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FORAGING STRATEGIES ON RANGELAND: EFFECTS ON INTAKE AND ANIMAL PERFORMANCE

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Abstract

Rangelands exhibit extreme spatial and temporal variability in forage quality and availability. The animals that utilise these rangelands have consequently evolved a range of foraging strategies in an attempt to cope with this variability and maintain nutrient intake. In general, animals respond to and exploit spatial variability at all scales by selecting those items or units which optimise the intake of digestible nutrients and hence animal production. Animals similarly employ a variety of strategies to cope with temporal variability on rangelands. These strategies may include adjusting foraging behaviour and/or exploiting critical resources or resource areas to buffer temporal variability in feed quality or supply.

While current understanding of short term foraging processes operating in small scale, relatively simple environments is acceptable, our understanding and ability to predict longer term processes operating at the larger scale in more complex rangeland environments is poor. Consequently, our ability to predict foraging behaviour on rangelands and hence animal intake and production or the impact of animals on specific areas is severely limited. The major challenge therefor, is to advance our current information, theory and models upwards from the small scale to accommodate and realistically simulate, the larger, more complex systems operating on rangelands.

Introduction

The rangelands of the world are incredibly diverse and vary widely in structure, species composition, productivity and in their ability to support animal production. Despite this diversity, a unifying characteristic common to most if not all rangelands, is the extreme spatial and temporal variability in forage quality and supply that occurs in these environments. Spatial heterogeneity occurs at many different, nested hierarchical scales on rangelands ranging from the variability encountered between different plant parts, upwards to the variability encountered at the plant, patch, landscape and regional level. Similarly, temporal variability may occur over different time scales ranging from periods of a few seconds to many months or years and may result in dramatic and significant shifts in feed quality and availability. Further, this spatial and temporal variability may often interact, markedly increasing the heterogeneity, complexity and unpredictability of resources in these environments.

In contrast, animals foraging on rangelands require a relatively constant supply of nutrients. Rangeland animals have consequently evolved a range of foraging strategies to cope with the variability inherent in these environments and meet the energetic demands of growth, maintenance and reproduction.

The foraging strategies applied by these animals are of critical importance as they define the cardinal link between different trophic levels and between primary and secondary productivity on rangelands (Laca & Demment 1996). Firstly, these foraging strategies determine the intensity, timing and spatial location of plant defoliation and hence the impact

of grazing or browsing on plant communities. These strategies thus have a major impact on vegetation trend and condition and ultimately on productivity, species diversity and sustainability. Secondly, these foraging strategies determine nutrient intake, and hence animal performance and production. Developing a predictive understanding of how animals respond to spatial and temporal variability on rangelands is therefore crucial for devising productive and sustainable management systems for these environments.

In this paper I address the issue of how animals cope with spatial and temporal variability in forage quality and supply on rangelands. In each section, the variability encountered at each hierarchical level is briefly described and the response of the animal discussed in terms of its foraging strategy. This review accordingly adopts a similar approach to that used by O'Reagain & Schwartz (1995). Where possible, the effects of these strategies on animal intake and production are described, using either empirical data or the results of computer simulations. In the final section the paper discusses shortcomings in our present knowledge base and concludes by highlighting the challenges and issues that need to be addressed in order to develop better predictive and conceptual models of foraging behaviour and processes on rangelands.

Spatial Variability

For the purposes of this review, I address spatial variability using a plant based approach which begins at the plant part and then extends upwards to the plant, patch, landscape and regional scale. I accept that these levels may not exactly match the animal's perceptions of its foraging environment and that the distinctions between these levels are somewhat subjective. Nevertheless this plant-based approach avoids confounding body size with scale which is a problem implicit in any animal based classification of spatial heterogeneity.

Plant part level

The finest level of spatial heterogeneity encountered by the foraging animal occurs at the level of the plant part and occurs over scales of a few millimetres to a few metres depending upon plant phenology and size. This variability arises due to inherent differences in nutritional quality, size and accessibility between different plant organs. The magnitude of such intra-species differences are frequently large and may exceed those encountered at the species level eg Wilson (1981). Marked variability in quality or accessibility may also exist within a particular plant part fraction due to differences in maturity and hence lignification.

Grazing animals select leaf in preference to stem and green in preference to dry or dead material eg Arnold (1960). As swards mature, animals become increasingly selective and can maintain high levels of green leaf in the diet over a fairly wide range of green leaf availabilities (O'Reagain & Mentis 1988; Forbes & Coleman 1993). Browsers tend to select fruit and flowers in preference to leaves and avoid lignified stems (Owen-Smith 1982). Both grazers and browsers also tend to select the largest, most accessible bites within the plant (Barthram 1981) but the extent to which this occurs depends upon the relative trade-off between bite size and bite quality.

Diet quality in grazers is strongly correlated with the proportion of green leaf in the diet eg Chacon & Stobbs (1976). This relation is logical: green leaf is the highest quality component in the sward and of significantly higher quality than either stem or dead material eg Wilson (1981). Dietary intake is also likely to be positively correlated with green leaf selection due to its higher digestibility and passage rate. Animal production is therefore largely determined by the amount of green leaf in the diet. Intense selection at the plant part

level is thus a critical step in allowing animals to cope with the fine scale, spatial variability encountered at this level in rangelands.

Plant level

At the plant level, rangelands consist of a fine-grained mosaic of different plant species that vary widely in quality, mineral composition, rate of ruminal degradation and secondary chemical content. Plant species also vary markedly in structural characteristics such as height, leaf density, and thorniness and hence in bite size and ingestion rate (Cooper & Owen-Smith 1986; O'Regain & Goetsch 1996; Illius *et al* 1999). Significant intra-species variability in plant structure and quality may also occur due to localised variation in soil characteristics and differences in defoliation history (Gammon & Roberts 1978a).

It is well documented that animals respond to spatial variability at the plant level by selecting strongly for certain species while avoiding others eg Theron and Booysen (1966). Despite this, understanding of the underlying factors determining species acceptability remains limited. In grazers, species acceptability appears to be determined by the interplay between leaf quality and ingestion rate in terms of the rate at which leaf material can be harvested by the animal (O'Regain & Mentis 1989a; O'Regain 1993, but see Illius *et al* 1999). For example, sheep grazing *sourveld* in South Africa selected short, non-stemmy species with leaves of high quality and low tensile strength but avoided tall, stemmy species with tough, low quality leaves (O'Regain 1993). For cattle, preferred species were leafy, with a high leaf table height and had high quality leaves of low tensile strength (O'Regain & Mentis 1989a). Given the lack or relatively low level of tannin-binding salivary proteins in grazing animals (Robbins *et al* 1987) secondary chemicals like tannins do not appear to be major determinants of plant selection for these animals.

In contrast, work conducted on browsing ungulates such as kudu and impala indicate that secondary chemicals are an important determinant of species selection, with acceptability being determined by the balance between leaf crude protein and condensed tannin content (Cooper *et al* 1988). Physical structures like thorns and spines, which reduce, bite size and intake rates are also important and strongly modify species acceptability (Cooper & Owen-Smith 1986). Both grazers and browsers therefore appear to select species based on the balance between nutrient content and the energetic costs of harvesting and processing (mastication, digestion and metabolism of secondary chemicals) a particular food or species.

Different plant species on rangeland vary widely in their ability to support animal production as would be expected given the large differences in ingestion rate and nutrient content observed between species eg O'Regain *et al* (1995). Thus simulation of potential animal production from different African *sourveld* grasses (O'Regain 1996a) using the measured digestion and ingestion rates for these species, indicated that there were major differences in the potential animal weight gains that could be expected from different grasses. As an example, there was a predicted 900 g difference in the potential daily gain for cattle in summer between the highest and lowest ranked species. Differences of a similar relative magnitude were also predicted for sheep but it is interesting to note that even in summer these animals would be unable to maintain body weight on certain grass species (O'Regain 1996a). Animals are thus able to achieve levels of production that are substantially higher than would be expected from non-selective feeding by exploiting the spatial variability encountered at the plant level. Selective grazing in rangelands thus confers a major advantage in terms of growth and production for the grazing animal.

Patch level

Extreme patchiness in forage quality and availability is an inherent part of most rangelands. Definition of what constitutes a 'patch' is, however, subjective and dependent upon the animal being studied, group size, observer bias, the activity in question and season. For present purposes a 'patch' is defined as *the level of variability encountered within a landscape unit*. Patches may thus differ markedly in species composition and/or structure but would nevertheless be identifiable as being part of the landscape unit in question (O'Reagain & Schwartz 1995). At a single site, patchiness could therefore occur simultaneously at multiple, overlapping scales ranging upwards from a few centimetres, to many hectares in extent.

Patchiness in landscape units arises primarily due to small-scale, localised variation in soil characteristics such as fertility, texture, depth etc. Superimposed over this variability are other differences created and driven by biotic and other abiotic processes such as grazing, fire and urine deposition. These two layers of variability reinforce and accentuate each other creating a dynamic, complex network of patches that vary in species composition, structure, nutrient quality and mineral content as well as the presence or absence of deterrents to grazing such as the presence of faeces or thorny plants.

The overwhelming response of animals to patchiness is to avoid low quality, unproductive patches and select high quality, productive patches within a particular landscape unit eg Du Plessis (1968), Mott (1985). With increasing patch biomass or height, bite size increases sharply as animals prehend a bigger volume of herbage through increased bite depth and bite area, eg Laca *et al* (1992). However, once plant height exceeds bite depth, bite size becomes limited by buccal cavity dimensions (Illius & Gordon 1987) and, thereafter remains constant eg Allden & Whittaker (1970). As instantaneous intake rate (IIR) is largely determined by bite size (Hodgson 1981), IIR responds in a similar fashion, and increases sharply in response to increasing patch biomass to reach an asymptote beyond which increasing biomass or sward height has no effect on this variable. For example, work done on mesic grasslands in South Africa indicated that for cattle and sheep IIR increased sharply with increasing sward heights to reach asymptotes at about 20 and 10 cm respectively (O'Reagain *et al* 1996). Similar responses of IIR to biomass or sward height have been recorded for a variety of other ungulates including Thomson's gazelle (Wilmshurst *et al* 1999) bison (Hudson & Nietfeld 1985), and elk (Wilmshurst 1995).

The response of IIR to increasing sward or patch biomass is a variation of the Type II functional response originally described by Holling (1959). This model has subsequently been extended by (Spalinger & Hobbs 1992) to account for the different abundances and spatial distributions of plants that the animal may encounter under grazing. In Process 1 foraging, potential bites are well dispersed and hidden, such as may occur in the dry season on swards of high biomass where green leaf is scarce and highly dispersed. In Process 2 foraging, potential bites are well dispersed but are apparent as may occur on very short, sparse regrowth following a fire or drought. Process 3 foraging occurs when bites are both concentrated and apparent (Spalinger & Hobbs 1992) as may happen in the wet season when swards are green and offer a dense array of accessible bites.

In Process 1 and 2 foraging, encounter rates are less than the maximum cropping rate, so IIR is constrained by searching and cropping time. Conversely, in Process 3 foraging, encounter rates with potential bites exceed the maximum cropping rate and in this situation IIR is constrained by cropping and chewing rates (Spalinger & Hobbs 1992). Accordingly, shifts between the different processes should occur with changes in biomass or sward conditions (Spalinger & Hobbs 1992) as has been documented by Bradbury *et al* (1996) with

Thomson's gazelle in Kenya: in the dry season, bite rates were positively correlated with protein density, suggesting that IIRs were limited by encounter rate as would be expected from Process 1 or 2 type foraging. Conversely, bite rates were negatively correlated with protein density in the wet season suggesting Process 3 type foraging with IIR being restricted by processing rather than encounter rates (Bradbury *et al* 1996). Switches between these different processes could also conceivably occur due to differences in species composition. For example, Process 3 type foraging should occur on 'good condition' rangelands dominated by preferred grasses whilst Process 1 or 2 type foraging could predominate on 'poor condition' areas where these species are relatively rare.

While the functional response provides a powerful conceptual and quantitative model of the relation between an animal's ingestive behaviour and its food supply, it nevertheless suffers from two related shortcomings which limit its general applicability to rangelands. First, the model deals only with short-term intake and neglects the fact that animals might be maximising intakes over longer time periods. Consequently, it does not address the problem that for ruminants, long-term intake is constrained by both ingestive and digestive processes. Secondly, the model assumes that there is no interaction between forage quality and availability, when in practice these variables are generally inversely related eg Wilmshurst *et al* (1995), O'Regain & Owen-Smith (1996). Consequently, there is likely to be a trade-off between IIR and digestion rate as sward biomass increases.

There should therefore be an optimum biomass where the intake of digestible energy is maximised, given the opposing constraints of short term IIR and the rate of digestion of material in the rumen. As an example, the effects of increasing sward height on production in cattle and sheep grazing *sourveld* in South Africa were modelled by O'Regain (1996b). Initial sensitivity analyses indicated that diet quality on this mesic grassland had a significantly greater effect on animal production than IIR through its effects on passage rate and hence long-term intake. The model consequently predicted that the intake of digestible energy, and hence animal production, would be maximised at sward heights of between 10-12 cm and 6-9 cm for cattle and sheep respectively. This is close to half the height at which short term IIR would be maximised. At heights below these optima, intake was restricted by ingestion rate while above this level, intake was restricted by the rate of passage of lower quality material through the rumen (O'Regain 1996b). Optimum heights or biomasses have similarly been identified for wapiti (Wilmshurst *et al* 1995) and Thomson's gazelle (Wilmshurst *et al* 1999). Comparison of the different optima reported in these studies reveals that the optimum sward biomass or height varies markedly between different grazing species as would be expected for animals functioning under different time: energy constraints.

Animals should therefore select patches which maximise the long-term rate of digestible energy intake rather than selecting those patches which simply maximise IIR. This has been termed the 'intermediate biomass hypothesis' (Wilmshurst *et al* 1995). Although this has not been widely investigated on rangeland, the available data tends to support this hypothesis. For example, Wilmshurst *et al* (1995) measured the relative time wapiti spent foraging in patches which ranged from 800 to 2900 kg/ha in available biomass. Although the animals grazed all patches, the bulk of foraging time was spent in the patch with an intermediate level of biomass (1100 kg/DM/ha) which was the biomass predicted to give the highest rate of energetic gain per day. In a similar experiment with red deer (Langvatn & Hanley 1993; Wilmshurst & Fryxell 1995), patch use strongly matched the estimated rate of intake of digestible energy from the different patches. Importantly, while animals spent the greatest proportion of their foraging time on patches offering the greatest rate of digestible energy intake, they nevertheless spent a significant proportion of time on 'sub-optimal' patches (Langvatn & Hanley 1993; Wilmshurst *et al* 1995). This matching behaviour has been attributed to factors such as the need to sample a heterogenous environment or simply

discrimination error (Krebs & McCleery 1984). Animals may also be trying to simultaneously optimise intake of different nutrients, so necessitating selection from a range of patches over time.

Landscape level

Landscapes are composed of landscape units, defined here as areas that differ markedly in species composition, vegetation structure, soil fertility, texture, depth, slope and/or rockiness. Superimposed over this variability are other factors such as the location of water and minerals, barriers to movement such as ravines, and refuges from predation such as thick scrub or cliffs (Stuth 1991). Landscapes may thus consist of a mosaic of units that vary not only in their ability to produce forage but also in proximity to water, accessibility and susceptibility to predation. Definition of what comprises a landscape or landscape unit is consequently partially subjective and depends to some extent upon the size and foraging behaviour of the species in question.

The primary determinant of landscape selection is the availability of water and physical accessibility by the foraging animal (Senft 1987; Stuth 1991). These abiotic determinants set the constraints within which all foraging strategies must operate (Senft 1987; Bailey *et al* 1996). The importance of water is readily apparent in semi-arid landscapes where landscape utilisation steadily declines with increasing distance from water. Upper limits for utilisation range from about 6 to 10 km for cattle (Squires 1982) but vary markedly depending upon the breed and class of animal.

Once the constraint for water is satisfied, selection for landscape units is, in general, strongly correlated with forage quality and availability eg Downing (1979); Gordon (1989). Conversely, animals select against areas of low forage availability or those dominated by low quality, unpalatable plants (McNaughton 1978; Senft *et al* 1985). Animals thus appear to select landscape units that offer the greatest return per unit of grazing time invested (Collins *et al* 1978). Nevertheless, animals seldom forage exclusively on the most preferred units but tend to spend at least some time foraging across all units in the landscape. As in patch selection, animals thus appear to *match* foraging time across units relative to their profitability rather than maximising time in the unit offering the highest rate of nutrient gain (Senft *et al* 1987). Animals on rangelands thus appear to follow the maxim proposed by Langvatn and Hanley (1993) of ‘use most of the best, least of the worst but some of everything’.

The utility of a particular landscape unit is however strongly dependent upon the animal species in question (Gordon 1989) and the specific anatomical, digestive and metabolic constraints under which it operates. Within a species, landscape selection is also strongly determined by the reproductive and metabolic state of the animal in question (Clutton-Brock *et al* 1982) in terms of its particular nutrient requirements and its vulnerability to predation (Berger 1991; Festa-Bianchet 1988). Landscape selection is therefore a complex process which is primarily determined by the availability of water and physical accessibility but which then involves a trade-off between forage quality and availability and a host of external factors such as predation risk, thermal stress or exposure to biting insects eg Duncan (1983). The position of this trade-off will be dynamic, and will vary according to environmental conditions, animal species and the state of the animal (O’Reagain & Schwartz 1995).

Current conceptual understanding of the general processes determining landscape selection is thus relatively good and is largely adequate to predict coarse, broad-scale patterns of landscape utilisation, eg productive areas close to water are likely to experience greater utilisation than unproductive areas distant from water. Unfortunately, our ability to predict utilisation at finer, more subtle levels such as between different soil types or vegetation

communities within the landscape remains poor. Consequently, even with access to detailed biophysical data, there is still no reliable *a priori* method of predicting the utilisation of different landscape units located at equivalent distances to water. This shortcoming needs to be urgently addressed if we are to accurately predict the utility of, and the impact of animal foraging on, different units within our extensive rangeland landscapes.

Regional level

At the regional level, rangelands consist of large-scale assemblages of landscapes (Rowe 1961, cited by Senft *et al* 1987) with regions being defined by major differences in climate, geology and soils and hence in vegetation. Regions may however simply differ in the seasonal availability of water or the presence of extreme heat or cold. Regions are equivalent in scale to migratory ranges in animal terms (Senft *et al* 1987) and to transhumance and nomadism in pastoral terms.

Animals essentially respond to regional and landscape heterogeneity in a similar fashion and tend to select regions based on a range of factors including forage quality and availability, predation risk and thermal stress (O'Reagain & Schwartz 1995). As an example, the large scale seasonal migration of ungulates across different regions in the Serengeti appears to reflect not only selection for forage quality and mineral content but also avoidance of predators, muddy soils and Tsetse fly (McNaughton 1990).

Temporal Variability

Short term variability

Short-term variability in the quality and availability of forage on rangelands may occur over the scale of a few seconds to a few hours and may be natural or grazing induced. Natural variability in the nutrient content of forage frequently occurs due to normal diurnal rhythms in plant physiological processes. For example, it is well documented that the concentration of non-structural carbohydrates tends to increase in plant leaves through the day due to the accumulation of photosynthate sugars eg Delagarde *et al* (2000). There is some evidence to suggest that animals adjust their foraging behaviour in response to these short-term fluctuations in forage quality. Sheep on temperate pastures, for example, have been shown to defer the bulk of grazing until the afternoon, presumably to capitalise on the increased leaf sugar levels present at that time (Penning *et al* 1991).

Most short-term variability in forage quality and availability is, however, grazing or browsing induced and is a direct consequence of patch depletion by the foraging animal. This depletion may occur over time periods ranging from a few seconds to a few minutes, depending upon the patch size involved. As the animal depletes a patch, IIR declines causing the cumulative rate of nutrient gain to flatten and depressing the rate of return relative to the costs of grazing that patch or moving to the next patch. For example, cattle bite sizes have been observed to decline from about 1.2g to 0.3 g with increasing time spent grazing ryegrass patches (Laca *et al* 1994). As the time taken per bite remained constant, the decline in bite size led to a decline in IIR with residence time, depressing the cumulative rate of intake (Laca *et al* 1994). Given that moving to another patch involves energy expenditure, the critical question for the grazing animal is therefore how long it should stay in a patch before giving up and moving on to the next patch, ie, what is the optimal patch residence time?

The Marginal Value Theorem (MVT) predicts that animals should utilise a patch until the rate of intake from that patch declines to the average available from the area as a whole

(Charnov 1976). The point at which an animal should leave a patch should therefore occur when:

$$H = P + C + MOC$$

where H= harvest rate of energy, C= energetic costs of foraging, P = predation costs associated with that patch and MOC = missed opportunity cost, ie, the benefits from alternative activities that the animal forgoes in consuming a patch (Brown 1988 cited by Kotler *et al* 1994). Accordingly, the basic predictions derived from the MVT are that (1) patch residence time should increase with patch richness and distance to the next patch, (2) distance walked to the next patch should be proportional to patch richness and (3) residence time should be inversely proportional to predation risk (Charnov 1976; Kotler *et al* 1994).

These predictions are, in general, corroborated by the available evidence. Work with cattle on temperate pastures (Laca *et al* 1993), Dorcas gazelles on desert shrubland (Baharav & Rosenzweig 1985) and impala on savanna (Fritz & De Garne-Wichatitsky 1996) indicates that residence time is strongly correlated with patch richness. Similarly, residence time appears to increase with increasing distance to the next patch (Laca *et al* 1993). Animals also appear to trade-off walking distance against patch richness (Dumont *et al* 1998; Dumont & Petit 1998). For example, in an elegant study conducted by Dumont *et al* (1998), sheep were offered hay of different quality at various walking distances. A constant reward: distance relationship was observed in the study with preference for the good quality hay declining as distance to the hay increased (Dumont *et al* 1998). Residence time also appears to be strongly related to predation risk: in Nubian ibex patch depletion levels and, by inference, residence times, declined as patch exposure to predation increased (Kotler *et al* 1994).

In theory, animals should use departure rules such as a threshold IIR to determine when to move between patches. Unfortunately, patch departure rules have not been widely investigated in ungulates due to the logistical difficulties of measuring individual bite sizes and short term gain functions in these animals. In elk, there is some, albeit weak, evidence to suggest that cropping rate or even neck angle are used as cues to determine when to leave patches (Jiang & Hudson 1993). Evidence from cattle grazing temperate swards indicates that an abrupt change in IIR occurs when the top horizon is depleted and animals begin grazing the lower horizon (Laca *et al* 1994). This change could conceivably be used as a departure rule to determine when animals should move to the next patch. Bailey *et al* (1998) have postulated that animals have some threshold of 'expectation' derived from recent foraging experience in an area so that when IIR declines below this threshold the animal moves to the next patch. In rangelands bite quality is also likely to play a critical role in determining when to leave a patch. Cues used here could be the amount of green material in a bite, or the time taken to harvest and separate bites out from surrounding low quality material. Unfortunately, these issues have yet to be investigated in any detail.

Finally, it is important to note that animals seldom, if ever, completely *deplete* a patch in the first pass or visit. For example, work with impala (Fritz & De Garne-Wichatitsky 1996) and kudu (Owen-Smith 1994) indicates that animals never entirely deplete trees but generally take a few bites from each tree before moving on. Animals are thus likely to revisit patches within a landscape unit a number of times, progressively depleting the patch at each visit and gradually depressing the average rate of return available from that landscape unit or area as a whole.

Medium term variability

In rangelands, marked temporal variability in forage quality and supply may occur in the medium term over time scales of a few days to a few weeks. Although such variability may be natural, such as the fluctuations in leaf N content that occur in response to rain or

short periods of drought eg Heckathorn & DeLucia (1994), the majority of variability at this time scale is grazing induced and results directly from the depletion of the foraging environment by the animal.

At a gross level, grazing depletes overall forage availability within landscape units, resulting in a decline in bite size and quality eg Chacon and Stobbs (1976) and potentially depressing animal production. Animals typically respond to such variability by moving to new landscape units where forage is more freely available eg Low *et al* (1981), presumably obeying departure rules similar to those used at the patch scale. However, where animals do not have access to other landscape units they may adjust foraging behaviour in an attempt to compensate for the reduced quality and availability of forage. Thus animals commonly extend grazing times and/or increase biting rates (Allden & Whittaker 1970; Hudson & Nietfeld 1985; Roguet *et al* 1998) in an attempt to compensate for reduced bite size. Animals may also increase travel speed in an attempt to increase encounter rates with food items eg Roguet *et al* 1998; Spalinger *et al* (1988). However, the extent to which these strategies can compensate for reduced forage availability is limited given that bite size is the major determinant of intake (Hodgson 1981). Further, these strategies may carry other costs such as reduced diet quality, increased vulnerability to predation (Fitzgibbon 1989) reduced digestive efficiency (Greenwood & Demment 1988) or increased thermal load (Owen-Smith 1994) that may ultimately negate the effects of maintaining intake.

In the multi-species communities encountered on rangelands however, the most significant impact of grazing occurs at the plant level and results from the selective defoliation of preferred species in the community. This impact is manifested as a progressive and often rapid change in the relative availability of different species to the grazing animal. The effect is particularly pronounced at high stocking densities where the relative availability of different plant species may change rapidly with time spent in a particular area or paddock.

Studies conducted on grassland in South Africa (Daines 1980; Danckwerts *et al* 1983; O'Reagain & Mentis 1989b; O'Reagain & Grau 1995) and on Australian savanna (Clarke 1999) indicate that both cattle and sheep graze species in a distinct sequence of selection with time spent in a paddock. This sequence occurs in three basic stages. In the first stage, animals select the most preferred species and, to a limited extent, may also lightly defoliate species of intermediate acceptability. The second stage is initiated when about 60 % of the tussocks of preferred species have been defoliated and is characterised by regrazing of these plants together with increased defoliation of the intermediate species. The third and final stage occurs when between 80 – 100 % of the plants of the preferred and intermediate species have been defoliated at least once and defoliation of avoided species is finally initiated. Stocking density appears to affect only the rate at which this sequence progresses and not the sequence *per se* (Daines 1980; Stoltz & Danckwerts 1990).

This sequence of species selection is in at least partial agreement with some of the basic tenets of optimal foraging theory (OFT). First, OFT predicts that dietary breadth should be widened as food availability declines (Emlen 1966). While this was observed, both cattle and sheep nevertheless showed strong resistance to consuming avoided species and usually re-grazed preferred plants one or more times before attempting to consume plants of lower acceptability. This resistance to grazing avoided species partly substantiates the prediction (Owen-Smith & Novellie 1982) that while ruminants should initially widen acceptance ranges when food availability declines, they should narrow dietary breadth when nutrient maintenance levels can no longer be satisfied. This is because for ruminants under conditions of nutrient restriction, addition of poorer quality items in the diet may exacerbate the problem of nutrient limitation by slowing down rates of digestion and ultimately decreasing nutrient intake (Owen-Smith & Novellie 1982).

Second, OFT predicts that certain foods should always be eaten or rejected when encountered, i.e., animals should display an all or nothing response to foods (Krebs & McCleary 1984). However, both cattle and sheep displayed partial preferences and grazed a small proportion of the tussocks of the intermediate and even the avoided group of species at the beginning of the grazing period, despite the ready availability of the preferred species (O'Reagain & Mentis 1989b; O'Reagain & Grau 1995). Partial preferences in large ungulates have been reported elsewhere eg Parsons *et al* (1994), and have been ascribed to the need to sample the environment (Westoby 1978), discrimination error (Illius *et al* 1999), matching (Senft *et al* 1987) and/or the need to maintain a balanced rumen micro-flora eg Parsons *et al* (1994). An equally plausible explanation may be that on rangelands intra-species variability in morphology and/or leaf quality may be sufficient to result in some plants being of higher or lower acceptability than would be expected from that particular 'acceptability group'.

A third prediction of OFT is that the decision to eat a lower ranked species (food) should be independent of its own abundance but depend upon the abundance of the more preferred species present (Pyke *et al* 1977). This was strongly supported by the data from species selection studies with cattle and sheep (O'Reagain & Grau 1995). In both animals, a distinct threshold effect was evident with the less preferred species only being grazed when the availability of ungrazed plants of the preferred species had declined below a certain threshold level. In general, thresholds were higher with less palatable species (O'Reagain & Mentis 1989b; O'Reagain & Grau 1995).

In the medium term, animals on rangelands are therefore faced with a series of foraging decisions about when to stop rejecting and start consuming species of lower acceptability when encountered. As the preferred, better quality species are depleted the energetic costs of locating a diminishing supply of tussocks of these species increases. At some point these costs will outweigh the potential benefits of consuming a food of greater nutritive value. This point will of course depend first, upon the relative nutritive value of the different species involved and second, upon the relationship between inter-tussock distance (d) and the density (D) of the remaining ungrazed tussocks. Where plants are regularly distributed, the distance walked to the next ungrazed plant d , increases in an exponential fashion as plants are depleted through grazing. Thus while there is initially little increase in d , once a certain proportion of tussocks have been grazed (60 – 90 % depending upon total population size), d increases sharply (O'Reagain 1996a). This suggests that the thresholds which determine when species from the next acceptability class are included in the diet, could arise from sudden increases in search time associated with locating a rapidly diminishing supply of ungrazed plants in a particular area.

Animal production is therefore likely to decline within a period of occupation in a paddock or landscape unit as animals deplete the better quality species present and are forced to consume lower quality species present in the community, depressing diet quality and intake eg O'Reagain & Mentis 1988; Clarke 1999. This process was modelled for *sourveld* swards in South Africa using measured digestion and ingestion rates of a number of *sourveld* grasses (O'Reagain 1996a). As expected, a general decline in animal production (AP) with time spent in a paddock was predicted, but the rate and extent of decline was strongly influenced by sward species composition. On all swards, the decline followed a distinct three-stage process as the plants in the different acceptability classes were depleted. In the first stage, animals consumed only the most preferred species present giving some relatively high level of AP. During this stage AP remained largely constant due to the exponential relation between plant density D and inter-plant distance d (see above) which ensured that IIR was largely unaffected as this species group was depleted through grazing. However, once plants in this class had been severely depleted, d increased sharply causing animals to start consuming the next most preferred species in the diet in order to maintain intake. In this second stage, AP declined due

to the increasing consumption of this lower quality species. This stage continued until all of the preferred plants were depleted and the diet consisted exclusively of the less preferred species. In the third stage, AP usually stabilised at some second, usually lower, level (O'Reagain 1996a).

Overall, the model indicated that a number of specific factors are important in determining animal production and its rate of change with time in a paddock or landscape unit (O'Reagain 1996a). First, the basic nutritive value of the major species present defines the limits to animal production from a particular area. While, the nutritive value of the most preferred species sets the upper production limits that can be expected, that of the less preferred species determine the extent to which production will decline with time. Second, the relative abundance of these different species will determine the rate and extent of the change in production over the grazing period. Third, the absolute species abundance or total basal cover will determine the period over which production can be maintained in terms of animal production and stocking density. These findings reinforce the basic tenet that species composition and basal cover are basic determinants of animal production on rangelands.

In practice, the sequence of species selection described above and its resultant effects on animal production are likely to be complicated by two important factors. First, *management variables* such as stocking rate, paddock size and the grazing system applied directly determine stocking density and the period of occupation in a paddock. These in turn determine both the rate and extent of species selection and the potential period available to re-graze previously defoliated plants respectively (Daines 1980; Stoltsz & Danckwerts 1990). Second, *plant growth rates* following defoliation will strongly influence the *extent* to which the sequence will occur, because animals consistently select the palatable regrowth on preferred species rather than grazing the next most preferred group of species present (Gammon & Roberts 1978b).

Consequently, where stocking densities are low, periods of occupation long and/or conditions suitable for rapid growth, preferred species may regrow sufficiently rapidly after defoliation to allow animals to return to this new regrowth without being forced to graze the intermediate or avoided species in the community. Conversely, where stocking densities are high, periods of occupation short and/or plant growth rates slow, animals will be forced to defoliate most species present in order to maintain intake. In rangelands the whole process may thus vary from being fairly simple with animals moving through the basic predictable steps as described above, to a more complicated process where animals graze and re-graze only certain groups of species or sub-populations of these species and only extend defoliation to other groups or ungrazed plants when growth rates decline and feed conditions become limiting. The latter, more complicated processes of species selection and their resultant effects of animal intake and production on rangelands have not been adequately investigated and require urgent attention.

Long term variability

Significant long-term temporal variability occurs over time scales of months to years on all rangelands causing marked fluctuations in forage quality and availability. For example, in the shrub-grasslands of east Africa, forage availability can decline by more than 66 % and quality drop to sub-maintenance levels within 8 weeks of the end of the wet season (Schwartz 1993). Temporal variability at this scale largely arises from the coupling of plant growth cycles with longer term, seasonal level changes in soil moisture and temperature. In rangelands that experience fairly regular seasonal changes in growing conditions eg Monsoon savannas, such longer term temporal variability is likely to follow fairly predictable, seasonal cycles. However, in many arid and semi-arid rangelands where rainfall is aseasonal and has a

high coefficient of variation, this variability is likely to be stochastic and relatively unpredictable.

A primary response by animals to such longer-term temporal variability is to exploit the different levels of spatial heterogeneity present in the environment to buffer seasonal changes in forage quality and availability. Thus animals may widen acceptance ranges over a range of spatial scales and start utilising species, patches or landscape units that were previously avoided or only lightly grazed. For example, in African savannas, browsers like kudu widen dietary breadth to include unpalatable species in the dry season and start utilising previously avoided landscape units (Owen-Smith 1979; 1994) while cattle may start browsing and consuming seedpods from woody species (Skinner *et al* 1984).

In an attempt to elucidate the relative importance of different food types through the seasonal cycle, Owen-Smith (2000) proposed a generic set of *resource types* for browsing and grazing animals. Although specifically intended to provide a functional categorisation for different food or plant types it can logically be extended upwards to the patch and landscape scales (Table 1). Thus *Quality resources* are high quality foods/ areas that provide high intake rates and support high levels of animal production. Such resources are, however, generally ephemeral, of restricted availability and/or of low persistence and so are generally unavailable in times of need. *Staple resources* supply adequate levels of nutrient intake for much of the year and provide the bulk of dietary nutrients for most of the season. *Restricted intake resources* are of very high quality but provide low levels of intake. *Reserve resources*, are generally of lower quality and less favoured but can sustain animals at or near maintenance levels in times of need. Reserve areas could also be dominated by staple species but due to other constraints such as limited accessibility or distance from water may be poorly utilised thus becoming moribund and of low quality. *Buffer resources* are of poor quality and cannot support animal maintenance requirements but nevertheless delay the onset of starvation during times of extreme need (Owen-Smith 2000)

The relative importance of different food resource types through the seasonal cycle was illustrated in a model constructed for kudu populations on an African savanna (Owen-Smith 2000). Model results indicated that greater populations could be maintained where kudu had access to a combination of staple, high quality and reserve resources than when animals had access to staple resources alone. Further, although of lower quality, the contribution of reserve resources towards population numbers was greater than that of the high quality resources because of their persistence and general availability in the dry season. Buffer resources similarly made a significant contribution to animal numbers because they provided food during the critical dry season period. Foods in the buffer and reserve type categories thus provided critical bridging resources that allowed animals to survive periods of extreme nutritional stress (Owen-Smith 2000). Although the model specifically focussed at the plant or food type level, the simulations provide an equally valid analysis of the importance of different resource types at the patch or landscape scale. The results clearly indicate that while staple resources maintain animal populations through most of the season, the ability of animals to access and exploit reserve and buffer resources is critical for ensuring survival through periods of extreme nutritional stress like the late dry season.

At larger spatial scales animals may migrate to different regions or land systems to cope with seasonal deficits in fodder quality or availability. A classic example is the annual migration of animals in the Serengeti between the woodlands in the dry season and the plains in the wet season (McNaughton 1990). At smaller landscape scales, animals that are dispersed over large areas in the wet season may contract to 'key resource areas' (*sensu* Scoones 1995) in the dry season. These key resources are analogous to reserve or buffer resource areas at the landscape scale but could also simply be areas along the landscape catena that remain green in the dry season or areas where water is available.

The importance of such key resource areas on population levels in large ungulates was demonstrated in a simulation model by Illius & O'Connor (2000): model results indicated that population levels were strongly dependent upon the size and relative proportion of key resource areas. Importantly, the presence of such key resource areas strongly buffered the effects of temporal variability in rainfall and hence forage biomass production, on population numbers (Illius & O'Connor 2000).

Animals have also evolved a variety of other strategies to cope with seasonal fluctuations in feed supply. As already noted, animals may employ a range of foraging strategies to cope with seasonal scarcity, such as extending daily foraging times eg Jarman and Jarman (1973) and/or increasing encounter rates with preferred species eg Owen-Smith (1994). Metabolically, animals may also respond by adjusting net energy requirements. This may involve storing fat reserves when conditions are good for use in times of scarcity. However, this strategy can incur other costs such as reduced mobility, increased risk of predation and reduced thermal tolerance (Owen-Smith 1994). Animals may also conserve energy by reducing activity levels during critical periods, eg Novellie (1978). Different digestive strategies may also be utilised to cope with poor quality forage. These may include expanding rumen volume to increase digestive capacity, increasing rumen retention times to increase the extent of digestion, reducing particle size through increased rumination and increasing rumen passage rates eg (Holand 1994; Lechner-Doll 1990).

In practice, animals are likely to employ a range of strategies to cope with seasonal level changes in feed quality and availability. For example, studies on kudu indicated that animals applied a number of strategies to maintain energy intake in the dry season (Owen-Smith 1994). Apart from widening dietary breadth, animals also increased the percentage of palatable species accepted for feeding, increased mean feeding duration per tree and increased encounter rates with evergreen species. Animals also increased the proportion of the day spent active from 60 to 72 % as well as increasing the proportion of that time spent foraging. There was also evidence that animals increased rumen capacity in order to cope with increased intake. Consequently, despite a substantial decline in both food abundance and quality, animals managed to maintain E intakes at or near requirements for maintenance, activity and growth over nearly all months. Simulation of daily energy balances indicated that without applying these strategies, kudu would have only achieved 30 – 40 % of energy requirements through the dry season. Dietary expansion made up *c.* 60 % of this shortfall, with the increased intakes being facilitated by increased rumen fill (Owen-Smith 1994).

In conclusion, animals have a variety of foraging, digestive and metabolic strategies to compensate for or at least buffer seasonal variability in the supply and quality of forage. However, the mechanisms chosen are likely to vary with the animal species concerned (O'Regain & Schwartz 1995), according to the particular physical, metabolic and digestive constraints under which it operates.

Discussion

In the last few decades there have been major advances in the general understanding of foraging behaviour, the development of foraging models and the application of foraging theory to ungulates. Despite this, understanding and prediction of ungulate foraging strategies on the extensive rangelands in general, and in particular, how these animals cope with the spatial and temporal variability inherent in these environments, remains poor. At present, most knowledge is limited to detailed understanding of short-term, small-scale processes operating in relatively simple environments. In contrast, with large scale, longer-term processes in more complex systems we are generally limited to broad generalities or conceptual models that have limited predictive power and hence are of restricted utility in

these environments. Consequently, our ability to predict foraging behaviour on rangelands and hence animal intake and production or the impact of animals on specific areas is severely limited.

This situation has arisen for a number of reasons: First, the majority of studies conducted on foraging behaviour have been conducted on temperate, usually mono-specific, cultivated pastures. Relative to most rangeland communities, such pastures are structurally simple, of low heterogeneity and of high quality. Further, most of these studies have been conducted at the small plot or micro-patch scale or, in some cases, using artificial swards or pasture boards. Second, those studies which have been conducted on rangelands have tended to be small scale (plot or small paddock level) and have often deliberately excluded or suppressed any elements of spatial or temporal heterogeneity. Many rangeland studies have also been largely descriptive and have not attempted to elucidate the underlying processes determining the foraging behaviour in question. Third, for reasons of simplicity and ease of handling, most studies on rangelands and cultivated pastures have tended to use non-reproductive animals and/or animals maintained on a high nutritional plane. This is problematic, given that animal 'state' is a major determinant of foraging behaviour and that the majority of stock on rangelands are breeding animals, often maintained under conditions of sub-optimal nutrition.

To overcome these deficiencies and develop realistic conceptual and predictive models of foraging processes on extensive rangelands, a number of issues need to be addressed.

1. Confronting environmental heterogeneity

It is critical that future work confronts the spatial and temporal heterogeneity inherent at all scales in rangelands and that projects be designed accordingly, rather than assuming that heterogeneity does not exist or attempting to reduce it to a minimum. However, it is also important that this heterogeneity be addressed at the scales relevant to the foraging animal. Thus studies need to focus on functional heterogeneity, rather than simply addressing heterogeneity at every possible level or focussing on heterogeneity for its own sake.

2. Quantifying environmental heterogeneity

It is essential that the spatial or temporal heterogeneity be quantified and analysed in an appropriate manner. Consequently, it is obvious that gross parameters such as 'mean sward height', do not provide a meaningful representation of the environment to the foraging animal. To this end the appropriate statistics and measurements need to be applied that capture the scale and extent of variability in the environment. For example, spatial statistics have been used to describe complex patterns of vegetation structure and patterning the resultant animal response to such attributes eg Owens *et al* (1995). While such statistics have an essential place in capturing and quantifying heterogeneity, a major problem nevertheless remains in terms of linking foraging behaviour in a meaningful and unambiguous manner to such parameters. In many cases however, all that is required is to ensure that vegetation measurements are conducted at the appropriate scale on the unit of relevance to the foraging animal. For example on multi-species swards, measurements could be focussed on the grazed sub-population of individuals of the preferred plant species.

For large spatial scales and/or more complex systems new technology exists to capture spatial heterogeneity at many scales. Examples here include satellite imagery, low-level aerial videography or ground-based sensing systems eg Clifton *et al* (1994). Linking such

technology with GIS systems allows such complex and detailed data to be analysed and integrated across the scales relevant to the foraging animal.

3. Quantifying the animal response to large scale heterogeneity

In the past, the ability to monitor and quantify the foraging response of the animal to the larger scale heterogeneity operating at the paddock and landscape level has been constrained by the available technology. Previous techniques were often highly intrusive, required frequent animal handling, non-robust and /or limited to small-scale application. For example, fistulated animals are of little use at large spatial scales where animals forage across a range of vegetation communities.

Recent technological advances have provided a range of tools that are largely non-intrusive, require minimum animal handling and integrate animal responses over a range of scales. For example, Near Infra-Red Spectroscopy (NIRS) analysis of faecal samples provides a rapid, cheap and reliable method of quantifying dietary quality, intake and, to some extent, even diet selection in free ranging animals. Relatively cheap Global Positioning Systems are also available that permit the collection of precise, detailed data on animal movement patterns across large, heterogenous landscapes. Other systems allow the automatic, long term collection of data such as grazing time, distance travelled and activity level in free ranging animals.

4. Elucidating the effect of 'state' on foraging decisions

There is compelling evidence that the 'state' of an animal (Mangel & Clark 1986) is a major determinant of foraging behaviour and resource use eg (Fiesta-Bianchet 1988). Consequently, the effect of 'animal state' on diet selection, spatial distribution and foraging behaviour needs further elucidation if realistic models of resource use for animals on rangelands are to be constructed.

5. Information transfer and learning

Work conducted under controlled conditions and/or at the small plot scale indicates that spatial memory, dietary learning and information transfer between individuals plays a significant role in improving foraging efficiency eg Laca (1998), Dumont & Petit (1998); Provenza (1995)). Group size may also play an important role in foraging behaviour (Fritz & DeGarne-Wichatitsky 1996). These processes are also likely to play a significant role on rangelands in determining, for instance, species selection and the spatial distribution of animal groups, and require investigation.

6. Spatial arrangement of patches

There is evidence that the size, arrangement and relative distribution of patches strongly determines patch (Hester & Bailie 1998), and probably landscape, utilisation. Moreover, different animal species appear to interact differently with these variables resulting in markedly different patterns of patch use (Hester & Bailie 1998) and ultimately, vegetation structure and composition. The inter-relation between spatial arrangement and utilisation in different animal species requires serious investigation at different spatial scales on rangelands, particularly in view of the current problems of degradation and fragmentation in these environments.

In conclusion, we have good understanding of short term processes operating in small scale, relatively simple environments, our understanding and ability to predict longer term processes operating at the larger scale in more complex rangeland environments is poor. The major challenge therefor is to advance our current information, theory and models upwards from the small scale to accommodate and realistically simulate the larger, more complex systems operating on rangelands. This will require first, the scaling up of existing information and models to larger spatial and temporal scales. And second, improving our understanding of the foraging processes that operate at the larger patch and landscape scale on rangelands and the effects that these processes have on animal intake and performance.

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Table 1 - Examples of different resource types at the plant, patch and landscape scale (After Owen-Smith 2000)

Resource Type	Plant level	Patch level	Landscape level
Quality resources	Flowers, fruits, seed pods.	High fertility patches dominated by ephemeral grasses	Productive areas only accessible in the wet season
Staple resources	Medium quality, perennial grasses eg <i>Themeda</i>	Patches of intermediate biomass	Medium productivity areas, accessible all year
Restricted intake resources	Small leaved, thorny, palatable, browse species	High quality grazing lawns on termitaria etc	Previously burnt areas etc
Reserve resources	Lower quality perennial grasses	Tall, rank patches dominated by such species	Poorly accessible areas dominated by staple species.
Buffer resources	Unpalatable, chemically defended plants eg <i>Cymbopogon</i>	Unpalatable patches, areas of faecal contamination etc	Steep rocky slopes, dominated by unpalatable species, areas of high predation risk