Spatial heterogeneity and grazing processes

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Review article

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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

Résumé — **Pâturage et hétérogénéité spatiale.** Les motifs d'hétérogénéité à large échelle, en terme de variabilité de hauteur, de densité ou de composition botanique du couvert, sont l'un des aspects les plus reconnus de l'hétérogénéité spatiale dans les systèmes pâturés. Afin de comprendre en quoi ils résultent du processus de pâturage, et ce qu'ils induisent pour l'évolution des couverts, les performances animales et les décisions des gestionnaires, il est indispensable de prendre en compte la composante spatiale des dynamiques de végétation et du comportement animal, ce qui représente en soi une approche innovante. Dans cet article, nous donnons une vue d'ensemble de ce que nous pensons

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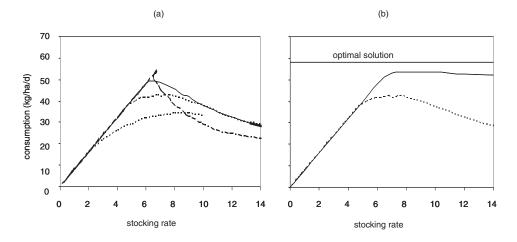
While we recognise the continuum of these impacts across the scales, we proceed systematically in an attempt to unravel the complexity of the phenomena that emerge in grazing systems. Our aim is to focus attention on those aspects of heterogeneity that might be manipulated or controlled with a view to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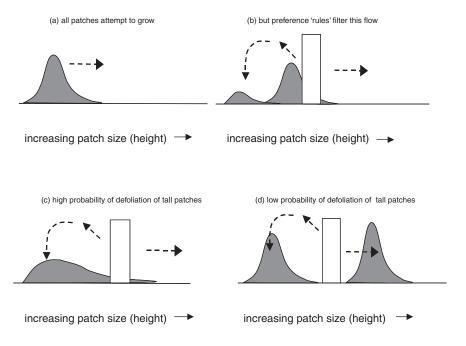
(a)　　　　　　　　　　　　　　　　　　　　　(b)

Figure 1. The effect of some fundamentally contrasting ways of placing bites in space and time on the yield (intake per ha) of the grazed system across a wide range of stocking rates. In (a) bites were grazed at random (solid line); in strict sequence (dashed line), or encountered at random but grazed preferentially with an 80% or 95% (lower line) partial rejection of tall patches (dotted lines). In (b) animals grazed as an enforced group (a 30 day regrowth: 1 day grazing rotation) which suppressed preference at high stocking rates (solid line), as compared with continuous grazing (dotted line). According to [44].

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 [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 [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.
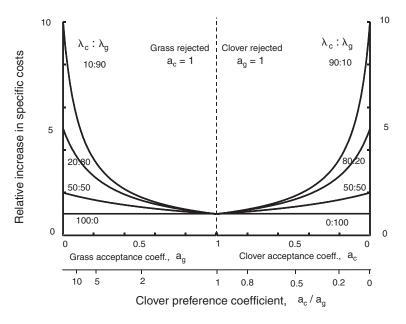
A bimodal frequency distribution of bite scale patch states will clearly be a powerful force to 'seed' spatial patterns at larger scales should there be other state-dependent processes that cause the subsets (e.g. tall and short) of the frequency distribution to become aggregated in space [5, 32].

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. The calculated *relative* increase in specific foraging costs (i.e. per unit mass eaten) in a 2 species mixture as affected by the acceptance coefficients (a_c, a_g) and the relative abundance ($\lambda_c : \lambda_g$) of the two species (assumed here to be clover and grass). From [48].

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.
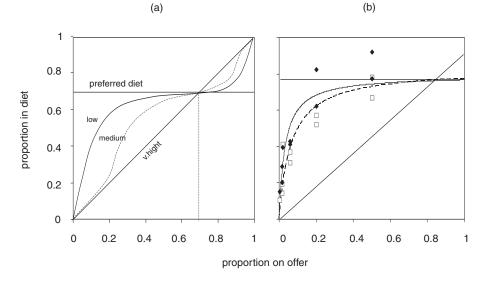
However, food may be distributed in patches (aggregated). To consider how this would intrinsically affect animals' expectation of finding the preferred food, we can start by imagining a situation where the same amount of food is distributed in one case in a large number of small patches, whereas in a 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.
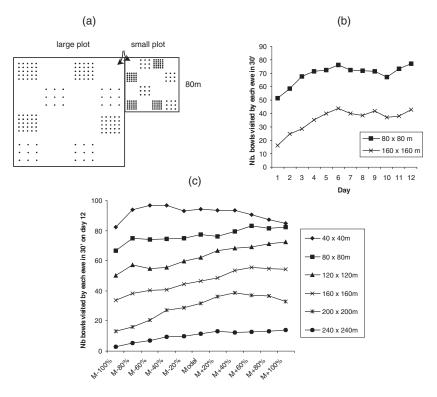
If animals were to search along a path but with a wider field of view, and were drawn toward any preferred food item within that, they would be sampling in effect, as if using contiguous 'quadrats' and their success would relate more to the 'frequency' and not the 'cover' of preferred items [29]. This 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. (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.

(a)

large plot   small plot

80m

(b)

(c)

Figure 5. (a) Layout of experimental plots with individual bowls shown as dots [15], (b) the increase in the number of bowls visited by each ewe in 30 min as animals learn the location of bowls, shown for different plot sizes [15], (c) simulation of the number of bowls visited by each ewe in 30 min after 12 tests according to the animals' memory capacity and plot size [14]. Model outputs were similar to that of the ewes in (b) ('Model'), and the predicted effects of increasing (or decreasing) memory size and memory persistence by 20%, 40%, 60%, 80% and 100% are shown.

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.
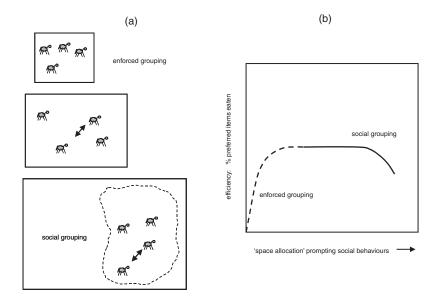
Conversely, when animals are aware of food location and when food is not limiting, social bonds within a group can favour patch and habitat selection. Boissy and Dumont [11] observed the behaviour of ewes in their motivation conflict procedure with animals being familiar (reared together from the young 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 m^2 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 m^2 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.
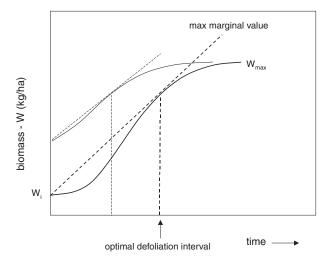
But fine scale foraging rules might be anticipated to change with scale as indicated in Figure 6b. Such a graph is, we feel, an essential component for a foraging model (either as an input or preferably an emergent property) that aims to analyse heterogeneity and its impacts across a range of scales. 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

*A*lthough 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
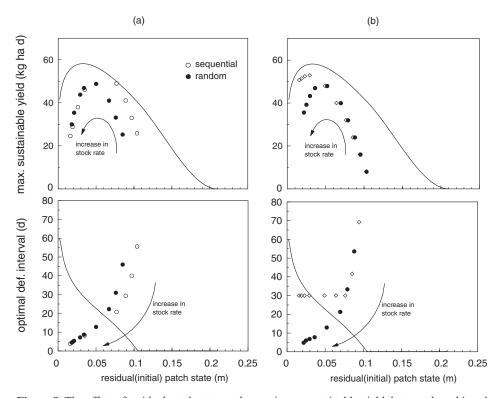
Figure 7. The theoretical basis for seeking optimal solutions for a sustainable harvesting of a hetero-geneous and regrowing resource is simple only at a bite-sized patch scale where defoliation is instan-taneous. Unique regrowth curves (only two shown here, one from a low residual state, one from a greater residual state) depend on the initial state of each patch, W_i, and there is an optimal time of har-vest for that patch [35]. At even greater residual patch states, regrowth is monotonic, implying the patch should be regrazed immediately. Foraging rules affect both these components and generate unique growth curves, but with simple to derive optimal solutions.

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 har-vest, which will achieve the maximum av-erage 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 com-bination of residual patch states, and defol-iation intervals would achieve (for full details see [35, 39]).

To understand the impact of the funda-mentally 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 de-foliation intervals) that these would gives rise to (the emergent properties), and we can relate these to what would be the opti-mal 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 so-lution which is achievable only by uniform cutting [38].

5.2. Model outputs in the different grazing scenarios

The modelling predicts that grazing se-quentially or at random, whether as individ-uals or a group, would lead to combinations of residual patch states and defoliation in-tervals 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

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].

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

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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