the total available patches in any one day, but there is no variance about the determinants of regrowth – the residual
patch state or regrowth duration. Even though animals would always be eating the next largest patch in the sward, a situation some have proposed as being optimal for intake \cite{51}, intake is low as there is little vegetation, so patches and bites are small. By contrast, under *random grazing*, some patches would escape grazing by sheer chance (there is now not only spatial heterogeneity but also variance in residual patch states and in regrowth duration). This gives the opportunity for more growth in those patches. Intake is greater purely because the system comes to equilibrium with a greater mean vegetation state (and so bites are larger).

Both these simple systems generate spatial heterogeneity in the sense that there would be a frequency distribution of patch states at the fine (bite) scale \cite{38}. Spatially explicit accounts of these methods for placing bites in space and time reveal that larger scale patterns can arise purely by chance under even spatially random grazing, whether it is portrayed as a Poisson process or if the animals are constrained to walking a random path. Such larger scale patterns are only transient however. But as we shall see later, these can become the focus for subsequent larger scale animal behaviours, and so could contribute to sustained vegetation patterns.

2.2. Adding preference at the fine scale

We now add to this framework what would be the effects of grazing with preference. Here we still consider the case where animals might encounter potential bites spatially and temporally at random, but now make local, state-dependent decisions whether to eat from the bite sized patches they encounter. There are numerous criteria by which animals might prefer one vegetation patch over another, but here we focus on size (density, mass or height). This highlights how, although preference is simple to conceive in a static system, it is more difficult.
to conceive dynamically. We have seen how grazing animals create a frequency distribution of patch states. All patches in this size-structured population will endeavour to regrow (move to the right in Fig. 2a). But preference rules filter this flow. Patches that are eaten will in effect be ‘thrown back’ down the size structure, to contribute to the small categories of the frequency distribution (Fig. 2b). Of the many simple state-based preference rules we tested [38], one in particular was seen to have a very deleterious impact – a partial rejection of ‘tall’ (relative preference for short). It was shown [44] with a simple dynamic model of this mechanism, that where there is a high probability of tall patches being eaten, a skewed but unimodal frequency distribution of patch states results (Fig. 2c). However, where there is a low probability of tall patches being eaten (a stronger stochastic rejection of tall) a bimodal frequency distribution of patch states emerges (Fig. 2d). This form of patch selection can lead dynamically to considerable reductions in intake, and so foraging success (dotted lines Fig. 1a). When animals partially reject tall, the mean state of the vegetation (even at high stocking rates) is larger, but intake by animals is reduced as they eat preferentially from the population of smaller patches. Intake is therefore reduced even at low stocking rates, where it would otherwise not have been constrained by vegetation. Bi-modal frequency distributions have been widely reported in field experiments [23].

Figure 2. Diagram to convey the impact in a dynamic context of stochastic preference ‘rules’ (here a partial rejection of tall) on the frequency distribution of patch states, and the possibility of the emergence of sustained markedly bi-modal distributions that could ‘seed’ larger scale patterns in heterogeneity. According to [38], using the same spatial model [44] as in Figure 1.
A bimodal frequency distribution of bite scale patch states will clearly be a powerful force to ‘seed’ spatial patterns at larger scales should there be other state-dependent processes that cause the subsets (e.g. tall and short) of the frequency distribution to become aggregated in space [5, 32].

2.3. Moving up a scale: adding foraging (search) costs

So far, we have considered the dynamic consequences of how animals place their bites in space and time, without considering the additional time costs of searching (to be precise, where search costs are less than handling costs and these are deemed to overlap, so there are no additional search costs for foraging) [37, 44].

Grazing selectively can, however, substantially increase the costs of foraging ([48] and Fig. 3). Costs increase as animals pass by less desirable items (‘lost opportunity’), in effect travelling further per unit preferred food. Grazing selectively is shown in Figure 3 to increase foraging costs in two ways. First, costs increase substantially with the degree of selectivity, and second, costs increase substantially if the preferred food is less abundant in the vegetation. Both are intuitive, though the scale of the increase is perhaps surprising. Grazing selectively may clearly create spatial heterogeneity, both at a fine scale and as a larger scale pattern, but it is important to consider next how the potential size of foraging costs might limit animals desire to graze selectively in the first place.

We can consider the expected feedback of search costs on animals desire to forage selectively by modelling the optimal solutions for trading off the benefits of eating a given diet component, against the costs of selecting for it, under different circumstances (for details see [48]). Optimising the cost-benefits of foraging, and a desire

![Figure 3](#)
for a mixed diet [36, 41] predict complex selective foraging phenomena. Figure 4a describes how the optimal proportion of preferred food in the diet should vary with the proportion (abundance by cover) of the preferred food in the vegetation. The model suggests that, if the searching costs are negligible, the animal would be expected to extract always its preferred diet (in this case presumed to be 70% of the preferred food). If search costs were very high, the animal would be expected to eat whatever was in front of it. With intermediate costs, seemingly complex behaviours would be anticipated, with animals sustaining their preferred diet while the composition of the vegetation is close to that mixture, but in situations where the abundance of the preferred food in the vegetation is lower, animals would be expected to progressively forego preference. In some cases, e.g. when the cost structure is very high, then at low abundance of preferred food, animals should resort again to eating whatever was in front of them. Experimental studies of the effects of the relative abundance of alternative foods, on selectivity, confirm these predictions in grassland [17].

3. INFORMATION GATHERING: ANIMAL RESPONSES TO POTENTIALLY PROHIBITIVE COSTS

Foraging (search) costs are modified by the way food is distributed (dispersed or aggregated) and the extent to which animals are able to exploit this opportunity spatially. It is well established that animals (including domestic herbivores) can use sensory cues (sight or smell) to detect food items at a distance; can form flexible, even abstract, associations between food appearance and its value [6, 19] and so learn, and use spatial memory [15, 18] to aid foraging. This, clearly and intuitively, can help them reduce foraging costs, though it is not a simple task to analyse to what extent, and under what circumstances, the benefits prevail.

3.1. ‘Theory’ for how spatial distribution per se affects rate of encounter

We can argue from the basis of probabilities alone that, if the distribution of preferred food is approaching random at a fine scale (or the distribution is for any reason cryptic), then for any level of abundance, the potential search costs for grazing selectively would be greatest. There would be little animals could do other than to respond, as in the examples above, by making very local decisions, trading off the benefits of being selective against the potentially high costs.

However, food may be distributed in patches (aggregated). To consider how this would intrinsically affect animals’ expectation of finding the preferred food, we can start by imagining a situation where the same amount of food is distributed in one case in a large number of small patches, whereas in a second case, it is distributed in a small number of correspondingly larger ones. Let us assume the density of food within the patches is the same and that there is therefore the same abundance (by cover) in the area to be searched. We can consider what problems the animals face, and their expected encounter with preferred food, from the well-established theory behind vegetation sampling techniques [29]. Totally random point sampling would clearly give an identical level of success in finding preferred food in both cases. But this is not the way ground-based animals can sample as they are constrained to walking a path. If animals were to sample only locally along a path (e.g. as with random line transects, or a random walk), then when food is distributed patchily, the expected rate of encounter with the patches is far greater where there are more smaller patches than with fewer larger ones. However,
this would be compensated for in that more food is found in each larger patch and so the expected rate of encounter with preferred *food* (as opposed to with *patches*) could be the same (though patch shape has some impact). There would however be greater variance about the rate of encounter with food when it is in fewer larger patches, with longer periods with no preferred food followed by longer periods with preferred food.

If animals were to search along a path but with a wider field of view, and were drawn toward any preferred food item within that, they would be sampling in effect, as if using contiguous ‘quadrats’ and their success would relate more to the ‘frequency’ and not the ‘cover’ of preferred items [29]. This sampling approach implies that for any given level of abundance (by cover), the probability of encountering a patch will depend on the size of the field of view relative to the ‘grain’ of the pattern of aggregation. There would be an optimal size field of view (cf. ‘quadrat’ size) which maximizes the rate of encounter with *patches* for each level of aggregation [29]. The probability of encountering *patches* would be far greater (in some cases approaching certainty) where the same amount of food is distributed in many small patches.

### 3.2. Learning and spatial memory

Where the distribution of food items is not detectable at a distance (e.g. when no visual or olfactory cues are available for locating them), learning and spatial memory become potentially more valuable. To study the use of learning and spatial memory by herbivores, and so the impact on animals of aggregated patterns of food distribution, experiments and models have been used in which preferred food is for example offered

![Figure 4](image.png)

**Figure 4.** (a) The complex effects of partial preference, and of low, medium, and high (specific) foraging costs on the proportion of preferred food in the diet, in relation to its abundance in the vegetation, as predicted by a model that seeks the optimal trade-off between the benefits and costs of foraging selectively [48]. (b) Data from a range of sources show the effect of aggregated (solid symbol) and dispersed (open symbol) spatial distributions of food are consistent with differences in foraging costs [17]. It is assumed that the preferred diet is a mixture in (a) of 70% and in (b) of 76% of the preferred species.
in bowls in an arena [18] or hidden within a pasture [15], or herbage species are planted in patches mown to look like surrounding vegetation [16]. The layout of one such experiment is shown in Figure 5a. When naïve animals are released into this arena, the results show a marked increase over time in the success of the animals in finding the preferred (pellet) food (Fig. 5b), typically demonstrating the capacity for learning and spatial memory, as the animals subsequently move more directly to and between the aggregated preferred areas [15]. It is notable animals did better, both initially, and even after learning, when the area to be exploited was smaller (as in this design, the overall density of the preferred food was simultaneously greater).

Independently manipulating the many aspects of the complexity of the environment in which animals forage, in experiments, would be prohibitively exhaustive. But following this experiment, Dumont and Hill [14] constructed an individual-based model to explore the adaptive value of spatial memory in relation to environmental complexity (e.g. plot size, and consequent overall density of the preferred food) using experimental data to calibrate the parameters of sheep searching behaviour. Comparison of
the real system behaviour and of model predictions was successful for both the visual features of animal movement paths and for the main model outputs, i.e. the simulated data were within the 95% confidence interval of real data. Some examples are shown in Figure 5c, which portrays the effects of manipulating the memory capacity of the animals (reducing or increasing by 20%, 40%, 60%, 80% and 100% the memory size and memory persistence parameters in the model) within a range of plot sizes.

This confirms, first, that when the area to be searched is small, animals should be more successful (both initially and after several days learning) in finding the preferred food, but adds that variations in memory capacity will have relatively small effect (the number of bowls visited in 30 minutes, after several days learning, differed little with major changes in memory capacity). Second, the benefits of spatial memory were greatest in intermediate-sized plots, foraging success increasing by 22–25 bowls with memory capacity. In the largest plot size considered, increasing memory capacity had less effect (only 11 extra bowls found) suggesting there is an upper limit to the benefits of using spatial memory in herbivores.

3.3. Area-concentrated searching within patches

Whatever means animals use to increase their chances of finding a food patch, or even if they encounter one by pure chance, it is recognized that animals can concentrate foraging within a preferred food patch, once any part of that patch has been found. This is achieved by increasing the rate of turning, to remain within the locality [16, 50, 53]. It can be shown easily (e.g. by taking simple transects across patches drawn on graph paper), that area-concentrated foraging should increase foraging success many-fold, compared to where the foraging path within a patch is not altered. More elegantly, Benhamou [8] determined the theoretical efficiency of area-concentrated searching using computer simulation. The model simulated searching with high sinuosity and low speed within high resource density areas, but low sinuosity and high speed between these areas. Tested in habitats having the same mean overall density, the efficiency of this movement control was higher in coarse-grained (a few large patches) than in fine-grained habitats (more smaller patches) and increased also with intra-patch resource density. Depending on the habitat, an animal exhibiting optimal spatial memory-based area-concentrated searching behaviour was able to harvest three to five times more food items than if it did not exhibit any area-concentrated searching behaviour but moved in a straight line with an optimal constant speed [9].

3.4. How well do animals exploit these abilities?

We can now return to the issue of heterogeneity and the prospects offered by these sensory behaviours to reduce foraging costs. Data from a range of studies, in which food was distributed in different ways, and at different abundances, are plotted together in Figure 4b, which shows animals (large herbivores grazing a range of vegetations) are more successful in selecting preferred food where it is more aggregated [17]. Relating this to the theoretical responses to different overall costs of foraging (Fig. 4a), the data suggest this is consistent with the aggregated food leading to lower foraging costs. But the benefits of foraging in patchy environments seen in such studies are not always as great, perhaps, as would be expected. In this context, we feel it would be of value if more studies of the foraging success of herbivores in different (patchy) environments, compared the observed results with some expectation of success (e.g. the expected encounter with patches if animals foraged without
knowledge; if they foraged close to random; or assessed how the outcome would be expected to increase from area concentrated foraging). Below, we discuss some possible reasons why, despite proven abilities in learning and spatial memory, animals may yet, in some cases, exhibit a foraging success closer to that expected by random.

Any increase in knowledge about food distribution offers animals the opportunity to devise travelling strategies to minimize the searching time costs of moving between patches of preferred food. But, even with total knowledge of the area to be grazed and of the location of all preferred food patches, it becomes progressively more difficult to exploit this knowledge as the number of these increases. Seeking minimum distance travel paths between patches poses complex ‘travelling salesman’ problems. Detailed analyses of the search paths observed in experiments are necessary to confirm if animals are responding to heterogeneity in an intelligent fashion, or opting to graze closer to at random.

Another reason for the distribution of animals eating not matching the distribution of food at any instant is that in situations where animals revisit areas of vegetation frequently, they may instead be responding more to the spatial patterns in the rate of replacement of resources. Spatially this alludes to there being an ‘ideal free distribution’ [22]. Some notable foraging experiments and models test ‘against’ some of the theories for the expected distribution of animals in a dynamic resource environment [20, 21]. Several of these emphasise how the expected outcome of foraging, in a dynamic system, is distinctly different from that in a static one, and how foraging may match, or both increase and decrease, heterogeneity in the vegetation [1]. But, a third explanation is that social interactions between animals can create motivation conflicts that can reduce (as well as enhance) foraging success.

4. FORAGING AS A GROUP AND ITS EFFECTS ON THE FORAGING OF INDIVIDUALS

Many large herbivore species forage in groups (flocks or herds), itself a recognition, in part, of the impacts of aggregating the distribution of food (themselves, as prey) on the expectations and foraging costs of their predators [28]. Herbivores have been domesticated more to enhance, rather than remove, the evolved flocking and associated anti-predatory (e.g. vigilance) behaviours, many being managed using wolf-like predators. When sheep are made to graze in only small groups (e.g. below five) grazing time per day decreases [40] and vigilance postures increase [13].

4.1. Costs and benefits of foraging within a group

Social behaviours can be both beneficial and detrimental to individual (and arguably even group) foraging success. Animals foraging within a group benefit from the feeding sites (e.g. preferred patches) discovered by other members of the group and from shared vigilance, but they can face the negative effects of intra-specific competition for food within the food patches. Even with perfect knowledge about food distribution, herbivores always run the risk of returning to a patch that has been largely depleted by other animals of the group. Sociability thus adds uncertainty in animal’s expectations of patch value and potentially increases foraging costs [25]. The way animals would be expected to optimise the trade-offs between ‘cooperation’ and competition has been considered for a number of species, using game theory [34], and social foraging theory has been established around this [24]. Several models have looked at the impact of these interactions on the expected distribution of grazing herbivores [7, 14].

Hence, group behaviour can impose motivation conflicts, as animals from socially
stable groups are very reluctant to graze away from their peers. This has been shown in intensive grasslands. Sheep were allowed to forage in a long narrow grass field which contained an area of preferred food (taller patch) at a distance of either 15 or 50 m from where, at the end of the field, there was a small sealed paddock containing a group of their social peers [13]. At 15 m, the tendency to eat from the preferred patch was unaffected whether animals grazed alone or in small groups. But their results suggest that a sheep is very reluctant to graze the preferred patch when it is located further away (50 m in their experiment, this critical distance varying with sheep breed) unless it is accompanied by several other peers, and even then (in groups as great as 7) time spent grazing the preferred patch was depressed.

Dumont and Hill [14] modelled that in an unfamiliar and complex environment, where the cost of finding preferred food items is high, the foraging success of an animal decreased together with the increase in conspecific attraction within the group, and this was for two reasons. First, ewes were frequently attracted by peers feeding on previously discovered sites and therefore missed the opportunity to discover new feeding sites. Second, animals faced the effects of feeding competition for a preferred and rare resource on sites. Their efficiency (in g of pellets consumed per minute of searching) therefore decreased with increasing social attraction index, while in the same time the number of bowls visited per minute increased.

Conversely, when animals are aware of food location and when food is not limiting, social bonds within a group can favour patch and habitat selection. Boissy and Dumont [11] observed the behaviour of ewes in their motivation conflict procedure with animals being familiar (reared together from the young age) or non familiar to them. The ewes with familiar companions more easily split from the paddock containing a group of peers to graze the preferred patch located away, vocalised less and were less vigilant than those with unfamiliar animals. Differences in the strength of social bonds within a flock are thus likely to affect the formation of subgroups and the way herbivores forage in patchy grasslands. Similarly, under more extensive conditions, cattle from the same herd share the use of a common home range, which is very similar to that of their mothers [26].

A third way in which social interactions may reduce foraging success is that competition with peers can encourage animals to leave a current patch prematurely. Likewise, a remaining animal may leave a rewarding patch to follow its group mates. It is well recognized that herbivores should leave patches before exploiting all the food these patches contain (this is a central tenet of the Marginal Value Theorem [12] discussed later) and there is a theoretical optimal time to leave a patch, which is modified by the time spent reaching the patch [47]. Social factors also alter patch residence times [24]. It has been proposed that, according to the departure criterion (intake rate falling below a threshold value or duration without finding a food item) and to the number of foragers that are likely to take this patch leaving decision (anyone or only a leader decides), living in a group can be either beneficial, neutral or detrimental to individual foraging success in this regard [42]. If grazing herbivores use a departure criterion based on an intake rate threshold, it has been proposed that foraging for patchily distributed food, as a group, would cause a reduction in food intake rate compared to as a solitary forager [52]. Any tendency for group foragers to leave rewarding patches prematurely would readily explain why the foraging success of herbivores in patchy environments falls short of what would be expected if they fully exploited their abilities in area-concentrated foraging.
4.2. Scaling issues: preferences may change with scale due to social interaction

One problem in interpreting the behaviour of animals foraging as a group, as a means to understanding how animal behaviour interacts with the vegetation, is that the phenomena may be dependent on scale (Fig. 6). At small scales (relative to natural range and herd size), animals may be comfortable and sense their preferred inter-animal distances are satisfied, while distributing themselves even randomly across the entire vegetation area, with consequently widely distributed impacts on the vegetation pattern. That is, at small scales, the desire for grouping may have no different impact on foraging success and vegetation dynamics than if animals forage independently. At larger scales, animals satisfying a desire for the same inter-animal distances would appear to be aggregated in their distribution (Fig. 6a). On a homogeneous sward, Sibbald et al. [45] measured the effects of space allowance on the grazing behaviour and spacing of groups of ten Scottish Blackface ewes. At space allowance from 50 to 133 m² per head, there were no significant differences between mean observed inter-animal distances and those expected by chance (i.e. there was no grouping pattern), but observed values were lower than expected values at 200 m² per head. In very heterogeneous environments, herds [30] and flocks [4] may split into subgroups, according to the size and distribution of vegetation patches.

What matters more, for the interaction of animals and vegetation, is whether the act of forming a group, or questions of space allocation, alter the very rules, at the fine scale, by which animals graze. The fact that animals might move around an area, foraging as a group, should not be seen as synonymous with them having an obvious

Figure 6. A speculative graph (b) on how fine scale foraging rules might be anticipated to change with scale by evoking social foraging behaviours. Preference may be constrained when animals graze as an enforced group (dotted line), or when grazing as a social group (fall-off at large scales), as shown in (a).
effect on the large scale spatial heterogeneity in the vegetation, nor on the fine scale heterogeneity. If the group of say 5 moves at random, and revisits areas on a fairly short time scale (e.g. where stocking rate is high), it is unlikely their impacts would be distinguishable from that of 5 individuals each moving at random. The group may act like a ‘meta-animal’. If the group grazed with the same fine scale rules as individuals, the outcome would be the same, and as seen in Figure 1.

But fine scale foraging rules might be anticipated to change with scale as indicated in Figure 6b. Such a graph is, we feel, an essential component for a foraging model (either as an input or preferably an emergent property) that aims to analyse heterogeneity and its impacts across a range of scales. But such an analysis is rarely presented, and is largely speculative here. The axis of ‘space allocation’ should be seen perhaps only as a surrogate for the extent to which various social behaviours are evoked. We propose that foraging efficiency (the apparent selection of preferred items) might decline at large spatial scales as a combination of environmental complexity and the constraints of group foraging limit the foraging success of individuals (as we have discussed earlier). What we add is that individuals’ foraging success might also be expected to decline when animals are forced into groups at very small spatial allocations. Consistently, increasing the instantaneous stocking rate from 50 to 150 ewes per ha and per day in an oak coppice where the availability of the preferred herbaceous layer was low resulted (for a same overall high stocking rate) in an increase of browse consumption by the ewes [31]. What is critical here is that not all animals are equal. Social groups impose constraints on subordinate individuals. In grazing red deer, for example, the subordinates do not have access to preferred patches [2] are less synchronised with the dominants [10] and have a lower biting rate when near the dominants [49]. Similar hierarchical social relationships may, for example, be expected to reduce the foraging efficiency of subordinate members of groups of domestic herbivores at the high stocking densities in each successive paddock in a rotational grazing system.

5. TO WHAT EXTENT DO ANIMALS COME CLOSE TO ACHIEVING THE OPTIMAL SOLUTION?

One final consideration about the consequences of how animals place their bites in space and time, is to ask to what extent animals moving as individuals, or as a group, come close to achieving the optimal solution for repeatedly harvesting the vegetation.

5.1. Optimal foraging modelled at the bite scale

Although the Marginal Value Theorem [12] elegantly describes the optimal means to exploit a succession of patches of vegetation, it is very difficult to conceive and apply in grazing systems where the vegetation is spatially more continuous (albeit heterogeneous), where grazing and regrowth are at a field scale simultaneous, and where patches may be frequently revisited, so that the rate of replacement of resources becomes paramount [3]. However, the optimal solutions can be perceived readily, even under continuous grazing, again by working at the fine (bite) scale [35]. Using the same, previously published models of bite scale foraging [39, 44], we can recognise that individual bites are discrete, assumed instantaneous, events and so generate a regrowth pattern specific to each and every bite taken. Just two of numerous possible examples are shown in Figure 7. The shape of the regrowth curve, and the amount that may be harvested subsequently, depends uniquely on the initial patch state (residual
after the previous bite), and the duration of regrowth in each case [35]. These are then two fundamental determinants of the rate of replacement of resources. For any initial patch state, (and any ensuing growth curve) we can identify an optimum timing for harvest, which will achieve the maximum average rate of yield. This (the maximal marginal value) is shown as the tangents from \( W_i \) to the growth curves in Figure 7. In Figure 8 (solid lines) we plot the optimal solutions for all possible initial (residual) patch states (x axis), in terms of the optimal defoliation interval that is required and the maximum sustainable yield that each combination of residual patch states, and defoliation intervals would achieve (for full details see [35, 39]).

To understand the impact of the fundamentally different ways in which animals may place their bites in space and time, we can now translate the contrasting animal foraging behaviours into the components of regrowth (the residual patch states and defoliation intervals) that these would give rise to (the emergent properties), and we can relate these to what would be the optimal solutions. Most important, we consider not just the mean values but the variance about these because achieving the optimal solutions would require that all patches are defoliated identically – a deterministic solution which is achievable only by uniform cutting [38].

5.2. Model outputs in the different grazing scenarios

The modelling predicts that grazing sequentially or at random, whether as individuals or a group, would lead to combinations of residual patch states and defoliation intervals that are clearly suboptimal (Fig. 8a). At low stocking rates, patches are grazed too leniently, and defoliation intervals are too long to approach optimal regrowth.
rates. At higher stocking rates, although residual patch states decline, so too do defoliation intervals. The sustainable yields fall short of the optimum possible, not only because the combinations of the components of regrowth are inappropriate, but also because under random grazing, there is variance about these components. Note that in the examples so far, the animals are at all times free to move around the whole area at will, motivated by attempting to meet intake demand.

Next, we consider the case where animals move around the area as a group, but where their rate of movement is regulated (e.g. by management with subdivision or fencing). In this way we impishly relate the expectations for social foraging behaviour to what is more widely observed in agriculture – rotational grazing. Grazing as a rotation, the models propose, comes considerably closer to the optimal solutions for exploiting resource replacement (Fig. 8b). This is because constraining the movement of the animals allows control over at least one of the two major components of regrowth. This means that it is now possible, e.g. at high stocking rates, to combine low residual

![Figure 8](image-url)

**Figure 8.** The effect of residual patch state on the maximum sustainable yield that may be achieved and the defoliation interval required to achieve this (solid lines) as predicted by a model that seeks optimal solution for all combination of residual patch state and the timing of harvest. In (a) we show the combinations of residual patch state and defoliation intervals that emerge (separate point for each of a range of stocking rates) when animals are assumed to graze patches either at random (solid dots), or in strict sequence (open circles) and in (b) the same for rotational grazing (open symbols, 30 days with animals not present: 1 day grazing) compared to continuous grazing (solid symbols), all as in Figure 1. Arrows show the direction of increasing stocking rate. According to [35].
patch states (severe defoliation) with long intervals between defoliation. Note, many defoliation intervals in a rotation are less than one day. What matters more to plant regrowth, however, is there is one interval (e.g. here 30 days) that has been imposed, which allows close to optimal resource replacement.

Finally, we combine all the impacts, some probable social changes in foraging rules with scale, and the concepts of exploiting the rate of replacement of resources, in a dynamic context, using the same models, in Figure 1b. Where animals graze as an enforced group, and where social behaviours modify their capability to graze selectively (e.g. at high stock densities in a rotation, selectivity is depressed in some if not all animals), foraging success per ha (and clearly per animal) is greatest and close to the maximum sustainable. The model runs, here, clearly demonstrate there is an optimal time to leave a patch (this is a simple extension of the MVT which includes resource replacement). However an animal moving through the vegetation intent on meeting its daily demand for intake, may fail to realise the maximum sustainable rate of yield. In this analysis, each and every animal would do better, in the longer term, to constrain its movements to optimise resource replacement. Presumably individual animals do not do this for fear their longer-term vision would be exploited by those who are more opportunists [24]. Clearly animals are not motivated by feeding alone and the social interactions necessary to ensure fitness and survival of individuals might mitigate against achieving the optimal solution for the whole group.

6. CONCLUSION

Although one of the most notable features of heterogeneity is what we regard (as humans) as large scale pattern, the challenge for us is to understand how such pattern could arise in the first place, and in any case, what heterogeneity means to foraging success and vegetation dynamics. The most satisfying explanations, we propose, are those that can generate pattern from an initially homogeneous state. The grazing processes described here will achieve this, though some spatially localising behaviours are necessary to aggregate the (e.g. tall or short, or species) components of the frequency distributions into large patches in space. As a final note, we cannot overemphasise how many sources of heterogeneity may yet be pre-determined e.g. by variations in soil quality; dung or urine return, or due to the nature of the mechanism of dispersal of plant species and their biotic interaction with soil [32]. Complex spatial and temporal phenomena can certainly arise from such vegetation interactions alone [43].

Given this complexity it is probable that only by combining models with carefully focussed experimentation, will we satisfy the desire to understand the role of heterogeneity and grazing processes in ecosystem function. Such work would need foremost to address issues of spatial scale. Analyses of the growth of vegetation resources in grassland are soundly based in the physiology and morphology of individual plants but have tended to be modelled as a continuous, deterministic process, as if homogeneous, at the field scale. This is in marked contrast to advances in animal foraging science and behavioural ecology which are predominantly individual based, where foraging is perceived at the bite (prey or patch) scale and considers the (stochastic) expectation of success of finding food. This disparity in scales can lead to substantial imbalance in models and discrete, stochastic, spatial accounts can give critically different predictions, e.g. of carrying capacity and stability, from conventional continuous, deterministic, homogeneous ones [39]. But we propose it is not only important to
address plant animal interactions at the same scale, but to seek ‘rules’ across a range of scales (e.g. in Fig. 6). Emphasis on individual based concepts must not, of course, overlook group foraging theory [24].

Major advances in combining vegetation and animal behaviour have been made recently, but one component of the system is substantially overlooked – that of human intervention in response to risk and uncertainty, and a confusion of regulatory, emotive and socio-economic goals. The models above are essential for understanding the biophysical system, but the challenge is then to capture these insights and rationalise them to a scale and level of detail that is more appropriate for tools for managing the complexity of grassland ecosystems, and sufficiently balanced to be able to seek optimal solutions for achieving the human, as much as the animals, multiple goals.

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Grazing and pasture management for biodiversity benefit

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Abstract — The primary role of grazing animals in grassland biodiversity management is maintenance and enhancement of sward structural heterogeneity, and thus botanical and faunal diversity, by selective defoliation due to dietary choices, treading, nutrient cycling and propagule dispersal. Most research on dietary choices uses model systems that require considerable extrapolation to more complex communities. Grazing animals’ diets are constrained by temporal and spatial changes in sward structure, plant defence mechanisms, herbage availability, plant phenology and animal physiological state. Potentially, these could be exploited to manipulate choice in diverse communities. Dietary choice differs between animal species, driven by factors such as body size, digestive physiology and dental anatomy. There is anecdotal evidence for breed differences but little experimentation, with genetic effects often confounded with background experience. There is information about landscape-scale breed and background effects but little about parameters such as bite and feeding station areas that allow reconstruction of the development of small-scale sward patchiness. An experiment at five European sites is examining breed effects on grazing behaviour, structural, floral and faunal diversity, animal production and economic impacts. In another project, calves are being reared by their own mothers or by cows of another breed allowing genetic effects on grazing behaviour to be separated from effects of early experience. ‘Designer animals’ may be needed to deliver desired grazing behaviour and biodiversity outcomes, either by breeding or by the use of training and previous experience to manipulate choices. Application of research results requires consideration of conservation goals, whether at landscape, habitat, plant community or plant species level. There is a need to replace stocking rate prescriptions with sward-based methods and to integrate biodiversity goals into intensive systems. Major gaps in our knowledge of grazing behaviour and its impact on biodiversity remain, necessitating greater integration of plant ecophysiology, plant community ecology and animal behavioural ecology research.

grazing / biodiversity / pasture management / dietary choices / animal type

pâturage / biodiversité / conduite de la prairie / choix alimentaires / type d’animal

1. INTRODUCTION

In this paper, we review the role of the grazing animal in the management of grasslands for biodiversity, and the mechanisms by which this role occurs. We identify some of the gaps in our knowledge and describe experiments at the Institute of Grassland and Environmental Research, North Wyke (UK) that are attempting to fill some of these gaps. We consider the goals of biodiversity management and some of the important current issues. In the light of these goals, we consider some of the potential management tools that may assist grazing managers to enhance biodiversity.

If we are to exploit current knowledge and to take sensible directions in applied research, it is necessary to consider the goals of our conservation management. To some extent, this is an issue of scale. The goal might be to manage for a cultural landscape, that is not just the physical features of the landscape but also the human aspects.
For example, the species and breed of animal employed might be chosen to reflect traditional local practices. The possibility that this might compromise biodiversity outcomes per se need to be considered. Another goal might be to manage at the habitat level over several different plant communities or at the community level. Alternatively, interest may centre on rare or emblematic species or on the fauna rather than the flora. These scenarios may require very different grazing management practices.

Having established the goals, there is also a need to consider some of the current issues in the management of grasslands for biodiversity. One of these is the need to move away from crude, though easily implemented, management methods such as stocking rates prescriptions on which many current agri-environment schemes are based, to sward based management guidelines such as sward height or sward height distribution [5]. Another pressing issue is to obtain reliable evidence about animal breed and background effects as many current management prescriptions rely heavily on anecdotal evidence. There is also a need to integrate biodiversity goals into intensive systems. Currently, many of our agri-environment schemes are aimed at farmers in marginal areas rather than at, for example the intensive dairy farmer.

2. THE ROLE OF THE GRAZING ANIMAL

Most temperate grasslands require periodic defoliation to control succession, if they are not to succeed to scrub and ultimately woodland. Except on very steep or uneven ground, it is usually possible to achieve this defoliation by mechanical harvesting of the herbage. Indeed some communities such as hay meadows have evolved in response to such management. However, the grazing animal has a unique role to play. This is to maintain and enhance structural heterogeneity of the sward canopy, which in turn has a vital influence on floral and faunal diversity.

3. MECHANISMS FOR CREATING HETEROGENEITY IN GRAZED SWARDS

Probably the most important mechanism by which grazing animals create sward heterogeneity is selective defoliation as a result of dietary choices both between species and between plant parts within species. This alters the competitive advantage between plant species both by direct removal of phytomass and by altering the light environment and competition for soil nutrients [3]. A second mechanism is treading which opens up regeneration niches for gap-colonising species. A third mechanism is nutrient cycling. This has the effect of concentrating nutrients into ‘hot spots’ at dung and urine patches and again may alter the competitive advantage between species, both directly and by feedback effects on dietary choice and thus on heterogeneity, as cattle in particular will not graze near dung patches. Grazing animals also have a role in propagule dispersal. This may be either endozoochorous (i.e. by seeds passing through the animal’s digestive system) or exozoochorous (i.e. by seeds attaching to the animal’s coat) dispersal but we particularly stress the role of the endozoochorous route as the mower can also effectively distribute many exozoochorous species. For a more comprehensive review of plant responses to grazing see [2].

The direct effects of grazing on sward canopy structure and the plant community lead to secondary effects on faunal diversity both by changing the abundance of food plants and by providing breeding sites. The direct effects on invertebrate diversity feed through to vertebrate diversity (e.g. [20]). Another secondary effect of the changes in...
structure and community brought about by grazing is the feedback on the grazing behaviour of the animals by changing the choices available to them.

4. DIETARY CHOICES

Since much of the system is driven by the animal’s dietary choices (both between species and between potential feeding stations), it is important to understand the mechanisms driving these choices. It should be stressed that most of our knowledge is derived from simple model systems, such as perennial ryegrass-white clover and that there has been relatively little detailed work in more complex communities, at least in temperate lowland environments.

Generally, behavioural ecologists have assumed that the animal is striving to optimise its evolutionary fitness. In the context of foraging, rate of energy intake has usually been taken as a surrogate measure for evolutionary fitness [18]. However, in many situations animals appear to behave sub-optimally. For example, grazed grass has a carbon/nitrogen ratio too low to be optimal for the animal’s requirements but both cattle and sheep offered a free choice with minimal physical constraints consistently chose a diet containing around 70% clover, with an even lower C/N ratio [17]. Furthermore, the mixed diet is not due to intake rate maximisation since in this case animals would choose 100% clover as this species can be eaten faster [17]. This suggests that rate of energy intake is not the currency that the animal is optimising, and that the true currency remains to be identified. To optimise fitness the animal has to trade-off many currencies, for example nutrient intake with predation risk and these trade-offs are not fully understood [17]. These limitations to our knowledge make it difficult to extrapolate from our simple model systems to the more complex swards of interest to biodiversity managers.

In discussing dietary choices, many people, particularly those working in conservation management use the term ‘palatability’ as a plant descriptor. Unfortunately, the term has been so misused as to have become almost meaningless. Palatability refers to the acceptability to an animal of a food based purely upon organoleptic properties independent of post-ingestive consequences. Animals can learn to associate post-ingestive consequences (for example toxicity) with the taste of a food and subsequently use taste as a cue to avoid this food but there are relatively few examples of choices being made solely on organoleptic grounds. Palatability is primarily an animal not a food characteristic as there are many situations in which an animal’s food choice is altered even though the foods themselves remain unchanged. We therefore recommend that the term is not used as a food descriptor and suggest that it is of little use in understanding the basis of dietary choices (for a fuller discussion see [14]).

It is more useful when describing food choices to regard the animal as having a potential intake but being constrained by various factors, including those inherent to the food. When grazing there are important physical constraints on intake and therefore on the choices between plants with different levels of these constraints. These constraints include sward structure (sward height, leafiness, tiller density and horizontal patchiness) and plant physical defence mechanisms (for review see [15]). This latter may be a driving force in patch formation in some situations, for example, the animals may avoid an area around Cirsium sp.

Dietary choice changes over time at all scales. This is due to the availability of herbage, phenology of the plant and the physiological state of the animal. An example of a relatively short-term temporal effect is the change in preference between grass and clover that has been observed over the day. Both dairy cows and sheep include
more clover in the diet in the morning and more grass in the evening [16]. It has been speculated that this might be either due to higher sugar levels in the grass at this time [11] and hence higher digestibility or, alternatively, it may be because the animal fills its rumen with relatively slowly digesting material (compared to clover) in order to maintain rumen microflora populations during the overnight fast. At present, it is not possible to offer a definitive answer. If a similar circadian effect was to be seen in choices between elements of plant communities of interest for biodiversity, it might be possible to exploit the effect to manipulate overall choice and hence effect on sward structure and diversity.

There are also spatial effects at many scales. Most animals in lowland systems in Europe have no opportunity to make choices at the landscape scale and hence much of our research in these systems relates to choice at the bite or feeding station (i.e. without moving the legs) scale. In hill and upland systems (and range systems in other countries), we know that animals establish home ranges within which they move on daily and longer time scales. Choice of location may be driven by other factors than food, such as water, shelter and social cohesion (itself an anti-predation strategy) (e.g. [6]).

5. ANIMAL TYPE

Animal type has a major effect on dietary choice. The most fundamental effect is that of body size. Because larger animals have relatively large gut capacity in relation to their metabolic requirements, they can retain digesta in the tract for longer and thus digest it more thoroughly. This means that they can deal with a lower digestibility diet and hence can forage less selectively than smaller animals which must of necessity select higher quality items [10]. The animal’s physiological state will also affect its selection. For example, hungry animals are less selective [12].

Species effects are of great importance. Some of these are driven by body size, for example, sheep are more selective than cattle. Digestive physiology is also important, for example, ruminants such as cattle have more efficient digestion than hind-gut fermenters such as horses [10]. The latter therefore rely on high throughput and this can necessitate long grazing times of up to 19 hours per day (e.g. [4]). Dental anatomy is also important; horses, with both top and bottom incisors can graze much closer to the ground than cattle and appear to concentrate their grazing in short areas that represent only a small proportion of the available area and thus produce a quite different sward structure [7]. The extent to which grazing by horses results in a different plant community to grazing by cattle is still the subject of some debate. Many horse grazed pastures are overstocked, leading to poor structure and loss of diversity [1]. This has probably resulted in an unjust, negative perception of grazing by horses as a tool for conservation management.

There is much anecdotal evidence (e.g. [19]) for breed differences in diet selection and hence in impact on sward structure and composition but little experimental evidence. In these anecdotal reports, true genetic differences between breeds are often confounded with the environmental effects, particularly prior experience of biodiverse pastures during early life that may affect subsequent selection.

Secondary evidence on breed effects is also patchy. There is some good information about breed and background effects on animal movements at a landscape scale. For example in an experiment in which Scottish Blackface or Suffolk ewes raised either lambs of their own breed or of the other breed [8], the distances between Blackface ewes was greater than between Suffolks but Blackfaces kept their lambs much closer to them, whatever the breed of the lamb. The
ewes had a choice of using upland or lowland pasture; the Blackface ewes made much more use of upland and this persisted in the lambs that they had reared whatever the lamb breed, although some effect of lamb breed was also evident (Tab. I).

While we have reasonable information on breed effects on movement at a landscape scale in heterogeneous environments, we know very little about differences at the scale of the grazing bout or feeding patch. There is information from single breeds grazing homogeneous pastures (e.g. [9, 13]); these provide information on parameters such those shown in Table II that allow the development of patchiness in the grazed sward to be reconstructed [2]. However, we have no idea if and how breeds differ in these parameters, how any such effects would be modified in heterogeneous pastures or how they would interact with the background of the animals, either immediately prior to moving to the target area or during early life. It is also possible that small-scale selection and the heterogeneity this creates will differ depending on the scale of enclosure in which the animal is allowed to make its choices. Some of the main gaps in our knowledge are summarised in Table III. Because of these gaps, we are currently ill-placed to predict effects of different grazing managements and breed on biodiversity.

6. CURRENT EXPERIMENTS

In this section, we describe two recently initiated experiments which illustrate research approaches to some current issues in biodiversity management. In an EU project (FORBIOBEN), we are comparing North Devon (a traditional breed) with Charolais × Holstein-Friesian (a commercial breed) yearling steers. The aim of this project is to test if there are any breed differences in grazing behaviour and impact on biodiversity. With the commercial breed, we will also look at grazing intensity. The animals are grazing agriculturally semi-improved grassland and rush pasture containing 5–10 species per m². We have chosen the North Devon as it was originally developed on this type of grassland, particularly rush pastures. We are monitoring botanical structure and flora and faunal diversity, herbage and animal production and economic outputs. Similar trials are taking place at 4 other sites across Europe (Tab. III).

In a second project (BEFOREBIO), funded by the UK Department for the Environment, Food and Rural Affairs, we are attempting to separate true breed (genetic) effects from the effects of early experience. North Devon or Hereford-Friesian suckler cows have been mated to North Devon and Charolais bulls, respectively. At birth we

<table>
<thead>
<tr>
<th>Ewe-Lamb</th>
<th>Blackface Blackface</th>
<th>Suffolk Blackface</th>
<th>Blackface Suffolk</th>
<th>Suffolk Suffolk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ewe-ewe distance (m)</td>
<td>12.77</td>
<td>5.30</td>
<td>12.01</td>
<td>3.84</td>
</tr>
<tr>
<td>Ewe-lamb distance (m)</td>
<td>6.03</td>
<td>11.64</td>
<td>5.45</td>
<td>10.88</td>
</tr>
<tr>
<td>% upland use (ewes)</td>
<td>78</td>
<td>10</td>
<td>82</td>
<td>2</td>
</tr>
<tr>
<td>% upland use (lambs)</td>
<td>82</td>
<td>28</td>
<td>55</td>
<td>4</td>
</tr>
</tbody>
</table>
will cross-foster half the calves onto cows of the other breed. Devon cows with their own or fostered calves will graze a fen meadow/rush pasture while Hereford-Friesian cows + calves will graze a fertilised ryegrass sward. In their second year, all the calves will graze on fen meadow/rush pasture and we will compare behaviour and impact on the sward of the different breeds and backgrounds.

### 7. MANAGEMENT OPTIONS

In this section, we consider some of options for biodiversity management that we believe current research findings in grazing behaviour make possible. We believe there is a need for ‘designer animals’ that are chosen to deliver desired grazing behaviour and hence biodiversity goals. This might be achieved by exploiting the animal’s genetics. We do not believe that genetically modified animals per se will be acceptable to European consumers in the foreseeable future, particularly in a conservation context. However, the new insights provided by genomic technologies open up opportunities for greater understanding of the genetic basis of behaviour and the use of marker

**Table II.** Examples of small scale (within head down grazing bout) movement parameters for heifers and ewes. According to Harvey et al. [9].

<table>
<thead>
<tr>
<th></th>
<th>Heifers</th>
<th>Ewes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bout duration (s)</td>
<td>180</td>
<td>51</td>
</tr>
<tr>
<td>Distance moved during bout (m)</td>
<td>7.3</td>
<td>1.8</td>
</tr>
<tr>
<td>Bites per m</td>
<td>32.3</td>
<td>37.4</td>
</tr>
<tr>
<td>Bites per bout</td>
<td>244</td>
<td>67</td>
</tr>
<tr>
<td>Bites per min</td>
<td>80</td>
<td>79</td>
</tr>
<tr>
<td>Bite area (cm³)</td>
<td>36.4</td>
<td>16.7</td>
</tr>
</tbody>
</table>

**Table III.** Gaps in current knowledge on the effects of grazing on biodiversity.

- Dietary choices of animals in temperate multi-species swards
- Small scale animal movements in heterogeneous swards
- Relative importance of genetics and environment
- Effects of spatial scale at which grazing management is applied

**Figure 1.** Minutes grazing clover or grass by dairy cows in each hour of the day (according to Rutter et al. [18]).
assisted selection to obtain animals with desirable traits. In the short term, we believe there is opportunity to better exploit the background of animals and to train them to produce the biodiversity outcomes that we desire. There is also much scope for exploiting temporal behaviour patterns to manipulate dietary choices so as to ensure that, whilst animals are productive and provide the farmer with an acceptable economic return, they also make the desired choices when grazing biodiverse pastures. An extreme example of this might be the use of folding systems (such as practiced in the past in many chalk downland systems) in which animals are removed to fallow arable land for part of the day as a means of exporting nutrients.

8. CONCLUSIONS

In conclusion, grazing animals have a vital role to play in the management of biodiverse pastures. However, major gaps in our knowledge of grazing behaviour in such pastures and its impact on biodiversity remain. We believe that there is a need for stronger integration between research on plant ecophysiology and plant community ecology and the behavioural ecology of foraging herbivores in order to address these knowledge gaps.

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