

Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates

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Abstract

Resident grazing ungulates in the Serengeti National Park, Tanzania, are conspicuously patchy in their distribution among regions of the Park. Linear programming models that maximize nitrogen (N) consumption by foraging ungulates in Serengeti regions having high and low resident animal densities were compared using forage ingestion rate and twelve nutritional requirements as simultaneously imposed constraints on forage choice. Model results indicate that (1) growing season N or crude protein is not limiting in either region although greater N ingestion is possible within the eastern corridor under other nutritional constraints, (2) grazing ungulates in the eastern corridor region occur in greater density and are capable of balancing dietary requirements solely from forage while simultaneously consuming more protein than ungulates in the northeast region, and (3) rarer landscape elements are most capable of providing ungulate dietary requirements in both the northeast and eastern corridor. These results provide a nutritional basis to understand patchy spatial distributions of grazers within Serengeti regions and landscapes, and provide a partial test of the hypothesis that large generalist herbivores should graze rare forages more frequently. The ability of uncommon landscape elements to support ungulate grazing over the growing season is supported by previous ecosystem studies that demonstrate the capability of grass forages for compensatory growth and the ability of grazing to stimulate rapid nutrient recycling.

1. Introduction

The Serengeti ecosystem is comprised of approximately 25,000 km², primarily in northwestern Tanzania, but spanning the border into southern Kenya. The extent of the ecosystem is delineated by the migratory wildebeests (*Connochaetes taurinus*) as they move between wet season ranges on the southeastern plains of the ecosystem to the northern reaches of the ecosystem during the dry season (Pennycuik 1975; Maddock 1979; Sinclair 1979a). Within the ecosystem, the Serengeti National Park, located totally within Tanzania, represents the core

area ostensibly protected from poaching and human encroachment. Across the ecosystem, generally from southeast to northwest, extend physical gradients of increasing rainfall and coarseness of the soil (Sinclair 1979b; Bell 1982; McNaughton 1985). Associated with these physical changes are southeast to northwest clines of decreasing soil fertility (Ruess and McNaughton 1987; McNaughton 1990), decreasing grazing intensity during the wet season (McNaughton 1985), and decreasing soil microbial biomass (Ruess and McNaughton 1987). Although plant community structure and composition also vary along these gradients, spatial varia-

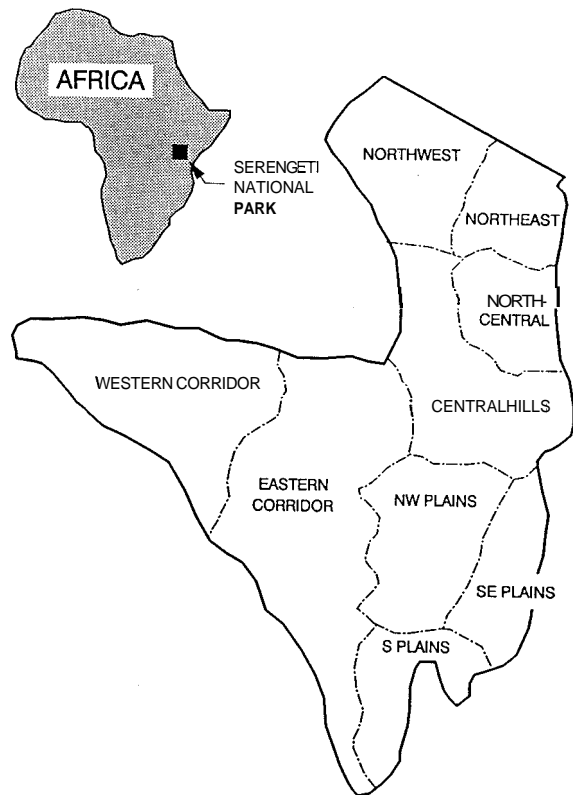


Fig. 1. Regions of the Serengeti National Park, Tanzania, based on soils and vegetative composition. In a south-southeast to north-northwest direction across the Park there exist gradients of increasing rainfall and sandiness of the soil, along with gradients of decreasing wet season grazing intensity, soil nitrogen fertility, and soil microbial biomass. Within these cross-regional gradients, these variables may vary locally because of landscape position. Resident grazing animals also vary in density within Park regions with, for example, the northeast region having notably fewer grazing ungulates than the eastern corridor.

tion in plant communities within different regions of the park is apparent (McNaughton 1983) and often associates with slope or catena position. Based on these variations in soil and vegetative composition, the Serengeti can be divided into several regions (Fig. 1) for comparative purposes. On an annual time scale, long-distance migratory ungulates obviously exploit the entire Serengeti as a heterogenous mosaic of regions and have been proposed to gain nutritional advantages by migrating among regions (McNaughton 1990). However, both migratory and resident grazers must view the various grass species and catena positions within

any single region as a mosaic of feeding choices during a single season of the year. While migratory animals may benefit on an annual basis from nutrient gains made by seasonal use of different regions, resident animals must meet all dietary requirements within a single region or landscape within that region. We suggest that differential food quality, reflected by ease in meeting dietary requirements, may select for regional and landscape-level distribution of ungulates and perhaps influence the production of grazing ungulates within these regions.

Wild grazing ungulates generally encounter an abundant food source that varies in quality both temporally and spatially (Westoby 1978; Belovsky 1984, McNaughton 1988, 1990). In order to clarify the role of spatial resource distributions in explaining ungulate grazing patterns, Senft *et al.* (1987) proposed a spatial hierarchy of foraging components with selection units ranging in scale from individual plants, through communities, to entire landscapes embedded within regions. Within such a hierarchy, free-ranging grazers must forage efficiently enough to meet energetic demands while balancing nutritional requirements. McNaughton (1989) presented a similar foraging hierarchy for the Serengeti ecosystem, along with forage nutrient analyses indicating that Serengeti ungulates confront substantial heterogeneity in forage quality during the growing season at each hierarchical level. Thus, Serengeti grazers are subject to balancing nutritional requirements for macro- and micronutrients through forage choice at a variety of spatial scales even during that season when forage is abundant. Evidence of deficient dietary balance for both domestic (McDowell *et al.* 1983) and wild (McNaughton and Georgiadis 1986) African ungulates suggests that the forage heterogeneity found in Serengeti grasslands may render a nutritionally balanced diet problematic despite the long evolutionary history of grasses and herbivores in African savannas (McNaughton *et al.* 1985).

The theory of optimal foraging (Emlen 1966; McArthur and Pianka 1966; Schoener 1971; Pulliam 1974; Pyke *et al.* 1977; Pyke 1984; Stephens and Krebs 1986) addresses the role of food quality in determining the diet composition and foraging

tactics of animals. Schoener (1971) put forth alternative strategies that animals might use in selecting the composition of their diets. These included energy maximization and foraging time minimization. However, the nutrient content of primary producers is associated with many environmental parameters and is more variable, both inter- and intraspecifically, than animal nutrient composition; thus Ellis *et al.* (1976) suggested that herbivores need be more selective in food choice to meet nutritional requirements than do carnivores. Therefore herbivores might display yet another foraging strategy: optimizing nutritional balance such that both nutritional and energetic needs are met (Emlen 1973). By the nature of their lower trophic position, herbivores have available a greater energy resource in food material and may not necessarily be energy limited either through sheer availability or effort expended in energy intake (Ellis *et al.* 1976; Belovsky 1984). For large generalist herbivores, Westoby (1974) argued that the main premises of optimal foraging theory were not applicable because these herbivores are limited to a fixed bulk of food, related to body size and gastric morphology, that is digestible. Thus the feeding strategy of large ungulates, for example, should be to achieve a balanced diet within an allometrically determined bulk of food. Westoby (1974, 1978), Pulliam (1975), and Belovsky (1978) presented the optimization of generalist herbivore diets as a linear programming problem, similar to that faced by domestic animal scientists in calculating feed ratios that meet dietary standards while minimizing cost of feed materials. In nature, rather than monetary costs, generalist herbivores are assumed to either maximize energy and protein intake, or minimize energy expended in foraging time, while balancing a suite of nutrient requirements. Senft *et al.* (1987) further refined the problems of understanding generalist herbivore foraging by combining elements of optimal foraging theory, landscape ecology, and hierarchy theory. In this context for herbivore foraging, we examine the potential influence of ungulate nutrition on regional distribution and landscape utilization, and present a partial test of Westoby's (1974) prediction that foraging ungulates should select relatively rare forages that confer

high nutritional content. In doing so we hope to provide insight to the basis for regional distributions of resident Serengeti grazers and ungulate utilization of patchy landscapes.

2. Methods

Based on field observations, both the number and density of resident animals vary among Serengeti regions. In particular, population numbers and densities seem much lower in the northeast region of the Serengeti as opposed to the eastern corridor region (Fig. 1). Regular aerial censuses of both resident and migratory animals within the Serengeti are carried out by the Serengeti Ecological Monitoring Programme (SEMP). Data collected by SEMP during 1988 were thus used to test whether the density of resident animals found in the northeast was lower than the density of residents in the eastern corridor of the Serengeti. These densities were calculated from SEMP counts using only grazing species that included primarily topi (*Damaliscus korrigum*), hartebeest (*Alcelaphus buselaphus*), buffalo (*Syncerus caffer*), Grant's gazelle (*Gazella granti*), waterbuck (*Kobus defassa*), and eland (*Taurotragus oryx*). Those non-migratory wildebeest and zebra (*Equus burchelli*) found in these regions were also included. Impala (*Aepyceros melampus*), a mixed feeder that grazes during the wet season and browses during the dry season (Jarman and Sinclair 1979), was included because our analyses focus on wet season forage attributes. Thomson's gazelle (*Gazella thomsoni*) was not included due to migratory habits and their recognized preference for feeding on forbs (Jarman and Sinclair 1979), which were not analyzed for nutrient content.

Our basic spatial units for considering grazer distribution in relation to forage nutrients were the northeast and eastern corridor regions of the Serengeti (Fig. 1). However, within each region, foraging landscapes are composed of a combination of structural elements (catena positions) and grass species. Catenas are long slowly sloping hillsides which, for our purposes were divided into top, middle and bottom. In addition, two other physiographic landscape components were considered:

(1) flats, which are open areas not associated with any slopes, and (2) rocky hillsides that are unique due to abundant stones and often relatively steep slopes. Collectively these five structural features were referred to as catena positions, with each often supporting unique grass species. These grass species-catena combinations represented our finest scale of resolution for foraging and were defined as landscape elements.

In order to assess the influence of forage quality within regions and landscape elements on the ability of ungulates to meet dietary requirements, an objective assessment of forage availability and nutrient content was needed. As part of a forage survey conducted by SJM during the wet season of **1986**, triplicate samples of young, actively growing leaf blades were collected from landscape elements in both the northeast and eastern corridor regions of the Serengeti. Grass samples were sun-dried in plastic mesh bags and transported to Syracuse University for nutrient analyses as described by McNaughton (**1988**). The concentrations of thirteen nutrients were analyzed for fourteen landscape elements in the northeast region and sixteen landscape elements in the eastern corridor. Estimates were also made of the proportion of each region that each landscape element represented by considering the topography of the region and the distribution of grass communities (McNaughton **1983**). Univariate (t-tests) and multivariate (discriminant analysis) statistical comparisons of the two regions were made using the SAS (**1985a**) statistical package. Log transformations were used in the discriminant analysis to re-scale widely varying nutrient concentrations and avoid having concentrations of great magnitude inordinately influence the analysis.

Although much information exists concerning wildlife nutrition (Robbins **1983**) and there is a body of literature on grazing ruminant nutrition in tropical climates (McDowell **1985**), relatively little is known about the specific nutritional requirements (other than energy and protein needs) of wild herbivores (Suttle **1987**). Thus ungulate dietary requirements were derived from McDowell's (**1985**) compilation of nutritional requirements for beef cattle in warm climates. Two dietary standards are

generally recognized. Absolute nutritional requirements represent those levels at which animals must receive nutrients to carry out daily and life cycle activities; performance standards are higher and represent those nutrient levels used for economic production. We felt that absolute nutrient standards represent more ecologically-oriented nutritional standards and utilized them in our analyses.

Linear programming models seek to maximize/minimize the value of a variable known as the objective function, under constraints imposed by the values of further variables identified in the model. Two choices for the objective function in such a model were apparent in our data set: (1) nitrogen (N) ingestion could be maximized, or (2) 'cost' or rareness of a forage item, calculated as the reciprocal of its regional percent, could be minimized as a proxy for energetic cost of foraging on that item. We elected to maximize N intake because (1) it is directly related to crude protein content (Moen **1973**) which is generally of greater importance to large herbivores than rate of digestible energy intake (Belovsky **1984**), (2) wild herbivores in the Serengeti carry little fatty tissue and catabolize body protein during the dry season (Sinclair and Duncan **1972**; Owen-Smith **1982**), leaving the wet season (the period during which forage samples were collected) for replenishing body mass and growth, (3) N/protein is known to be a limiting nutrient for large herbivores in seasonal environments (Bell **1971**; Sinclair **1975**), and (4) energy availability to grazing herbivores is largely a function of microbial fermentation rates in the rumen and have not been accounted for analytically. Absolute feeding requirements were used to set minimum ungulate nutrient intake levels as constraints in the model. As noted by Westoby (**1974**), grazing ruminants are also constrained by rumen volume. We used an herbivore mass of **153 kg**, which is the average mass of a wildebeest (Georgiadis **1985**) and represents the approximate median mass of those ungulates included in the resident animal density estimates. Thus, in addition to nutrient constraints, a daily intake of **3%** of body mass (Owen-Smith and Novellie **1982**; Ruess and McNaughton **1988**) represented a model constraint on daily forage mass intake. Although these are reasonable mass

estimates, the linkage between body size and forage intake capacity, combined with evidence for little difference in nutrient requirements among wild ungulate species once genetically determined body size is accounted for (Taylor and Murray 1987), made choice of average ungulate body size arbitrary. Model results would be identical unless nutrient requirements were varied, perhaps to represent different age classes. If energetic requirements were being analyzed the choice of body size would have been critical because energetic requirements scale with body size. To summarize, a linear programming routine using the simplex method for analysis (SAS 1985b) was applied separately to the northeast and eastern corridor data to assess the potential for a resident grazing ungulate to balance daily dietary needs while foraging from the array of landscape elements within each region, with absolute standard nutrient requirements and daily mass intake as constraints in the model. These analyses allowed (1) comparison of nitrogen intake and dietary nutritional balance for ungulates foraging in the two regions, and (2) description of predicted landscape element use within each region.

3. Results

3.1 Animal densities

Based on the most recent data (1988) compiled by SEMP, the eastern corridor of the Serengeti averages approximately 50.1 resident animals/km²; the northeast region has only 44.7% of that density with 22.4 animals/km². Given the inherent variability in aerial animal censuses, we intend these densities to be only approximate estimates. However, other indications of regional variation in resident ungulate densities have been documented (e.g., Sinclair 1972) and also observed by the authors during field activities. This variation suggests that resident grazers, at the least, select different regions for habitation, and that ultimately population regulation may be different within the two regions.

3.2 Forage distributions and nutrients

Differing distributions of both catena positions and forage species create distinct landscape element compositions for the northeast and eastern corridor regions (Table 1). The northeast is heavily dominated (50%) by middle catena with a grass cover of *Themeda triandra*; in contrast, the eastern corridor's most common landscape element is the flats with a cover primarily of *Pennisetum mezianum* (24%). The variety of landscape elements within each region, however, provide a diverse template for grazing ungulates.

Several forage sample nutrients differ significantly between the northeast and eastern corridor regions (Table 2). Sodium (Na) and phosphorus (P), two nutrients of obvious importance in animal nutrition, display the greatest differences between the two regions. The eastern corridor mean Na concentration was 21.5 times that of the northeast, due primarily to the presence of Na accumulating plants within the corridor; P mean concentration was 1.9 times greater in the eastern corridor. Magnesium (Mg) and zinc (Zn) were also significantly different, while potassium (K), manganese (Mn), and molybdenum (Mo) showed marginal significance. Of these nutrients, Mn and Zn average higher concentrations within northeast forages. Nitrogen, the variable to be maximized in our analyses, is not significantly different between the landscape elements of the two regions. This lack of significance does not impede our analyses because our goal is not to model maximal N intake alone, but to maximize N intake by grazers given a suite of nutritional constraints.

These different constraints are reflected when the northeast and eastern corridor regions are compared in a multivariate sense using discriminant function analysis. Only one observation from each region is misclassified as belonging to the other, resulting in a 93% correct classification proportion for the northeast and a 94% correct proportion for the eastern corridor. Although these classifications do not test the utility of the discriminant function as a classificatory tool because the set of observations used in the analysis also made up the classified set, the high level of accurate classification and the

Table 1. Grass species distribution by catena position within the northeast and eastern corridor regions of the Serengeti. Each existing species-catena combination is considered to be a landscape element. For each landscape element triplicate samples were collected in the field at a single site unless multiple sites are indicated in parentheses. The eastern corridor is richer in both forage species and physiography as represented by total percentages of catena positions.

REGION	SPECIES	CATENA PERCENTAGES				
		FLAT	BOTTOM	MIDDLE	TOP	ROCKY HILLSIDE
Northeast	<i>Themeda triandra</i>					
	<i>Sporobolus pyramidalis</i>	3				
	<i>Themeda triandra</i>	2	2	50(4)	10	
	<i>Echinochloa haploclada</i>		1			
	<i>Bothriocloa insculpata</i>		5			
	<i>Chloris gayana</i>		2			
	<i>Sporobolus pyramidalis</i>			20		
	<i>Loudetia kagerensis</i>					1
	<i>Heteropogon contortus</i>					4
	Σ =	5	10	70	10	5
E. Corridor	<i>Pennisetum mezianum</i>	24(2)				
	<i>Chrysochloa orientalis</i>	6				
	<i>Themeda triandra</i>		9(2)			
	<i>Panicum coloratum</i>		4			
	<i>Cymbopogon excavatus</i>		2			
	<i>Sporobolus fimbriatus</i>			10		
	<i>Digitaria macroblephara</i>					
	<i>Sporobolus ioclados</i>			10		
	<i>Sporobolus ioclados</i>			5	5(2)	
	<i>Digitaria macroblephara</i>				5	
	<i>Heteropogon contortus</i>					17(2)
	<i>Eustachys paspaloides</i>					3
	Σ =	30	15	25	10	20

interpretability of the discriminant function (Table 2) reflect the regional differences in landscape elements available for selectively foraging resident ungulates. Correlations of the nutrients with the discriminant function corroborate the univariate analyses (Table 2); only those variables significant or marginally significant in the univariate tests correlate significantly with the discriminant function. These correlations reflect once again the importance of Na and P in defining differences between the two regions, but do not specifically address ungulate foraging to achieve nutritional balance.

3.3 Regional diet analysis and landscape utilization

Although significant differences between forage nutrient concentrations within the two regions

reflect different foraging mosaics for grazing ungulates, they do not indicate the relative ability of grazers to balance dietary requirements while maximizing N or crude protein consumption. Solving this problem using a linear programming maximization algorithm indicates that grazers in the northeast region can consume 121.6 g N per day (760.3 g crude protein) with 3% body mass intake, but still be deficient in Na intake by 1.5 g. For the eastern corridor, grazers can obtain 147.8 g N/day (923.6 g crude protein), 21.5% more N per day than in the northeast, while meeting all nutrient requirements (Table 2). Both northeast and eastern corridor analyses resulted in N or crude protein consumption surpassing the minimum daily requirement of 70.5 g N or 440.6 g protein.

The predicted diets maximizing N ingestion are

Table 2. Univariate and multivariate comparison of forage nutrients from the northeast (N = 14) and eastern corridor (N = 16) regions of the Serengeti. Regional means were compared using *t*-tests which were adjusted for regional differences in variance when necessary; significance levels for these tests are indicated in column P. Pearson product-moment correlations between individual nutrients and the discriminant function (DF) resulting from comparing the two regions indicate those nutrients contributing most significantly to regional differences. Nutritional standards used in the diet analysis are presented and are based on a 153 kg grazer consuming 3% of its body weight per day.

NUTRIENT	REGIONAL MEAN (PPM)		P	CORRELATION WITH DF	REQUIREMENT (g/day)
	NORTHEAST	E. CORRIDOR			
Ca	3689.7	3433.4	.59	-.08	8.3
Co	.2	.3	.39	.17	3.0×10^{-4}
cu	5.9	5.8	.93	.01	1.8×10^{-2}
Fe	108.4	125.1	.34	.17	2.3×10^{-1}
K	15955.9	19597.1	.07	.33	2.3×10^1
Mg	1432.2	1778.4	.04	.45	2.2
Mn	75.7	37.9	.11	-.54	9.2×10^{-2}
Mo	1.9	2.9	.12	.39	4.6×10^{-5}
N	16785.7	18631.3	.34	.22	7.1×10^1
Na	151.9	3267.2	<.01	.67	2.8
P	2224.1	4103.2	<.01	.73	8.3
Se	.7	1.1	.26	-.13	2.0×10^{-4}
Zn	19.6	16.3	.05	-.47	9.18×10^{-2}

informative about landscape use by grazing ungulates. The bottom catena position seems paramount for ungulate diets in the northeast, perhaps owing to greater nutrient leaching through the sandier soils, while top and middle catena positions seem more important for eastern corridor grazers (Table 3). In comparing the calculated diet percentage of each landscape element with the actual percentage of that combination within the region (Table 3), two points emerge. First, selected landscape elements each represent 10% or less of the regions. In neither case was the most common landscape element (Themeda triandra-mid catena represents 50% of the northeast, *Pennisetum mezianum* in flats represents 24% of the eastern corridor) selected by the model to help balance dietary needs. Second, the dietary solutions most closely satisfying the dietary standards results in suggested use of a much greater proportion (15% more) of the eastern corridor than the northeast. Overall, rarer landscape elements seem most capable of contributing to a balanced ungulate diet and collectively these rarer elements make up a greater percentage of the eastern corridor than the northeast.

4. Discussion

Three primary points emerge from our analyses: (1) growing season N or crude protein does not appear limiting in either region although greater N ingestion is possible within the eastern corridor given other nutritional constraints, (2) grazing ungulates in the eastern corridor occur in greater density and are capable of balancing dietary requirements solely from forage while simultaneously consuming more protein, and (3) rarer landscape elements are most capable of balancing ungulate dietary requirements in both the northeast and eastern corridor. Collectively these results have implications for the spatial distribution of grazers at both the regional and landscape scales, and are discussed in the context of plant-animal interactions over evolutionary and ecological time scales.

Our linear programming models have considered N as a nutrient to be maximized, with other macro- and micronutrients as constraints in the model. In empirical studies, herbivore selection for forage high in nutrient content has clearly been demonstrated; both wild (Swift 1948; Heady 1964; Botkin

Table 3. Landscape elements (grass species-catena combinations) that represent the best solution in model analyses when grazer nitrogen intake is maximized subject to nutritional and forage mass intake constraints. Diet percentage indicates the amount of daily consumption a landscape element should comprise. Region percentage represents the approximate regional area covered by each landscape element.

REGION	LANDSCAPE ELEMENT			
	SPECIES	CATENA	DIET (%)	REGION (%)
Northeast E. Corridor	<i>Echinochloa haploclada</i>	Bottom	100	1
	<i>Digitaria macroblephara</i>			
	<i>Sporobolus ioclados</i>	Middle	82	10
	<i>Digitaria macroblephara</i>	Top	18	5

et al. 1973; Hanley 1984) and domestic (Cook 1959; Senft *et al.* 1985) species selectively forage for specific nutrients, often apparently N in the form of plant protein. Mattson (1980), in reviewing the relationship between herbivory and plant N content, recognized that many herbivorous insects have life cycles synchronized to 'flushes' of N-rich plant material (McNeil and Southwood 1978; Schwertzer 1979). In severely seasonal environments like the Serengeti, grazing ungulates also time reproduction coincident with onset of the growing season which brings a flush of young protein-rich grass, with migratory animals focusing on regions where forages are high in other nutrients as well (McNaughton 1990). Although this initial flush of protein-rich forage occurs over large areas of the Serengeti as the wet season begins, our results suggest that resident ungulates cueing on plant N can gain larger amounts of N and simultaneously balance their entire suite of nutrient needs in particular regions of the Serengeti that correspond to areas of high resident animal density. By definition resident animals do not migrate and select among regions. It is thus plausible that greater densities of animals within those regions where forage resources meet all dietary requirements and body mass is most readily restored before the dry season result from positive dietary feedback to survivorship and fecundity. Thus, at the larger spatial scale of regional comparisons, our results carry multiple-generation, evolutionary implications such as derive from traditional foraging theory (Senft 1989).

In comparison, our results within each region reflect on patterns of landscape mosaic utilization in ecological time (Senft 1989). At this scale, our

results concur with Westoby's (1974) hypothesis that grazing ungulates should utilize rarer forages a disproportionately large percentage of the time. In addition to providing a nutrition-based explanation for Westoby's (1974) hypothesis and further explanation for the patchy distribution of ungulates within Serengeti landscapes (McNaughton 1988), our results raise further questions about controls on Serengeti ungulate abundance and distribution. Westoby (1974) developed his hypothesis under the assumption that the amount of any forage consumed is independent of its availability. Grazing herds concentrating on rare landscape elements could theoretically deplete the forage resource and be forced to forage in less suitable portions of the landscape. Thus the temporal stability of foraging on a rare landscape element must be questioned. Our nutrient analyses were performed on young, actively growing leaf blades that would be higher in protein content than older senescent grass tissue (Owen-Smith 1982; Jones and Wilson 1987). For this highly nutritious resource to be maintained throughout the growing season, as is assumed by our analysis, the animals must either move along a productivity gradient or maintain the grasses in an actively growing state. Large productivity gradients, as would be maintained by a rainfall gradient, do not occur within single regions over the extent of a growing season, much less within smaller landscape elements, but ecosystem studies focusing on grazer-plant interactions and nutrient recycling explain the ability of relatively small landscape proportions to support long-term grazing. Intensive grazing, which sustains grasses in an actively growing, highly nutritious state (Seagle *et al.*

1992), and the capacity of Serengeti grasses for compensatory growth after defoliation (McNaughton 1979, 1985; Coughenour *et al.* 1984) demonstrate adaptations allowing grazers to take advantage of rare landscape elements that supply unique dietary opportunities. Empirically, McNaughton (1979) has demonstrated that grazing ungulates can indeed maintain small productive areas within which grass forage is not only kept in a state of active growth but also is higher in overall nutrient content (McNaughton 1988) than surrounding areas. In this way, resident species can maintain a nutritious forage base within those small landscape percentages capable of most closely balancing dietary needs. Perhaps, then, the ultimate control over regional resident abundance is the existence of small edaphic areas vegetated by grass species with appropriate physiologies in which grazers can either create through grazing (Georgiadis and McNaughton 1990) or take advantage of the potential for this positive feedback to dietary demands. The inability of *Themeda triandra*, the most common species in the northeast, to tolerate intense grazing (Coughenour *et al.* 1985) supports this supposition. Analogous to the resident animal strategy, Serengeti migratory ungulates have been suggested to time their inter-regional movements to exploit forages of high nutrient concentrations during the season of calving, mating, and replenishing of body mass (McNaughton 1990). This wet season range in the southeastern Serengeti is maintained as an extensive grazing lawn (McNaughton 1984) with compensatory grass growth maintaining the herds (McNaughton 1979, 1985) and rapid nutrient recycling maintaining grassland productivity (McNaughton *et al.* 1988). Both resident and migratory ungulate populations have apparently solved the problem of replenishing lean body mass catabolized during the dry season (Sinclair and Duncan 1972; Owen-Smith 1982) while simultaneously balancing dietary needs during reproduction through radically different strategies. The evolutionary stability of these two strategies is especially interesting in light of the fact that different populations of the same species utilize different strategies. This stability may result from the fact that most herbivores within nutrient-poor environments, such as tropical

savannas (Montgomery and Askew 1983; Cole 1986), must be 'behavioural-anatomical specialists', behaviourally adapted to focus on protein flushes yet anatomically adapted with digestive systems efficient at extracting energy and nutrients (Mattson 1980).

The number and diversity of grazing ungulates in the Serengeti have inspired many studies that describe niche separation of grazing ungulates in East Africa (Lamprey 1963; Bell 1970; Field 1972; Jarman 1972; Ferrar and Walker 1974; Sinclair 1977), suggesting that successful avoidance of competition may allow the observed high diversity and large numbers of savanna ungulates. Generally these studies are non-experimental and suffer from the tautological argument of whether niche separation reflects current or past competition (Connell 1980). Nonetheless, empirical observation of the patchy distribution of grazers at both regional and landscape scales can lead one to the opposite question of why there are not more animals? Or, why should niche separation have evolved when so much of the forage resource is not utilized? Our results have direct bearing on this question. If one assumes that the nutritional requirements of most grazing ungulates are similar, then our results suggest that niche separation may be an evolutionary result of many species feeding within relatively rare landscape elements where nutritional requirements are most readily met, while much of the landscape is used only marginally.

Our analyses have not analytically considered other potential constraints on resident ungulate foraging, such as energy obtained in the diet, secondary chemicals (Rhoades 1979), nutrient imbalances (Ruess 1984), and silica content of grasses (Van Soest and Jones 1968). We have assumed that ungulate energetic needs can be met by the activities of rumen microbial symbionts for most of the species. This assumption seems reasonable during the growing season when grazers are feeding on relatively high protein and nutrient rich forage that help sustain rumen microbial populations as well as themselves. However, energetic constraints may play a larger role for ungulates during the peak of the dry season (Bell 1971; McNaughton 1985). Therefore, we hypothesize that a less selective diet

and grazing of more common landscape elements would result from a similar analysis applied to dry season forage samples. Although forages can contain a variety of secondary compounds (Barry and Blaney 1987), grasses are generally lower in defensive chemicals (Malachek and Balph 1987), such as tannins (Cates and Rhoades 1977), than other forages. Excessive nutrient concentrations and nutrient imbalances, however, can also be toxic to grazing ruminants (Ruess 1984; McDowell 1985). Within those diets predicted by our analyses, no single nutrient reached toxic levels of ingestion listed by McDowell (1985) and the NRC (1984) in either region. Dietary imbalances resulting from nutrient interactions, such as milk fever (Ca/P imbalance), grass tetany ($K/(Ca + Mg)$ imbalance), and Cu deficiency (Cu/Mo imbalance) are difficult to predict, but occur commonly in tropical grazing ruminants (McDowell 1985). At nutrient ingestion rates predicted by the model, no Cu deficiency is apparent. Model grazer diets were high in K content, yielding $K/(Ca + Mg)$ ratios in the range resulting in grass tetany in the eastern corridor; however, relatively high total Mg consumption (8.8 g above dietary standard) makes this condition unpredictable. Milk fever is a likely result from a high Ca intake in the northeast region (36 g greater than dietary standard). Thus, overall, only the northeast region, with a lower resident animal density, seems to have a clear potential for serious nutrient imbalance. McNaughton and Tarrants (1983) found in laboratory experiments that Serengeti grass clones native to heavily grazed regions of the Serengeti accumulated greater leaf blade silica than those from more lightly grazed areas, especially when defoliated. However, variation in silica content was apparent among plants even with defoliation. Although contradicting results have been obtained for North American grasses (Cid *et al.* 1989), induced concentration of silica seems warranted for further investigation as a feeding constraint, especially should those grass species from landscape elements predicted for utilization by our model have naturally high, or inducible, silica content.

One key element of major importance to animal diets (Weir 1972; Jones and Hanson 1985; Risenhoover and Peterson 1986) and standing out in our

analyses is Na. The presence of Na accumulating grasses within the Serengeti has been pointed out by McNaughton (1988) who also noted the rarity with which animals can meet their Na requirements solely from forage. Presence of Na accumulators in the eastern corridor allow all dietary requirements to be met, while Na is the sole nutrient lacking from ungulate diets projected for the northeast. Nonetheless the northeastern region does have significant numbers of resident grazers that must somehow meet Na requirements, probably from 'salt licks'. Thus access to licks may be a major factor controlling northeastern resident ungulate populations who must balance other nutrient requirements within proximity of these resources. These ungulate populations might thus be classified as central place foragers. In contrast, eastern corridor grazers may not be as limited to such a localized edaphic resource, but to the distribution of Na accumulating grasses. The fifteen fold greater percentage of the eastern corridor available to modeled grazers suggests this to be the case.

By analyzing ungulate nutritional requirements in a comparative, ecological sense we find that there are plausible links among ungulate grazing strategies, regional abundance of resident grazing animals within the Serengeti, and the patchy utilization of Serengeti landscapes. The ultimate importance of nutritional balance to individual fitness provides a strong argument for viewing landscape and regional ungulate distributions from a forage nutrition stance. We thus feel that nutritional ecology can play an important explanatory role in understanding the distribution and abundance of animal species within ecological landscapes.

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