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Dietary selection and foraging strategies of animals on rangeland - coping with spatial and temporal variability

Rangelands occur throughout the world, from the polar circle to the inner tropics, from sea level to higher altitudes and from semi-desert to mesic environments. These different rangelands support vastly different vegetation communities ranging from annual desert grasslands support vastly different vegetation communities ranging from annual desert grasslands to sub-tropical savannas and from arid scrublands to mountain heath lands. The world' s rangelands are thus extremely diverse and vary widely in species composition, structure, productivity and, ultimately, in their capacity to support animal production.

Despite this diversity, a unifying property common to all rangelands is the extreme spatial and temporal variability of these environments. Spatially, this variability occurs at scales ranging from the plant part to the regional level, resulting in pronounced patchiness in the quality and availability of forage in the environment. Temporally, variability may occur over time periods ranging from a few seconds to a few years, resulting in dramatic fluctuations in both forage quality and availability with time. Spatial and temporal variability also frequently interact, creating a mosaic of patches which vary in both time and space.

In contrast, the animals utilising these rangelands require a relatively constant intake of nutrients to satisfy the requirements of metabolism, growth and reproduction. These nutrients must be located, harvested and digested within the constraints imposed by factors such as muzzle width, body size and gut capacity in the foraging behaviour, metabolic requirements and digestive efficiency of the animal concerned. Animals on rangeland are therefore faced with the problem of obtaining a relatively constant supply of nutrients in an extremely variable and fluctuating environment. This paper addresses the problem of spatial, temporal and spatio-temporal variability for animals on rangelands. In each section, the variability commonly encountered at different hierarchical levels in rangeland is first described. The theoretical and observed responses of the animal in terms of dietary selection, foraging behaviour and digestive strategy to this variability are then discussed. The paper concludes by discussing the relevance of spatial and temporal variability for the grazing animal in terms of foraging behaviour and resource management. The focus of the paper is on domestic herbivores in general and grazing ungulates in particular but where necessary, examples are cited from work involving browsers or wild ungulates.

1. Spatial Variability

In this paper, spatial variability is addressed using a plant based approach which starts at the level of the individual plant part and moves upwards to the plant, patch, landscape and regional levels. It is accepted that these hierarchical levels are somewhat subjective and may not necessarily coincide with the perceptions of the foraging animal. However, this approach avoids confounding body size with scale is a problem associated with any animal based classification of spatial variability.

1.1. Plant part level

At the smallest scale, animals are confronted with spatial variability within the plant canopy, due to inherent differences in the nutrient content of different plant parts. Generally, fruits and flowers are of higher quality than leaves, while green leaves are of higher quality than either stems or dead material (Arnold 1960). Considerable variation in quality within different plant parts also exists due to differences in maturity and hence, tissue lignigication (Wilson 1981). Plant parts may also differ in potential bite dimensions due to size or specific mass while potential ingestion rates may vary due to tensile strength or location and spatial arrangement within the canopy. Spatial variability in bite size and quality may occur at the scale of a few millimetres to a meter or mire depending upon plant size and phenology.

Animals respond to such variability by selecting leaf in preference to stem and green in preference to dry material (Arnold 1960, Juko and Bredon 1961). Selection also occurs within particular plant fractions with young leaf being selected in preference to mature leaf (Arnold 1960). Animals also select the most accessible leaf which offers the largest bite size or rate of intake, such as that growing at the canopy surface (Barthram 1981) or clustered at the base of stemmy tufts (Ruyle *et al* 1987).

1.2. Plant level

Rangelands are typically comprised of a large number of plant species which vary widely in nutritive value e.g. Juko and Bredon (1961), and ruminal degradation rate (O' Reagain *et al* 1995). Species also vary widely in morphology and structural geometry and thus in bite size and potential rate of ingestion (Cooper and Owen-Smith 1986, O' Reagain 1994). Marked intra-specific variability may also arise due to individual differences in defoliation history. This pattern is usually initiated in the early season when some plants are grazed through chance (Gammon and Roberts 1978a) while others remain undefoliated. As animals tend to select previously grazed plants in subsequent grazings (Gammon and Roberts 1978b), with time, ungrazed tufts

become rank and stemmy while grazed tufts remain green and leafy. This creates a mosaic of grazed, partly grazed and ungrazed plants within a single species, varying widely in forage quality and potential ingestion rate (Ruyle *et al* 1987).

Animals respond ti inter-specific variability by selecting species which are nonstemmy and have accessible leaves of high nutrient content and low tensile strength. Conversely, low quality, stemmy species with inaccessible leaves of high tensile strength are avoided (Theron and Booysen 1966, Field 1976, O' Reagain and Mentis 1989a, O' Reagain 1993). Grasses such as *Cymbopogon validus* which contain secondary compounds like terpenes are also generally avoided. Species selection therefore appears to be based upon the interplay between plant structure, which determines intake rate, and leaf quality, which determines nutrient content (O'Reagain 1993). However, the relative importance of these two factors appears to vary between animal species according to the particular constraints under which they operate (O'Reagain 1993). For example, leaf quality is likely to be of greater importance for sheep than for cattle given the relatively greater energy requirements and lower digestive ability of the former animals.

In terms of intra-specific variability, animals tend to select previously defoliated plants (Gammon and Roberts 1978b) largely because ot their high quality, accessible regrowth (Bakker *et al* 1983). Conversely, ungrazed tufts which are rank and contain senescent material are avoided or only lightly grazed (Mott 1985, Ganskopp *et al* 1993). For example, *Agropyron desertorum* tufts artificially supplemented with cured stems were less likely to be grazed by cattle and had less forage removed than plants in which stems were absent (Ganskopp *et al* 1993). Animals thus appear to respond to inter- and intra-specific variability by selecting species or individual plants within species, which maximise their rate of intake of digestible nutrients.

1.3. Patch level

Patchiness is inherent to natural vegetation and is apparent in all rangelands. A patch is defined here as the unit of variability commonly encountered within a landscape unit. Patches may vary in sward structure, phenology, nutritive value or even species composition, but will be identifiable with the landscape unit as a whole. Patches may therefore vary in size from a few centimetres in diameter, as in sites of urine deposition, to a few meters in area such as around a gate or watering point, to macropatches hundreds of metres in extent resulting from fires or other phenomena. At the smallest scale, a patch could therefore be an individual plant while at the upper limit, a patch could be equivalent to a landscape unit. Delineation of what

constitutes a 'patch' is thus subjective and dependent upon animal size, group size, the foraging activity under consideration and observer perceptions.

Patches largely reflect natural spatial variability within rangeland environments, particularly with regard to edaphic features. For example, in a supposedly uniform 1.5 ha area of South African grasslands the P and clay content at 40 randomly selected points was found to vary between 4.9 – 15 mg/kg and 4.7. – 9 % respectively. This resulted in a large degree of spatial variability in the quantity and quality of herbage produced (Barnes *et al* 1991).

This variability is compounded by various biotic processes, of which the most important is grazing. Selective defoliation of the sward creates a mosaic of grazed and ungrazed patches (Bakker *et al* 1983, Mott 1985, Willms *et al* 1988) of varying size. Once initiated, mosaics are maintained by selective grazing with grazed patches remaining short (Bakker *et al* 1983) while ungrazed patches become rank and stemmy (Mott 1985). Due to spatial variability in fuel distribution, rangelands also frequently burn in a patchy manner (Hobbs *et al* 1991) creating a mosaic of burnt and unburnt areas. Regrowth on burnt patches is of significantly higher quality than that on unburnt areas (Hobbs *et al* 1991) partly because it is undiluted by stem and senescent material and partly because of the increased availability of soil nutrients following fire.

Urine deposition also creates patches of high quality herbage which may persist for between 2 to 12 month (Ledgard *et al* 1982, Jaramillo and Detling 1992). High quality, productive patches may also develop around gates, watering points and other sites of localised nutrient deposition or through the actions of other animals such as termites (Steinke and Nel 1989) or prairie dogs (Coppock *et al* 1983a). In savannas, nutrient cycling and a more favourable micro-climate beneath isolated tress may also produce patches of significantly greater herbage productivity and quality (Belsky 1992) than the inter-canopy zone.

Apart from more obvious patches created by grazing or nutrient deposition, patchiness also arises from the relative distribution and abundance of different plant species in the sward i.e. even in relatively uniform vegetation, animals should 'create' patches by only feeding at points where the density of a particular species exceeds some threshold (Arditi and Dacoragna 1988). This assumes that below the threshold density it is energetically more profitable for the animal to move on and continue searching for other patches (Kacelnik and Bernstein 1988).

The consistent response of animals to patchiness is to select high quality, productive patches but reject those of low quality. Both wild and domestic ungulates persistently

select the higher quality herbage on grazed in preference to that on ungrazed patches (Mott 1985, Bakker *et al* 1983, Ring et al 1985, Willms *et al* 1988, Gordon 1989, Hobbs *et al* 1991). When grazed patches are depleted or collapse, new patches may be initiated in previously ungrazed areas or grazed areas expanded until patches coalesce (Ring *et al* 1985). Grazers also select strongly for burnt in preference to unburnt patches (Du Plessis 1968, Frost 1984, Van Wilgen 1990). Movement onto burnt areas occurs a few days to a few weeks after fire (Du Plessis 1968, Frost 1984) depending upon animal size and position in the grazing succcession. Selection for burnt patches usually persists for two to three mounth (Du Plessis 1968), until herbage quality declines to that unburnt areas (Hobbs *et al* 1991). Animals also select the relatively nutritious patches of herbage on sites of urine deposition (Bazely 1990, Jaramillo and Detling 1992), around termitaria, gates (pers. obs.), under trees (Skinner *et al* 1984) and on prairie dog towns (Coppock *et al* 1983b) in preference to the lower quality herbage in surrounding vegetation. animals respond to spatial variability at the patch level by selecting high quality patches within the general matrix of low quality vegetation.

1.4. Landscape level

At the landscape level, rangelands consist of a mosaic of different vegetation communities clustered in conjunction with geomorphic features (Senft *et al* 1987). Landscapes consist of different landscape units, here defined as areas which differ markedly in species composition, vegetation structure and/or some physical characteristic such as slope, rockiness or soil fertility. Landscape units thus differ not only in forage quality and availability but also in accessibility, potential predation risk and exposure to the elements. Superimposed on this variability are other factors such as the location of water, shade and minerals and the position of local barriers to movement such as gullies, cliffs or dense scrub (Stuth 1991).

The utilisation of different landscape units is primarily dependent upon their location relative to water (Stuth 1991). This is most obvious in arid and semi-arid rangelands where utilisation is largely confined to a 6 to 10 km radius around water (Squires 1982b). However, in the wet season or in more mesic environments, animals may obtain most of their water requirements from plants allowing more uniform landscape utilisation.

Aside from the primary requirement for water (Stuth 1991), selection for different landscape units is strongly correlated with the abundance of preferred species and the quality and availability of forage (Downing 1979, Low *et al* 1981, Harrington 1986,

Novellie *et al* 1988, Gordon 1989). Areas dominated by unpalatable species or those which give a low rate of intake of nutrients are avoided and seldom utilised (Collins *et al* 1978, McNaughton 1978, Harrington 1986). Animals therefore appear to select areas which give the highest return in dietary nutrients per unit of foraging time (Collins *et al* 1978).

The utility of a particular landscape unit is however, strongly dependent upon animal species (Gordon 1989) and the particular constraints within which it operates. Even within species, the utility of landscape units varies with the metabolic and reproductive state of individuals (Clutton-Brock *et al* 1982) and their vulnerability to predators (Festa-Bianchet 1988, Berger 1991). For example, in the western United States pregnant bighorn sheep with high nutrient requirements accept increased predation risks in order to utilise high quality forage on exposed areas. In contrast, lactating ewes, with similar nutrient requirements, select safer, inaccessible, habitats with lower quality forage due to their greater vulnerability to predation (Berger 1991). The selection of units within the landscape is therefore a complex process involving a trade-off between nutrient requirements, distance to water and predation risk, as well as other factors such as exposure to the elements and biting insects e.g. Duncan 1983. Within any animal species, this trade-off will be dynamic, reflecting current environmental conditions and the nutritional requirements and metabolic status of the animal.

1.5. Regional level

Regional systems are large scale assemblages of landscapes (Rowe 1961 cited by Senft *et al* 1987) defined by major differences in geology, climate and/or soils and therefore, vegetation. Different regional systems may however, simply reflect the availability of water or the presence of some physical stressor like extreme cold or heat. In animal terms, regional systems are defined by ranges (Senft *et al* 1987) and in pastoral terms by transhumance and nomadism.

Regional selection largely mimics, landscape selection, with animals tending to select regions according to forage availability and quality. Selection may also be determined by other factors such as the availability of water, extreme weather conditions or predation (Senft *et al* 1987), McNaughton 1990). An example of regional selection is the migration of grazing ungulates in the Serengeti with animals moving to the short grass areas of low rainfall in the wet season but returning to high rainfall areas in the dry season. Here selection is not only dependent upon forage quality and mineral content but may also reflect avoidance of muddy soils, predators and Tsetse fly

(McNaughton 1990).

2. Temporal variability

Temporal variability may be natural or grazing induced. Natural variability arises through normal changes in plant physiology, phenology and growth associated with seasonal or even diurnal changes in environmental conditions. Such changes operate at the cellular level but are expressed at spatial scales from the plant part upwards to the plant, patch, landscape or even regional level. Grazing variability arises through the actions of the animals themselves, through the depletion of available resources. This may operate over time scales ranging from a few seconds to many months and at spatial scales of the plant to regional level. In practice, natural and grazing induced variability interact, increasing the complexity and amplitude of temporal variability encountered by the foraging animal.

2.1. Short term variability

Short term variability in herbage quality and availability occur over a few seconds to a few hours. Natural temporal variability arises from diurnal variation in plant chemical composition due to normal, daily fluctuations in photosynthesis, transpiration and other physiological processes. This results in predictable fluctuations in water content and the levels of carbohydrates (Smith 1973) and secondary chemicals, like alkaloids (Fairburn and Suwal 1961). Evidence suggests that animals may match foraging behaviour with diurnal changes in plant composition. Sheep on temperate pastures commonly defer the bulk of grazing until late afternoon when leaf carbohydrate concentrations are highest (Penning *et al* 1991), presumably maximising their net intake of energy. Similarly, springbok in the arid Kalahari select the inflorescences of desert shrubs before dawn when water contents are highest (Nagy 1994). However, aside from these few examples the animal response natural, short term variability has not been widely researched and warrants further investigation.

Short term temporal variability also arises when grazing depletes the size and quality of bites available at the plant or patch level. This depletion may occur a few seconds within a single plant or feeding station e.g. Laca *et al* (1994) or over a few minutes or hours in a single patch (Jiang and Hudson 1993). In all cases, bite size and intake rate decline with time causing a flattening of the cumulative gain function (Laca *et al* 1994). Theoretically, bite quality should also decline but this effect has not been quantified.

The marginal value theorem predicts that animals should graze a patch (or plant)

until the rate of nutrient gain drops to the average for the environment as a whole (Charnov 1976). Residence time should therefore increase with patch richness and increasing distance to the next patch. This is corroborated by the available evidence which indicates that both domestic (Laca *et al* 1993) and wild ungulates (McNaughton 1978, Baharav and Rosenzweig 1985) have longer residence times in rich than in poor patches. For example, patch residence time in Dorcas gazelles is strongly correlated with shrub density (Baharav and Rosenzweig 1985). Patch residence has also been shown to increase with increasing distance to the next patch. Thus Laca *et al* (1993) observed that cattle increased patch residence times from 40 to nearly 70 seconds as the distance between patches increased from 1.2 to 8.4 m.

The giving-up or departure rules used determine when leave a patch are, however, obscure. For example, while elk appear to leave patches when cropping rates decrease below the seasonal expectation they appear to use neck angle rather than some more obvious cue like grazing time or total bites taken, as cue for leaving feeding stations (Jiang and Hudson 1993). This indicates that different departure rules may be used at different spatial levels within the environment (Jiang and Hudson 1993).

2.2. Medium term variability

In the medium term, temporal variability in forage quality and availability may occur over the space of a few days to weeks. Natural temporal variability in the availability of soil N (Birch 1958) and hence in herbage quality, occurs in conjunction with soil wetting and drying cycles in many grasslands. Consequently, dietary quality frequently declines sharply during periods of water deficit but subsequently recovers when soil moisture levels are replenished (McKay and Frandsen 1969, O'Reagain 1994). Natural changes in plant phenology and growth, and hence in sward structure, which directly affect herbage quality and availability may also occur over the medium term, these are discussed below in section 2.4.

Grazing induced temporal variability in the medium term usually occurs within landscape units at two different levels. At a gross level, grazing depletes overall herbage availability, depressing bite size and bite quality (Chacon and Stobbs 1976). Animals usually respond to such variability by moving to other landscape units where forage is more readily available (Low *et al* 1981, Squires 1982a), presumably obeying departure rules similar to those used at the patch scale. However, under fenced conditions or where other landscape units are unavailable, animals respond by

adjusting foraging behaviour. Typically, animals increase biting rates and/or grazing time in an attempt to compensate for reduced bites sizes (Allden and Whittaker 1970, Chacon and Stobbs 1976, Hudson and Nietfeld 1985, Spalinger *et al* 1988) or may walk faster to increase encounter rates with food items (Wickstrom *et al* 1984, Spalinger *et al* 1988, Baharav and Rosenzweig 1985). These strategies may be successful within fairly narrow limits but generally fail to maintain intake rates when bite sizes are severely restricted, as bite size is the major determinant of intake (Hodgson 1981). For example, when herbage availability was moderately restricted, East African cattle allowed access to night grazing achieved growth rates 30 % higher than a control group but this effect was not observed when herbage availability was either abundant or severely restricted (Joblin 1960). Increased biting rates and grazing times may also carry costs like increased energy expenditure, increased predator attrition (Fitzgibbon 1989)or decreased digestive efficiency through a reduction in the number of mastication bites (Greenwood and Demment 1988).

At the plant level, grazing affects the relative availability of different plant species, through the selective defoliation of the more preferred species in the community. This is particularly pronounced under rotational grazing where the relative availability of different species changes rapidly over the grazing period (O'Reagain and Mentis 1989b). Animals are thus confronted by a series of foraging decisions when to stop rejecting and start consuming species of lower acceptability when encountered. Evidence from African grasslands indicates that both cattle and sheep exhibit a distinct sequence of species selection over a period of occupation in a paddock (Daines 1980, Danckwerts *et al* 1983, O' Reagain and Mentis 1989b, O'Reagain and Grau 1995). Generally, preferred species are grazed first with some utilisation of less preferred species also occurring. When c. 60 % of the tufts of preferred species have been defoliated these plants are regrazed and the rate of utilisation of less preferred species is increased. Only after nearly all the preferred and mist of the less preferred species have been defoliated are any unpalatable species utilised. Stocking density appears to affect only the rate which this sequence proceeds and not the sequence *per se* (Daines 1980, Stoltz and Danckwerts 1990).

The above sequence is in agreement with basic predictions of optimal foraging theory that first, dietary breadth should be widened as food availability declines (Enlen 1966) and second, that the decision to eat a less preferred food (species) should be independent of its own abunddance but should depend upon the abundance of more preferred species (Pyke *et al* 1977). Accordingly, a threshold effect was evident in

some studies with the utilisation of unpalatable species only occurring when the availability of ungrazed, preferred tufts had been depleted below a certain level (O'Reagain and Mentis 1989b, O'Reagain and Grau 1995). Generally, the less palatable the species, the higher the threshold O'Reagain and Grau 1995.

Cues used to decide when to include the next ranked species in the diet could be some minimum intake rate, similar to the marginal capture rate proposed by Krebs and McCleery 1984) or search time cue (MacArthur and Pianka 1966). Interestingly, where plants are regularly distributed, the distance (d) to the next ungrazed plant increases in a exponential manner as tufts are grazed i.e. while there is initially little increase in d, once a certain proportion of tufts have been grazed (60 – 90 % depending on population size), d increases sharply (O' Reagain 1994). This suggests that the thresholds discussed above, could arise from sudden increases in search time associated with locating a rapidly diminishing supply of ungrazed plants.

2.3. Long term variability

Long term temporal variability results from seasonal cycles of vegetation growth and dormancy, caused by seasonal changes in moisture availability and temperature. These cycles frequently result in major changes in forage availability as for example, in the shrub-grasslands of east Africa where the peak herbaceous biomass of 3000 kg can decline by c. 66 % within eight weeks of the end of the wet season (Schwartz 1993). Forage quality may also show distinct seasonal trends with quality usually being highest in the early growing season but declining ti sub-maintenance levels in the dormant season e.g. Schwartz 1993. Sward structure may also change between seasons, reducing leaf accessibility (O' Reagain 1994) while the relative availability of different plant species may change through dormancy or senescence (Schwartz 1993).

Animals have evolved a variety of foraging, metabolic and digestive strategies in response to such seasonal variability. A primary foraging tactic is for animals to simply move to a different landscape or regional system in search of better grazing. This previously occurred in South Africa where animals and pastoralists 'trekked' between the low quality 'sourveld' in summer and the high quality 'sweetveld' in winter. Where such spatial compensation is not possible, animals respond by adjusting foraging behaviour. Thus in times of scarcity animals may widen dietary breadth by including other, less palatable species in the diet, as observed in kudu (Owen-Smith 1994) or utilising other vegetation layers, as observed in savannas

where cattle browse and consume seed pods and leaf litter in the dry season (Skinner *et al* 1984). Daily foraging times may also be extended to compensate for reduced intake rates (Joblin 1960, Jarman and Jarman 1973, Owen-Smith 1994) or to allow increased selectivity (Novellie 1978). Encounter rates with forage species may also be increased by seeking out areas where such species are most common (Owen-Smith 1994) or by increasing travel velocity (Collins *et al* 1978). Metabolically, animals may respond to seasonal fluctuations in forage quality and availability by adjusting net energy requirements. In species like sheep, this may be partly achieved by accumulating fat reserves when conditions are good, for use in times of deficit. However, this strategy may incur costs associated with reduced thermal efficiency or increased vulnerability to predation. Alternatively, energy may be conserved by reducing activity levels at critical times in the season. For example, blesbok in winter markedly reduce activity levels by walking slowly, decreasing grazing time and basking in the sun (Du Plessis 1968, Novellie 1978). Some northern hemisphere cervids show a photoperiod-induced reduction in metabolic rate with approach of winter. A dry season reduction in metabolic rate has also been reported for springbok (Nagy 1994), but whether this reflects a decline in basal metabolic rate per se. or simply a response to decreased energy intake is unclear.

Animals may also utilise a range of digestive strategies to cope with poor quality forage. This may involve increasing digestive capacity e.g. Holand (1994), increasing particle retention time in the rumen (Lechner-Doll *et al* 1990), increased rumination or improved urea recycling (Lechner-Doll *et al* 1990). For example, Lechner-Doll *et al* (1990) compared the digestive parameters of cattle, sheep, goats and dromedaries grazing the semi-arid savannas of Kenya in the wet and dry seasons. In all species the volume of rumen fluid increased in the dry season as did the retention time of particles in both the fore-stomach (figure 1) and the digestive tract as a whole. Such measures may compensate for increased dietary fibre content by prolonging bacterial degradation and hence increasing the extent of ruminal digestion (Lechner-Doll et al 1990). Where forage quality s particularly low, animals like the roe deer may increase passage rates e.g. Holand (1994), in an attempt to maintain a reasonable intake of digestible nutrients. This suggests that animals have some element of control over the rumino-reticulo orifice.

The range of foraging, metabolic and digestive strategies discussed above indicate that animals have a variety of mechanisms to compensate for, or at least buffer, seasonal variability in the supply and quality of forage. However, the mechanisms chosen vary between different animal species. For example, in semi-arid east

African savannah, goats appear to rely on their superior selective ability to select a high quality diet when conditions are limiting, while sheep apparently rely on greater digestive efficiency and the accumulation of fat reserves to survive the dry season. The precise strategy chosen therefore varies with the animal and the particular physical, metabolic and digestive constraints under which it operates.

2.4. Very long term variability

Many rangelands experience major fluctuations in herbage quality and availability between years due to rainfall variability. As mean annual rainfall is inversely correlated with its coefficient of variability (Tyson 1986), inter-seasonal fluctuations in herbage productivity are particularly extreme in arid and semi-arid areas. For example, in the semi-arid Acacia savannas of Zimbabwe, Dye and Spear (1982) recorded a 12 fold difference in herbage production between average and bad years. The potential response of animals to such variability is limited but may involve migration to other landscapes or regions in search of forage. In many cases animals retreat to less favourable marginal areas in poor years which then act as buffer or escape zones. Due to the high energetic costs of reproduction and lactation, females may not come into oestrous under extreme conditions or may abort or abandon neonates in an attempt to reduce energy expenditure.

3. Spatio-temporal variability

Spatial heterogeneity frequently inteacts with temporal variability in the amount and distribution of rainfall to increase rangeland complexity (Danckwerts *et al* 1993). In arid and semi-arid areas this results in pulses of productivity and quality which are stochastic and poorly predictable in both space and time (Ellis and Swift 1988). Consequently, animals in these environments are usually highly mobile, responding opportunistically to pulses of productivity across the landscape. For example, cattle in Australia' s arid interior (Squires 1982a) and wildebeest in the Serengeti (McNaughton 1979) track storms, frequently appearing on sites within days of a rainfall event. Such strategies increase individual animal production and overall landscape productivity.

4. Discussion

Animals have evolved a range foraging, digestive and metabolic strategies in response to the inherent variability of rangeland environments, allowing them the flexibility to survive under a wide range of environmental conditions. The particular

strategies adopted, and their relative success, vary both between within animal species, according to the particular constraints under which a species operates and the metabolic and physiological 'state' of the individual animal.

All strategies however, impose costs which ultimately reduce the long term fitness of the animal. These costs may be obvious such as reduced digestive efficiency or increased predator attrition or more insidious such increased tooth wear or metabolic turnover. The choice of strategy will therefore ultimately depend upon its cost-benefit ratio, which will be unique for each animal. At present, the relative costs and benefits associated with different strategies are poorly understood and these require further investigation.

Given the spatio-temporal complexity of rangelands, how do animals identify and locate the highest quality patches or plant species in these environments? First, animal may track environmental changes by constantly monitoring the quality and availability of different plants species or patches. This may be achieved by sampling at both the plant and patch level e.g. Illius *et al* (1992), to detect changes in forage quality and availability. Such 'sampling' may explain the wide diversity of plant species commonly observed in herbivore diets. Second, cattle and probably most ungulates, appear to have well developed, long-term spatial memories (Baily *et al* 1989, Laca 1993) allowing them to remember both the location and amount of food present in the environment. This, coupled with an intimate knowledge of their range, would enable animals to easily locate spatially dispersed patches in complex environments. Third, information transfer between individual animals about the location and quality of different food resources may occur. This is most common from mother to off-spring, but may also occur from adults to unrelated juveniles and between individuals in the same herd. The above processes increase overall foraging efficiency by increasing nutrient intake and decreasing the time and energy expended in locating these nutrients in a complex and fluctuating environment.

While the spatial and temporal variability of rangelands may be seen as a challenge, paradoxically this variability also provides a major opportunity to the foraging animal. By grazing selectively, animals can achieve nutrient intake rates higher than the average available from the environment as a whole, allowing them to survive in areas which on average, are incapable of supporting animal production. Small, scattered, high quality patches also allow animals to exploit surrounding low quality vegetation communities, either as a source of fodder or for cover and shelter. Although small, these patches frequently supply a disproportionate amount of animal nutrient requirements e.g. Collins *et al* (1978), or may stimulate the rumen sufficiently to allow

utilisation of the surrounding low quality vegetation (Goodchild an McMeniman 1994). Most importantly however, spatial variability enables animals to cope with temporal variability by allowing them to switch between spatial units in response to fluctuations in forage quality and availability. This ability to exploit spatial variability at the landscape or regional level improves individual animal production, increases total carrying capacity and reduces the probability of environmental degradation (Barnes 1979). Where animals are denied access to spatial variability large scale of fodder or supplements are periodically required to avert mass mortality resulting from fluctuations in herbage availability or quality. Spatial variability therefore provides the critical flexibility to survive in a changing and unpredictable environment.

Summary

Rangelands exhibit extreme spatial and temporal variability in the quality and availability of forage. Spatial variability occurs from the plant part upwards, to the plant, patch, landscape and regional levels, while temporal variability may occur over time scales ranging from seconds to many years. Spatial and temporal variability may also interact, resulting in pulses of productivity which fluctuate in space and time. This variability is problematic for rangeland animals whose nutrient requirements are relatively constant.

Aside from the basic requirement for water, animals respond to spatial variability by selecting patches or areas which offer the highest intake of digestible nutrients. This selection may also be influenced by other factors such as predation or cover. Animals compensate for temporal variability in forage quality and supply through a range of foraging, digestive and metabolic strategies. The particular strategies adopted and, their success, vary between species and individual animals, and the particular constraints under which they operate. Although problematic, spatial and temporal variability paradoxically allows animals to successfully exploit unpredictable and low quality rangeland environments.

Key-words: dietary quality, ingestive behaviour, landscape, patch, region, species selection.

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