

Invited Synthesis

Functional Resource Heterogeneity Increases Livestock and Rangeland Productivity

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Abstract

Most of the world's rangelands are subject to large spatial and temporal variation in forage quantity and quality, which can have severe consequences for the stability and profitability of livestock production. Adaptive foraging movements between functional seasonal resources can help to ameliorate the destabilizing effects on herbivore body stores of spatial and temporal variability of forage quantity and quality. Functional dry-season habitats (key resources) provide sufficient nutrients and energy to minimize reliance on body stores and are critical for maintaining population stability by buffering the effects of drought. Functional wet-season habitats dominated by short, nutritious grasses facilitate optimal intake of nutrients and energy for lactating females, for optimal calf growth rates and for building body stores. Adaptive foraging responses to high-quality focal patches induced by rainfall and disturbance further facilitate intake of nutrients and energy. In addition, focused grazing impact in high-quality patches helps to prevent grassland maturing and losing quality. In this regard, the design of many rotational grazing systems is conceptually flawed because of their inflexible movement of livestock that does not allow adaptation to spatial and temporal variability in forage quantity and quality or sufficient duration of stay in paddocks for livestock to benefit from self facilitation of grazing. Similarly the fixed intraseasonal resting periods of most rotational grazing systems might not coincide with the key pulses of nitrogen mineralization and rainfall in the growing season, which can reduce their efficiency in providing a functional recovery period for grazed grasses. This might explain why complex rotational grazing systems on average have not outperformed continuous grazing systems. It follows, therefore, that ranchers need to adopt flexible grazing management practices that allow adaptation to spatial and temporal variability in forage quantity and quality, allow facilitation of grazing (season-long grazing), and allow more effective recovery periods (season-long resting).

Resumen

La mayoría de los pastizales del mundo está sujeta a gran variación espacial y temporal en cantidad y calidad de forraje, lo cual puede tener severas consecuencias con la estabilidad y rentabilidad de la producción de ganado. El movimiento adaptativo del pastoreo entre la funcionalidad temporal de los recursos puede ayudar a reducir el efecto desestabilizador en la reserva corporal de los herbívoros de la variabilidad espacial y temporal de la cantidad y calidad del forraje. Hábitats funcionales de temporada seca (recursos clave) proveen de suficientes nutrientes y energía para minimizar la dependencia de reservas corporales y son críticas para mantener la estabilidad de la población y efecto amortiguador de la sequía. Hábitats funcionales de temporada húmeda dominados por pastos cortos nutritivos facilitan el consumo óptimo de nutrientes y energía para hembras lactantes para las tasas de crecimiento óptimo del becerro por la construcción de reservas corporales. La respuesta adaptativa al pastoreo en áreas específicas de alta calidad inducidos por la lluvia y disturbio además facilita el consumo de nutrientes y energía. En suma, focalizando el impacto del pastoreo en parches de alta calidad ayuda a prevenir la maduración del pasto y pérdida de calidad. En este contexto, el diseño de varios sistemas de pastoreo tiene la falla conceptual en la nula flexibilidad del movimiento del ganado que no permite la adaptación espacial y temporal en la variación en la calidad y cantidad del forraje o suficiente tiempo de estancia en el potrero por el ganado para beneficiarse de auto facilitación del pastoreo. De manera similar, los periodos de descanso fijos intratemporales de la mayoría de los sistemas de pastoreo no podrían coincidir con los pulsos claves de la mineralización del nitrógeno y lluvia en la época de crecimiento la cual podría reducir la eficiencia en proveer recuperación funcional del periodo de los pastos pastoreados. Esto podría explicar porque sistemas de pastoreo complejos tienen en promedio un bajo desempeño comparado con el pastoreo continuo. Se desprende por lo tanto, que los rancheros necesitan adoptar prácticas de manejo de pastoreo flexible que permita adaptar la variabilidad espacial y temporal de la cantidad y calidad del forraje permitiendo facilitar el pastoreo (temporal-permanente pastoreo) y periodos de recuperación más efectivos (temporal-permanente descanso).

Key Words: adaptive grazing, forage quality, grazing management, key resources, nutrient loss rates, seasonal variation

INTRODUCTION

The “carrying capacity” of grazing ecosystems (wildlife, pastoral, and ranching systems) will largely be determined by

grassland productivity because primary productivity ultimately determines the limits of secondary productivity (McNaughton et al. 1989; Fritz and Duncan 1994). Thus, the potential of an ecosystem to support a given level of herbivore biomass will be determined by inherent abiotic factors determining grass production such as rainfall and soil fertility (McNaughton et al. 1989; Fritz and Duncan 1994), and biotic factors such as grazing pressure and its feedbacks on soil productivity and

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Manuscript received 5 August 2011; manuscript accepted 26 February 2012.

grass quantity and quality. Grazing impacts that result in erosion of soil, reduced infiltration, and death of productive perennial grasses will negatively impact ecosystem productivity (Milton et al. 1994; Fynn and O'Connor 2000; Rogues et al. 2001), whereas grazing impacts that improve soil moisture retention, increase rates of nutrient cycling and increase grass quantity and quality will increase ecosystem productivity (McNaughton 1985, McNaughton et al. 1988, Frank et al. 1998).

However most of the world's grazing ecosystems are subject to great spatial and temporal variability in grass quantity and quality with associated severe bottlenecks in nutrient and energy intake (Sinclair 1975; Parker et al. 1999; Owen-Smith 2007), which can destabilize the relationship between average grass production and herbivore biomass (Ellis and Swift 1988; Clutton-Brock et al. 1992; Scoones 1993; Illius and O'Connor 1999). Most commercial livestock systems are relatively stable in that there are rarely any major crashes in livestock population numbers during droughts because ranchers generally have sufficient economic capital to supply supplementary feeds, thereby preventing animals depleting their body stores below a reproductive or survival threshold (e.g., Fig. 1). By contrast, many of Africa's pastoral systems, where supplementary feeds are less accessible, exhibit much weaker stability, displaying large population crashes during severe droughts (Ellis and Swift 1988; Scoones 1993). Similarly, the functioning of natural wildlife systems is purely determined by natural properties internal to the system, with no access to supplementary feeds. It is important to note, however, that in both pastoral and wildlife systems, some systems display much greater inherent stability than others (Walker et al. 1987; Clutton-Brock et al. 1992; Scoones 1993; Parker et al. 2009). This informs us that some systems must possess some internal property that endows upon them greater stability in the face of environmental instability. In the major drought of 1982–1984 in Zimbabwe, cattle herds that were moved between resources had much better survival rates (40% vs. 3%) than sedentary cattle herds (Scoones 1993). In this same drought, wildlife areas that had greater spatial heterogeneity of vegetation experienced far less ungulate mortality than more spatially uniform areas—

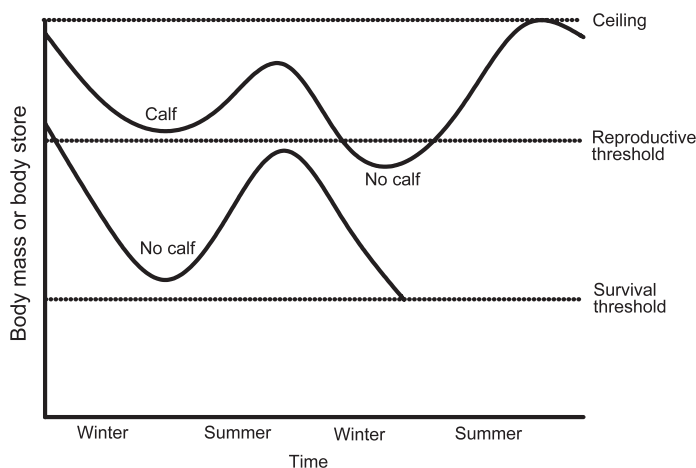


Figure 1. Conceptual model of body store dynamics of herbivores as influenced by differences in access to functional heterogeneity of resources (reproduced with permission from Parker et al. 2009).

although this might be partially confounded by differences in stocking rate that influenced this heterogeneity (Walker et al. 1987). These two examples, one from a wildlife system, and another from a pastoral system, provide insights into the nature of these internal stabilizing properties, which it appears is related to the ability of herbivores to move and access key functional vegetation resources.

Although this synthesis focuses primarily on concepts related to the foraging ecology of wild grazers and to livestock management in grassland and savanna ecosystems, there are potential parallels of these adaptive foraging concepts in grasslands to adaptive foraging in shrublands. This is because all large herbivores, whether browsers, intermediate feeders, or grazers, have to deal with the same seasonal bottlenecks and spatial variation in forage quality (see Parker et al. 1999; Owen-Smith 2002; Pettoirelli et al. 2003), as well as with their foraging effects on their forage resource base. Thus the density of a browser such as Kudu is strongly related to functional heterogeneity in woody browse (Owen-Smith 2002). In addition, selective browsing on palatable shrub and tree species without sufficient recovery periods between browsing events can be expected to result in similar undesirable shifts in community composition toward unpalatable species (e.g., Pastor et al. 1988) as is observed with selective grazing in grasslands (to be discussed later). Moreover, browsers have been shown to create and maintain high-quality browsing lawns that increase nutrient flow to themselves in a similar manner to the positive feedbacks between grazers and grazing lawns (Fornara and du Toit 2007). Thus, the potential exists for similarities and parallels in concepts between grasslands vs. shrublands and browsers vs. grazers, but the degree of overlap will probably differ for specific situations and regions.

The objectives of this paper are to review and synthesize an extensive literature in the field of wildlife and rangeland ecology to: 1) examine how marked spatial and temporal variability in forage quantity and quality in grasslands and savannas affects the productivity and stability of herbivore populations; 2) extract and discuss key processes determining the productivity and stability of herbivore populations in grazing ecosystems; 3) develop a conceptual understanding of how the pattern and scale of grazing might influence the productivity and sustainability of grazing ecosystems through its influence on palatable perennial grass persistence, productivity, and quality; and 4) from the foundation laid by the preceding objectives, critically examine the conceptual validity of popular grazing management models, as well as make suggestions that will help to facilitate future focus and direction in rangeland management and research.

DETERMINANTS OF HERBIVORE POPULATION PRODUCTIVITY AND STABILITY

Herbivore productivity (at both the individual and population level) is dependent upon body stores (fat and protein) remaining above a reproductive threshold, whereas individual survival and population stability is dependent upon body stores remaining above a survival threshold (Fig. 1). The energy and protein content of forage, which is a critical driver of mass gain and body store in herbivores (Cook et al. 1996; Owen-Smith

Table 1. Grass standing biomass at which various herbivores are expected to maximize energy intake. Herbivore mass is the upper range limit obtained from Smithers (1983). Optimum grass standing biomass derived from the equation: $\text{antilog}_{10}y = -0.088 + 0.86 \times \log_{10} \text{body mass}$ (Wilmshurst et al. 2000).

Species	Herbivore mass (kg)	Optimum grass standing biomass ($\text{g} \cdot \text{m}^{-2}$)
Springbok	47	22.4
Impala	65	29.6
Tsessebe	140	57.2
Wildebeest	250	94.2
Cow	500	171
Buffalo	800	256.2

2002; Pettorelli et al. 2003; Parker et al. 2009), is highly variable both spatially (Verlinden and Masogo 1997; Wallis De Vries 1998; Wilmshurst et al. 1999; Marell et al. 2006; Stokes et al. 2006; Hobbs et al. 2008; Holdo et al. 2009) and temporally (Sinclair 1975; Breman and de Wit 1983; Ellis and Swift 1988; Wallis De Vries and Daleboudt 1994; Wallis De Vries 1998; Parker et al. 1999; Owen-Smith 2007). As the dry season sets in, perennial grasses translocate limiting nutrients such as nitrogen (N) from photosynthesizing organs in shoots to storage organs (Clarke 1977), resulting in low concentrations of nutrients in senesced leaves (Sinclair 1975; Heitschmidt et al. 1982; Murray and Illius 2000). In addition, as grasses mature in age and size, structural compounds such as cellulose and lignin make up an increasing proportion of grass tissue (Wilmshurst et al. 2000), resulting in decreasing digestibility of grasses as the growing season progresses (Sinclair 1975; Wilmshurst et al. 2000; Owen-Smith 2007). These effects result in protein and energy intake declining over the growing season (Hiernaux and Turner 1996; Voeten et al. 2009; Table 1). By the time complete sward maturity and senescence is reached in the dry season/winter, nutrient and energy intake has dropped to well below the maintenance levels of herbivores in African (Sinclair 1975; Ellis and Swift 1988; Owen-Smith 2007) or northern (Parker et al. 1999) environments. Consequently, herbivores must rely on body stores (Fig. 1) to survive this season of protein and energy deficit (Ellis and Swift 1988; Shrader et al. 2006; Parker et al. 2009) or move to better habitats where deficits are minimized (Fig. 2). The problem with relying on body stores to survive seasonal deficits in protein and energy intake is that during extended dry seasons or severe winters, body stores are unlikely to be sufficient to carry herbivores through the extended period of deficit, and severe mass mortalities are often observed (Walker et al. 1987; Ellis and Swift 1988; Scoones 1993). Large fluctuations in body stores are likely to negatively affect fecundity (Fig. 1), and it makes ecological sense to forage adaptively to maximize nutrient and energy intake during good periods and minimize depletion of body stores during resource-limited periods (Figs. 1 and 2). Thus adaptive foraging in relation to spatial and temporal variability in forage quantity and quality (functional heterogeneity of forage resources) is critical for free-ranging herbivores to maintain their body stores at stable and productive levels (Figs. 1 and 2).

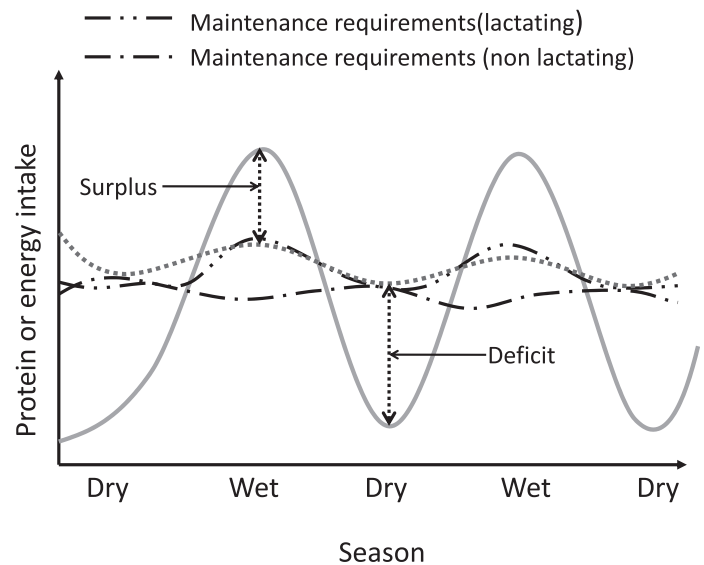


Figure 2. Conceptual model of habitat influences on protein and energy intake in wet and dry seasons relative to maintenance requirements. Note that lactating individuals have greater maintenance requirements than nonlactating individuals during the wet season (e.g., Murray 1995; Parker et al. 1999). Solid green line, optimal wet-season habitat; dotted red line, optimal dry-season habitat. Note how high-quality, wet-season habitats result in a surplus of protein and energy intake during the wet-season to enable building of body stores, but that these same habitats generally result in severe protein and energy deficits during the dry season (e.g., Ellis and Swift 1988; Parker et al. 1999; Owen-Smith 2007). Note that good dry-season habitats result in minimal deficits of protein and energy intake during the dry season but offer little surplus (or even a deficit) for building body stores during the wet season (e.g., Vesey-FitzGerald 1960; Fryxell and Sinclair 1988a), especially if the individual is lactating (e.g., Murray 1995; Parker et al. 1999).

For many large herbivores, functional heterogeneity can be defined as a mix of areas providing nutritious wet-season grazing and other areas that are able to provide adequate-quality forage during the dry season. In this regard, functional wet-season habitats are generally dominated by short, digestible grasses with high nutrient and energy status for this time of high nutrient and energy demand by herbivores (milk production, calf growth, and building fat and protein stores). Functional dry-season habitats are dominated by more productive grasslands that have access to soil moisture during the dry season, thereby enabling the provision of green leaf at a time when all other habitats have only low-quality dry leaf (Fig. 3). This enables herbivores to minimize the rate of decline of body stores during the dry season, a time when protein and energy become extremely limiting (Fig. 2). For example, poorly drained grasslands (dambos or wet meadows) accumulate a large amount of water over the wet season which can maintain sufficient soil moisture during the dry season (deep sands provide a similar effect) for growth by deep-rooted perennial grasses (Ellis and Swift 1988; Illius and O'Connor 1999; Scoones 1995; Fig. 3a). Similarly, high water tables on floodplains provide deep-rooted perennial grasses with moisture throughout the dry season, allowing them to produce relatively protein- and energy-rich green leaf (Vesey-FitzGerald



Figure 3. Examples of green grazing in the late dry-season provided without the incidence of rainfall by functional dry-season habitats. **A**, Zebra foraging on green regrowth after fire in low-lying poorly drained grasslands (dambos or wet meadows) of the Chobe Enclave, Botswana; **B**, a herd of buffalo and **C**, zebra foraging on the green grazing on the floodplains of the Savuti channel, Botswana (photo credits, R. Fynn).

1960; Fryxell and Sinclair 1988a, 1988b; Figs. 3b and 3c). Note in the foreground of Figure 3c the seepage of water from the high water table into local depressions. It is this high water table that allows the maintenance of green grass throughout the dry season without the incidence of rain—a key functional aspect of classic dry-season resources. In addition, high-rainfall regions can receive sufficient rain during the dry season (McNaughton 1985; Fynn and Bonyongo 2011) to support the production of green grass (McNaughton 1985; Fryxell and Sinclair 1988a; Fynn and Bonyongo 2011). It is the availability of habitats in a region that are able to provide green leaf during the dry season (key resources) that determines the size and stability of herbivore populations because they prevent catastrophic die-offs during drought (Vesey-FitzGerald 1960; Sinclair et al. 1985; Fryxell 1987; Ellis and Swift 1988; Illius and O'Connor 2000; Owen-Smith 2004). Consequently, in African environments, herbivore movement to floodplains, bottomlands, and high-rainfall regions during the dry season was once widespread (Bell 1970; Fryxell and Sinclair 1988a; Fynn and Bonyongo 2011). Similarly, many northern ungulates move to low-altitude regions during winter where snow depths are lower, forage is more available, and temperatures are warmer (Skogland 1980; Albon and Langvatn 1992; Festa-Bianchet 1988; Frank et al. 1998; Marell et al. 2006). The rate of use of body stores is influenced not only by forage quality, but also by temperature (Parker et al. 1999), indicating that adequate shelter from cold winds during winter can make a big difference to body condition at the end of winter.

Herbivore population productivity, however (such as calving percentages, milk production, calf growth rates, calf survival and age at first conception), is generally determined by the protein, energy, and mineral content of forage in the summer or wet-season resource (Murray 1995; Cook et al. 1996; Wilmshurst et al. 2000; Person et al. 2003; Parker et al. 2009); these elements also are known as multiplier effects on population productivity (White 1983). The optimal height and biomass of grass at which nutrient and energy intake is maximized varies as a function of mouth anatomy (Murray and Illius 2000; Arsenault and Owen-Smith 2008) and body mass (Wilmshurst et al. 2000). For example, it has been shown that the optimal biomass of grass at which energy intake is maximized generally increases with increasing body size (Table 1). It is important to note from the data presented in Table 1 that most herbivores are predicted to maximize energy intake on swards of less than $100 \text{ g} \cdot \text{m}^{-2}$, which is very low productivity grassland. Even an 800-kg buffalo is predicted to maximize energy intake on moderate productivity swards around $250 \text{ g} \cdot \text{m}^{-2}$. It is well-recognized that there is a negative correlation between grass height/productivity and quality (Jarrell and Beverly 1981; O'Reagain and Owen-Smith 1996; Wilmshurst et al. 2000), which will affect intake of nutrients and energy (Wilmshurst et al. 2000). The body size–intake relationship can be strongly modified by mouth anatomy, however, because very large-bodied herbivores with wide (lawn mower) mouths, such as white rhino and hippo, prefer short, low-biomass grazing lawns. This is because their wide mouths and specialized lips for cropping grass allow high intake rates on short grazing lawns (Arsenault and Owen-Smith 2008). The point is that, despite the extremely large body size of white rhino and hippo, they still prefer short grass during the wet

season. In general, functional dry-season resources, such as high-rainfall regions, floodplains, and wetlands, are very productive often exceeding $500 \text{ g} \cdot \text{m}^{-2}$ of dry matter production (Bremner and de Wit 1983; Knapp et al. 1993; Osem et al. 2004; Jacobs and Naiman 2008). From the data presented in Table 1 it is evident that although these winter/dry-season resources are able to provide higher-than-average forage quality during the winter/dry season (Fig. 2), their high productivity is likely to reduce rates of nutrient and energy intake during the critical period of high-nutrient and -energy demand during the summer/wet season (Langvatn and Hanley 1993; Wilmshurst et al. 2000; Parker et al. 2009; Fig. 2). For example, cattle (Edye et al. 1978; Fynn and O'Connor 2000) and bison (Craine et al. 2009) weight gain have been shown to drop in years of high grass production associated with very high rainfall. In another example, increases in the extent of high-quality-forage grazing lawns resulted in increased growth rates and gosling mass of Brant geese, a critical factor in their survival (Person et al. 2003). Similarly, growth rates of roe deer fawns and elk calves have been shown to be strongly positively related to the digestible energy content of their summer forage (Cook et al. 1996; Pettorelli et al. 2003).

Several environmental factors, largely through their influence on grass biomass and productivity, give rise to short, nutritious grazing. Shallow upland soils, being more moisture-limited than deeper lowland soils, generally provide lower-biomass grassland dominated by short grasses (Knapp et al. 1993; Osem et al. 2004; Jacobs and Naiman 2008). Consequently, wild and domestic herbivores tend to prefer these upland areas during the wet season, switching to the more productive lowlands during the dry season (Bell 1970; Knapp et al. 1999; Macandza et al. 2004; Arsenault and Owen-Smith 2008; Moyo et al. 2010)—this seasonal foraging pattern is often reversed in sandy regions (relic dune topography) where short grasses dominate in the higher-clay valleys and taller grasses on the deep sandy soils of the dunes (e.g., Senft et al. 1985; Winter et al. 2011). Alternatively, intermediate feeders such as impala and elephant, in addition to the option of spatial shifts on landscape-determined productivity gradients, often adapt to the seasonal decline in grass quality by shifting to browse on shrubs and trees during the dry season (McNaughton and Georgiadis 1986). Similar to these patterns on landscape-determined productivity gradients, herbivores tend to migrate down the rainfall gradient during the wet season to lower-productivity grassland in low-rainfall areas (Fryxell and Sinclair 1988a; Holdo et al. 2009; Fynn and Bonyongo 2011). It appears that herbivores migrate to these low-rainfall regions for the wet season because important minerals such as sodium (Na) are able to accumulate in soils with reduced leaching under conditions of low rainfall (Anderson et al. 2007, 2010). In fact, most major migratory wet-season grazing areas in Africa are relatively saline grasslands (Fynn and Bonyongo 2011), supporting high concentrations of Na, magnesium (Mg), and phosphorus (P) in the dominant grasses (Murray 1995; Grant and Scholes 2006; Anderson et al. 2010), minerals essential for lactating females (Murray 1995). Adaptive foraging and habitat selection in a landscape mosaic by free-ranging cattle was poorly explained by models incorporating an energy intake maximizing function alone but was much better explained by inclusion of intake of minerals such as sodium (Wallis De Vries

and Schippers 1994). Thus, productive herbivore populations, in addition to requiring high protein and energy concentrations in their wet-season forage, also require high concentrations of minerals (Murray 1995). This suggests that whereas protein and energy are the major factors limiting herbivore populations during the dry season, minerals become important limiting factors, colimiting with protein and energy during the wet season, because it is during this period that females are calving and lactating, and therefore have elevated requirements for minerals, protein, and energy (Fig. 2).

Apart from soil type and rainfall as determinants of grassland productivity and quality, fire is another factor that has been shown to greatly increase forage quality. Regrowth after fire or clipping has higher levels of N, P, potassium (K), calcium (Ca), and Mg than undisturbed vegetation (van de Vijver et al. 1999). Thus high-quality green regrowth after patchy fire events is a powerful determinant of wildlife and cattle foraging movements (Knapp et al. 1999; Fuhlendorf and Engle 2004; Archibald et al. 2005; Fuhlendorf et al. 2009). Similarly, the stimulation of new green leaves after rainfall is well known as a powerful attractant for free-ranging herbivores (Verlinden and Masogo 1997; Wilmshurst et al. 1999; Holdo et al. 2009). In addition, new growth after snowmelt generates high-quality “green waves” following the receding snowmelt upslope, which are tracked by a variety of herbivores (Festa-Bianchet 1988; Albon and Langvatn 1992; Frank et al. 1998; Marell et al. 2006). Finally, trampling and grazing effects of large herbivores have been shown to remove coarse stems and dead leaves and stimulate high-quality green regrowth (Vesey-FitzGerald 1960; McNaughton 1976, 1985; Frank et al. 1998; Anderson et al. 2007; Archibald 2008). By preventing grasses from maturing and losing quality and by stimulating growth of high-quality forage, it has been proposed that large herds of herbivores can facilitate their own grazing, thereby increasing nutrient and energy flow to themselves (Heitschmidt et al. 1982; McNaughton 1984; Fryxell 1995; Murray 1995; Hiernaux and Turner 1996; Archibald 2008)—a critical concept that is ignored by many livestock grazing strategies.

The transient and patchy nature of snowmelt, rainfall, fire, and grazing events act to draw herbivores around the landscape in an associated transient and patchy manner. An area heavily grazed in one year might not be grazed the next year if the pattern of rainfall and fire are different (e.g., McNaughton 1979; Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009). Combined with seasonal movements between wet- and dry-season resources, adaptive foraging in response to the patchy and transient occurrence of high-quality forage creates a natural “built-in” resting regime for grasslands in large-scale, heterogeneous systems. Another key factor contributing to the sustained grassland productivity of large-scale grazing ecosystems is the observation that herbivores avoid drier drought-stressed patches in these systems (e.g., McNaughton 1979; Bremner and de Wit 1983; Verlinden and Masogo 1997; Wilmshurst et al. 1999; Holdo et al. 2009). This is likely to reduce mortality of perennial grasses, which are negatively affected by grazing during drought (O'Connor 1995; Ash et al. 2002, 2011).

Thus there is now an overwhelming amount of empirical (Bremner and de Wit 1983; Walker et al. 1987; Albon and Langvatn 1992; Scoones 1993, 1995) and theoretical (Illius and O'Connor 2000; Owen-Smith 2004; Fryxell et al. 2005; Wang

et al. 2006; Hopcraft et al. 2010) support for the notion that access by herbivores to greater functional resource heterogeneity is critical for maintaining productive and stable herbivore populations (Figs. 1 and 2), which also might be responsible for the sustainability of these systems (McNaughton 1985; Frank et al. 1998). Both modeling and empirical evidence show that density-dependent effects on animal performance decline with increasing spatial scale (Scoones 1993; Ash and Stafford-Smith 1996; Wang et al. 2006; Hobbs et al. 2008). It has been empirically demonstrated that migratory red deer had greater body weight and skeletal size than nonmigratory individuals because they were better able to track optimal quality forage than nonmigratory individuals (Albon and Langvatn 1992). Large-scale mobile pastoral systems have been demonstrated to be more productive and sustainable than sedentary systems (Breman and de Wit 1983; Coughenour et al. 1984; McAllister et al. 2006). It is also important to note that functional heterogeneity in the landscape is not a spatially or temporally fixed entity but has a patchy transient nature in response to flooding, rainfall, fire, snowmelt, and grazing events at a range of scales (*sensu* Senft et al. 1987). Thus, optimal adaptive foraging can only occur with mobile, flexible herbivore populations at multiple scales—the reason proposed for dominance of the Serengeti fauna by highly mobile grazers (McNaughton 1985).

EVALUATING GRAZING MANAGEMENT STRATEGIES

There appear to be several critical conceptual and theoretical flaws underlying the design of many fixed rotational grazing systems. One major problem with systems that employ a short period of stay in the paddock followed by a long period of rest is that livestock are continually rotated through paddock after paddock of grown-out, low quality grass (after a long rest period)—a movement pattern completely at odds with natural adaptive herbivore movements (Bell 1970; Langvatn and Hanley 1993; Fuhlendorf and Engle 2004; Arsenault and Owen-Smith 2008) and optimal foraging theory (McNaughton 1984; Langvatn and Hanley 1993; Fryxell 1995; Wilmshurst et al. 2000; Owen-Smith 2002; Parker et al. 2009). A short period of stay in the paddock does not allow livestock to maintain and benefit from a short, high-quality sward (Bakker et al. 1983; McNaughton 1984; Hiernaux and Turner 1996; Langvatn and Hanley 1993; Wallis De Vries and Daleboudt 1994; Fryxell 1995; Murray 1995; O'Regain and Owen-Smith 1996; Anderson et al. 2007). This is likely to have a negative impact on livestock growth rates, conception rates, and age at first conception (Edye et al. 1978; White 1983; McNaughton 1984; Cook et al. 1996; Fynn and O'Connor 2000; Person et al. 2003; Pettoirelli et al. 2003; Craine et al. 2009; Table 1). For experimental demonstration of the negative effect of increasing time of regrowth of grasses on livestock growth rates see the study (and citations therein) by Barnes and Dempsey (1992).

Proponents of a short period of stay in paddocks base this practice on the spurious belief that palatable perennial grasses are negatively affected by repeated grazing in a season. This belief is only correct if repeated grazing happens every season, but not if the grass was rested in the season prior to grazing—if

rested in the previous season, up to six regrazing events in the season can actually stimulate perennial grass productivity relative to an ungrazed control (Turner et al. 1993). Thus, grazing management that incorporates season-long resting of paddocks followed by season-long grazing of sufficient intensity during the following season to allow the maintenance of short grassland (e.g., Venter and Drewes 1969; Kirkman and Moore 1995) will likely stimulate productive regrowth of high-quality forage in the grazing season following resting (Turner et al. 1993; Kirkman 2002). Another advantage of a season-long recovery period is that it ensures that grasses are rested during all the key pulses of N mineralization over the growing season, whereas these pulses can be missed by shorter intraseasonal recovery periods, reducing or nullifying the effectiveness of the recovery period. Finally, a season-long recovery period will likely facilitate maximum seed production for establishment of new tufts. Thus, season-long grazing and resting is expected to have two key influences: 1) increase grass production during the year of grazing, and 2) prevent grassland growing out and losing quality (facilitation of grazing). The combination of these two factors will facilitate maximum nutrient and energy flow to livestock (Table 1), thereby increasing the productivity of the ranch (Kirkman and Moore 1995). This facilitation effect was empirically demonstrated in Kenya where exclusion of wildlife grazing impact during the wet season resulted in higher grass cover and lower grass quality, with resultant reduced cattle growth rates (Odadi et al. 2011). Thus, grazing management that incorporates these important grazing facilitation and recovery effects (e.g., Venter and Drewes 1969; Kirkman and Moore 1995) is far better grounded in optimal foraging theory and known herbivore foraging strategies than are many of the popular rotational grazing systems.

Linked to these artificial grazing-system-imposed constraints on selection and maintenance of optimal quality grassland is the observation that certain areas in the landscape will be better for wet-season grazing, such as lower productivity uplands and areas with mineral-rich soils, whereas more productive lowland areas on deeper soils as well as on floodplains and wetlands would be better for dry-season grazing (Fig. 2). Most rotational grazing systems do not take this into account, forcing the livestock through paddocks in a systematic, time-driven system that might have no relevance to spatial and temporal shifts in forage quality across the ranch or the seasonal needs of the livestock. As a consequence, livestock might miss the opportunity to access optimal quality grasslands at critical periods during the year (van de Vijver et al. 1999; Holdo et al. 2009). The theory described in this review, together with studies of free-ranging cattle movements (Wallis De Vries and Schippers 1994; Moyo et al. 2010), suggests that fixed time-driven rotational grazing systems are unlikely to optimally satisfy the varied energy and mineral requirements of livestock, whereas greater adaptive options might be available to livestock in continuous grazing systems with functional heterogeneity of habitat types (Wallis De Vries and Schippers 1994; Moyo et al. 2010). With these factors taken into account, it is not surprising therefore, that on average, rotational grazing systems have failed to demonstrate any appreciable advantages over continuous grazing systems (Briske et al. 2008).

It should be noted, however, that this paper is not attempting to promote continuous grazing, but rather attempts to illustrate

that in certain rangelands fixed time-driven rotational grazing systems might not offer many advantages over simple continuous grazing systems (especially when the extra costs of fencing and management are considered). The relative merits, however, of continuous vs. rotational grazing will depend on the vegetation and environmental characteristics of individual rangelands (Fig. 4). The potential for degradation of a rangeland under grazing would be determined by the proportion of small- vs. large-mouthed grazers (Morris et al. 1999; Kirkman 2002) and the presence or absence of grazing-tolerant lawn grasses in the species pool, which will be influenced by the evolutionary history of grazing (Milchunas and Lauenroth 1993). Regions that supported large migrations of native ungulates (e.g., the prairies with bison or certain African grasslands with wildebeest and zebra) or millennia of livestock herding (e.g., the Middle Eastern and Asian rangelands) are likely to have grazing-tolerant lawn grasses in the species pool. The local presence of grazing-tolerant lawn grasses will, however, be modified by soil type because lawn grasses do not appear to be successful on very sandy soils (McIvor et al. 2005; Cromsigt and Olf 2008). The significance for rangeland management of having grazing-tolerant lawn grasses in the species pool will be discussed in the next section.

SPECIES REPLACEMENT AND DOMINANCE IN RANGELANDS

A mechanistic theoretical framework is essential for guiding our understanding of species replacement and dominance in grassland (Tilman 1988). In certain rangelands, long-term repeated grazing of palatable perennial grasses can result in degradation and homogenization of rangeland through the uniform rangeland-wide replacement of palatable by unpalatable grasses under selective grazing (Morris et al. 1992; Anderson and Briske 1995). Heavy stocking rates accelerate this degradation process (Briske et al. 2008), and especially under heavy continuous grazing (see Morris et al. 1992). In other rangelands, however, long-term repeated grazing of

palatable perennial grasses can result in the creation of functional heterogeneity through the formation of heavily utilized grazing lawns dominated by palatable, low-growing grasses embedded within a matrix of less palatable erect grasses (Bakker et al. 1983; Wallis De Vries and Daleboudt 1994; Morris et al. 1999; Teague and Dowhower 2003; Coetsee et al. 2010).

An understanding of this dichotomy of rangeland responses to grazing (Fig. 4) can be provided by the concept of relative nitrogen (N) loss rate under grazing, which is underlain by a robust theory (Tilman 1988; Holland et al. 1992; Tomlinson and O'Connor 2004), and is supported by experimental studies (Berendse et al. 1992). For the purposes of this discussion loss of N is defined as loss from the grazed plant via tissue removal under grazing; it does not refer to loss of N from the ecosystem via volatilization or leaching. In addition, although this discussion focuses on loss of N in grazed tissue, other factors such as reduced root mass, loss of carbohydrates, and reduced photosynthetic area under grazing will likely also contribute to reduced productivity and persistence of a grass plant under grazing. Loss of N in grazed tissue has major consequences for the productivity and persistence of a grass plant because N is the primary limiting nutrient for grass production in most of the world's rangelands (Cargill and Jefferies 1984; Tilman 1988; Tomlinson and O'Connor 2004; Crawley et al. 2005; Fynn and O'Connor 2005) and is difficult to replace when lost through tissue removal by grazers (Tomlinson and O'Connor 2004). Thus, once N is taken up by a grass plant, it is strongly conserved through internal recycling over many years, even decades (Clarke 1977; Tomlinson and O'Connor 2004). A large proportion of seasonal N mineralization is completed in the early growing season after the first spring rains, where high soil moisture (rewetting of dry soil), combined with warm weather, facilitates high rates of N mineralization (Read and Mitchell 1983; Pfeifer-Meister and Bridgham 2007; Xing-Ren et al. 2010), during which time plants can indulge in luxury uptake of N for later use when N availability is low (DeAngelis 1992). The finding that current-year grassland productivity can be affected by as far back as the previous 4 yr rainfall and temperature events (Wiegand et al. 2004) provides convincing evidence for later use of N by the plant, stored after previous luxury uptake during periods of high rainfall and temperature.

It is in this context of the primary limitation of N to grassland productivity and the associated importance of N retention by grasses that it is not surprising that the productivity of perennial grasses is greatly reduced if grazed in the previous season (Turner et al. 1993; Kirkman 2002). In this regard it is also important to note that not all grass species lose N at the same rate (relative to their total N pool) under grazing. Livestock generally select palatable perennial grasses while avoiding less palatable grasses, such as those with tough leaves and lower digestibility (Morris et al. 1992; Kirkman 2002; Anderson and Briske 1995). Thus, palatable grasses are likely to be grazed more heavily and lose more N to grazers than unpalatable grasses. If this grazing-induced N deficit is reinforced over the long term, palatable perennial grasses are likely to be replaced by unpalatable perennials or less productive annuals (Morris et al. 1992; Anderson and Briske

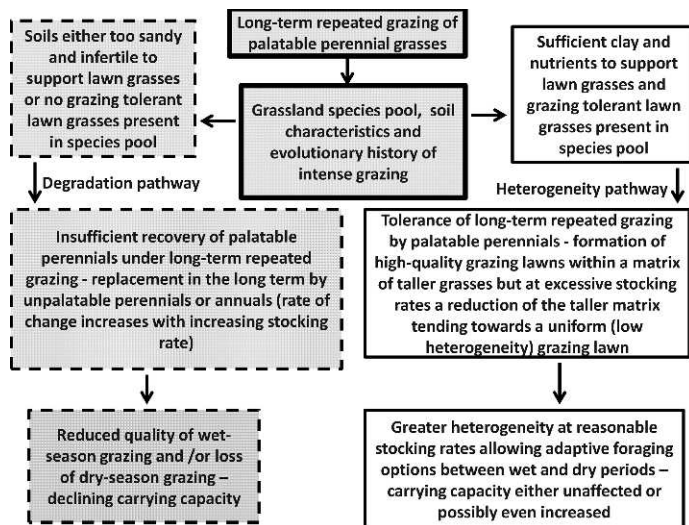


Figure 4. Conceptual model of rangeland change under grazing.

1995; Ash et al. 2011; Fig. 4). This negative selective grazing effect on palatable grasses is exacerbated by small-mouthed selective grazers such as sheep (Morris et al. 1999; Kirkman 2002) and at high stocking rates (Morris et al. 1992).

In addition, owing to their erect growth habit and the associated greater height at which leaves are initiated, palatable caespitose perennial grasses lose more N under grazing than palatable, prostrate-growing lawn grasses, which maintain a greater proportion of their leaves below the grazing height of livestock (Carman and Briske 1985; Polley and Detling 1988; Berendse et al. 1992; Holland et al. 1992). Consequently, grazing-tolerant lawn grasses are able to maintain greater growth rates and competitive ability than caespitose grasses under sustained heavy grazing (McNaughton 1985; Polley and Detling 1988; Hodgkinson et al. 1989; Berendse et al. 1992; Holland et al. 1992).

Although N might become more available for plant uptake under heavy grazing because rates of N mineralization are often increased and N immobilization decreased (McNaughton et al. 1988; Holland et al. 1992), it still remains that less palatable grasses or prostrate-growing grasses will experience lower loss rates of N than palatable or caespitose grasses. Thus, in certain rangelands, long-term repeated grazing of palatable grasses can result in increased functional heterogeneity with patches of preferably-grazed, high-quality lawns embedded within a matrix of rarely-grazed taller grasses (Fig. 4). Nutrient and energy flow to herbivores is facilitated by increased rates of N cycling and high forage quality on the lawns (McNaughton et al. 1988; Holland et al. 1992), while the taller grasses in the matrix provide a forage buffer resource during dry periods and droughts (Walker et al. 1987; Owen-Smith 2002, 2004). Exceptionally high stocking rates, however, are likely to result in loss of heterogeneity by expansion of the grazing lawns and ultimately in complete dominance by grazing-tolerant short grasses (e.g., Walker et al. 1987). This would result in an unstable system because it lacks a dry-season buffer or key resource of taller grasses (e.g., Walker et al. 1987; Illius and O'Connor 1999; Owen-Smith 2002, 2004; Fig. 2).

Rangeland scientists have traditionally considered patch/area selective grazing as counter-productive for sustainable livestock production, but creation of patchy heterogeneity is likely to provide greater adaptive foraging options than if the rangeland was managed for uniformity. Modeling has demonstrated that adaptive grazing between short- and tall-grass patches can increase the carrying capacity of the rangeland (see Owen-Smith 2002, 2004). Several specific examples now follow to further illustrate why a rangeland with a patchy mosaic of short and tall grasses can result in more stable and productive livestock production. In Hluhluwe–Imfolozi game reserve (HIP), a long evolutionary history of grazing combined with good soils and rainfall resulted in the development under heavy grazing of a patchy mix of short-grass lawns embedded within a taller-grass matrix (Coetsee et al. 2010). Short grasses provide high-quality grazing to a suite of herbivores when sufficient soil moisture is available for growth (O'Reagain and Owen-Smith 1996; Arsenault and Owen-Smith 2008; Coetsee et al. 2010; Table 1). In addition, large deep-rooted grasses in the taller matrix are able to access soil moisture at greater depths in the soil profile during dry periods than shallow-rooted grasses, thereby maintaining more growth and greenness during these

moisture-stressed periods (Shrader et al. 2006; Arsenault and Owen-Smith 2008). It is these adaptive foraging options provided by the patchy heterogeneity of grassland structure and composition of the HIP system that enables the maintenance of stable and high levels of herbivore biomass (Fynn and Bonyongo 2011).

Similarly, in Botswana, zebra are often observed to select for upper leaves of taller grasses and avoid short grasses during localized dry periods, even though the short grasses often have an abundance of green leaf. It appears that the taller grasses may still be able to access soil moisture and maintain more fresh growth than short grasses during these localized dry periods (K. Sianga, unpublished data, 2012).

Pyric herbivory creates an interannual shifting mosaic of heavily-grazed burned patches among a taller ungrazed/unburned matrix (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2009) and has been shown to result in greater and more stable cattle performance in certain rangelands (Limb et al. 2011). For similar reasons to the HIP example, these effects on livestock performance and stability are likely to be produced by maintenance of a short high-quality sward in focal grazed patches, which, combined with greatly increased rates of N mineralization in these focal grazed patches (Anderson et al. 2006), is likely to increase nutrient and energy flow to livestock. Lightly grazed (rested) taller grasses in the unburned matrix provide a buffer resource during dry periods as well as a season-long recovery period (usually longer) for these grasses to ensure maximum vigor when they become focal grazed patches (e.g., Turner et al. 1993; Kirkman 2002).

Another consequence of this increased productivity is that pyric herbivory has been demonstrated to greatly reduce invasion of alien species relative to uniform grazing systems (Fuhlendorf and Engle 2004). In fact, one of the major causes of increasing woody encroachment in rangelands (Van Auken 2009) could be because of increasing fragmentation of rangelands (Hobbs et al. 2008) and the associated loss of migrations of native herbivores on large-scale resource gradients. Focal grazing under mobile and flexible herds of native grazers generally stimulates grassland productivity (McNaughton 1985; Frank et al. 1998). By contrast, dispersed and sedentary livestock populations under the popular uniform grazing management regimes of today generally have neutral or negative effects on grassland productivity (Milchunas and Lauenroth 1993). Grass competition has been widely demonstrated to strongly suppress tree growth rates (Stuart-Hill and Tainton 1989; Mopipi et al. 2009; Riginos 2009). This suggests that the pattern and scale of grazing management and its effects on grass production can affect woody encroachment in savannas (e.g., Fuhlendorf and Engle 2004). Thus, pyric herbivory may provide a solution to the increasing threat of woody invasion of rangelands (Van Auken 2009).

MANAGEMENT IMPLICATIONS

A key lesson to learn from the foraging strategies of productive herbivore populations is that ranching systems must be sufficiently flexible to allow adaptive foraging to spatial and temporal variability in forage quantity and quality. In this regard, the Australian initiative of agistment, where ranchers

manage by agreement beyond the scale of their own ranches (McAllister et al. 2006), allows for greater adaptation to large-scale shifts in forage quantity and quality on functional resource gradients (e.g., Breman and de Wit 1983; McNaughton 1985). Agistment also allows greater adaptation to the predicted (e.g., Smith et al. 2009) increase in spatial and temporal variability of rainfall and forage production under climate change.

As demonstrated in previous sections of this synthesis, ranchers have the potential to increase the stability and productivity of livestock production on their ranches by creating induced functional heterogeneity (see Limb et al. 2011), which is also wildlife-friendly (Shamhart et al. 2012). Induced heterogeneity can be created by irrigation of pastures adjacent to rivers to increase the availability of green grazing for the dry season as well as by creating a patchy mosaic of short and tall grassland under pyric herbivory or mowing. Ranchers profits should be increased under pyric herbivory because there is much less reliance on expensive internal fencing to manage cattle movement and distribution (Fuhlendorf and Engle 2004).

Thus, there appear to be several obvious directions to take in the future of rangeland research: 1) examine the use of flexible grazing management approaches that incorporate adaptation to inherent and induced functional heterogeneity in resources at various scales, even at the regional scale; and 2) test the hypothesis proposed in the previous section that increasing fragmentation of rangelands and an associated change over time in the pattern and scale of herbivory has been responsible for an increase in woody encroachment in grasslands and savannas (for the importance of scale see Sandel and Smith 2009). Thus it appears that future prospects for rangeland management and research are looking up!

ACKNOWLEDGMENTS

Insightful comments by Tim O'Connor played a key role in shaping the direction and focus of this paper. Additional comments by five anonymous referees helped to greatly improve a previous version of this manuscript.

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