

# The Ecology of the Earth's Grazing Ecosystems

*Profound functional similarities exist between the Serengeti and Yellowstone*

Douglas A. Frank, Samuel J. McNaughton, and Benjamin F. Tracy

As recently as 150 years ago, most of Earth's grasslands supported large migratory populations of hoofed herbivores belonging to the Artiodactyla, Perissodactyla, and Proboscidea—that is, ungulates. These herbivores included bison (*Bison bison*) on the North American plains, saiga antelope (*Saiga tatarica*) on the Eurasian steppe, wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) on the African savanna, and the ecologically equivalent kangaroos (Macropodidae) on the Australian savanna.

As a result of the post-industrial global expansion of cropland and cattle ranching, most grasslands grazed by Pleistocene megaherbivores were eliminated. Today, they are restricted to the world's few large grassland reserves that protect all seasonal ranges of the animals. In this article, we describe profound functional similarities between two of the most celebrated of these remaining habitats, the Serengeti ecosystem of east Africa and Yellowstone National Park (YNP) of the North American intermountain west, which previously have been considered to

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The grazing ecosystem is among Earth's most endangered terrestrial habitats

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be markedly different. We contend that the Serengeti and YNP are extant members of a once-widespread ecosystem type that we refer to as a "grazing ecosystem." This ecosystem is distinguished from other habitats by its prominent herbivore-based food web and by the extent to which ecological processes are regulated by dynamics within that food web.

## Structural and climatic differences

The Serengeti and YNP have been described as being dissimilar largely because of their structural, boundary, and climatic characteristics (Berger 1991). Annual movements of the major ungulate species delineate the Serengeti ecosystem, of which 85% is protected in the Serengeti National Park, Masai Mara Game Reserve, and numerous other, smaller game reserves. By contrast, the boundaries of YNP were originally drawn to protect the area's thermal features, with little regard to the migratory patterns of animals. Consequently, ungulates regularly migrate across park boundaries to habitats that are not protected (Figure 1). The Serengeti is almost three times

the size, possesses almost four times the ungulate species, and has approximately 52 times the number of ungulates as YNP (Table 1).

There are several additional differences between the Serengeti and YNP. First, the Serengeti is a sloping, broad plateau covered primarily by grassland and savanna, whereas YNP is a mountainous reserve occupied by coniferous forest (80%) and grassland (20%), the latter being the focus of this discussion. Serengeti grass species all possess the  $C_4$  photosynthetic pathway, whereas grasses of YNP all have the  $C_3$  pathway. Moreover, the Serengeti and YNP support warm, tropical grasslands and cool, temperate grasslands, respectively, which are about as dissimilar climatically as any two grassland ecosystems on Earth (Figure 2). Nevertheless, within the constraints imposed by some of these differences, the ecosystems exhibit a high degree of functional similarity.

## Energy dynamics of grazing ecosystems

Grazing ecosystems support more herbivore biomass than any other terrestrial habitat (Sinclair 1975, Detling 1988, McNaughton et al. 1989, 1991, Huntly 1991). A functional consequence of this disparity in trophic structure emerges by comparing the relationship between aboveground production and herbivore consumption in the Serengeti and Yellowstone ecosystems with that in other terrestrial ecosystems (Figure 3). For consumption measure-

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Douglas A. Frank (e-mail: dafrank@mailbox.syr.edu) is an assistant professor, Samuel J. McNaughton (e-mail: sjmnaug@mailbox.syr.edu) is a professor, and Benjamin F. Tracy (e-mail: bft2@psu.edu) was a graduate student in the Department of Biology, Syracuse University, Syracuse, NY 13244-1220. They study the effects of large herbivores on grassland processes in the Serengeti and Yellowstone National Park. © 1998 American Institute of Biological Sciences.

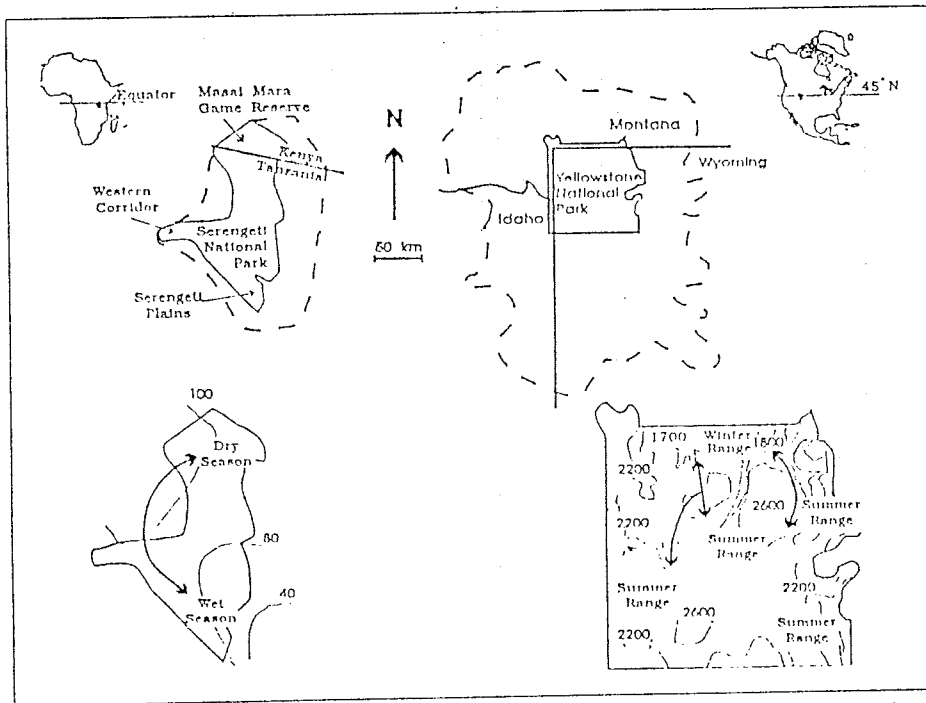


Figure 1. The locations of the Serengeti and Yellowstone National Park (YNP) in Africa and North America, respectively. The boundaries of both ecosystems (dashed lines) are determined by the migratory patterns of ungulates. Isoleths of mean annual precipitation are shown for the Serengeti, and isopleths of elevation are shown for YNP. These variables are the principal environmental factors controlling habitat variability and seasonal migrations (denoted by arrows) in the two ecosystems.

ments, we included plant material removed by all important herbivores, both vertebrates and invertebrates. All values were energy equivalents (kJ), converted from biomass measurements using standard conversion factors (Golley 1968). For productivity measurements, we considered only the nonwoody fraction of aboveground productivity—that is, net foliage production (NFP)—because woody production is largely unavailable to herbivores.

Plotting plant production against consumption revealed that terrestrial ecosystems fall into two groups that are distinguished by the intensity of herbivory ( $F_{1,78} = 88.2, P < 0.0001$ ; Figure 3). The first group includes low-herbivory habitats: desert, tundra, temperate forest, tropical for-

est, and small grassland sites lacking large herbivores. The second includes the Serengeti and Yellowstone, which exhibit high herbivory rates. On average, herbivores removed 57% (SE = 3.4,  $n = 40$ ) of NFP in the Serengeti and Yellowstone, whereas they removed only 9% (SE = 1.4,  $n = 40$ ) of NFP in other terrestrial ecosystems. For example, only 10% (SE = 2.1,  $n = 14$ ) of the aboveground production was consumed in temperate grasslands that lack large herbivores, showing that the removal of migratory grazers dramatically affects the energy dynamics of grasslands. Slopes of the relationships did not differ statistically between the two groups ( $P > 0.10$ ) and were greater than 1, indicating that the proportion of available primary production

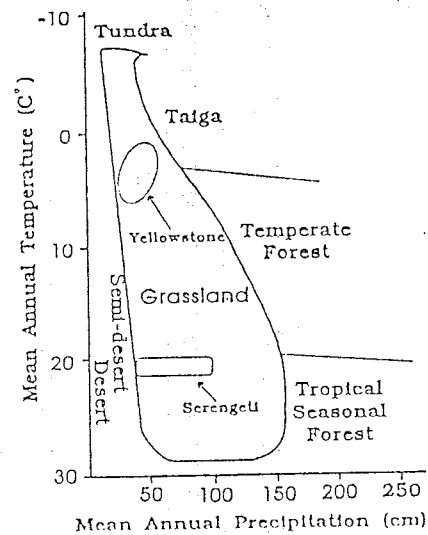


Figure 2. Approximate placement of the Serengeti and grassland habitat of Yellowstone National Park in Whittaker's (1975) climate-biome diagram. The area designated as grassland includes shrub-grassland, savanna, and open woodland habitat. The Serengeti and Yellowstone are climatically disparate grassland ecosystems.

consumed increased as NFP increased for both groups of habitats.

The low level of dispersion of samples around the regression line characterizing plant productivity and consumption in the Serengeti and Yellowstone grasslands suggests that the relationship describes a continuum from cool, temperate to warm, tropical grazing ecosystems. Primary production is greater in the Serengeti (average =  $11,118 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , SE = 978,  $n = 28$ ) than in Yellowstone (average =  $3168 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , SE = 530,  $n = 12$ ), most likely because of a combination of several factors: solar radiation and temperature are higher in the tropical system; some areas of the Serengeti receive more precipitation (range = 40–100 cm/yr) than Yellowstone (range = 40–75 cm/yr); a greater proportion of precipitation results in runoff in the Yellowstone ecosystem; and the  $C_4$  photosynthetic pathway of the Serengeti vegetation confers greater water-use efficiency than the  $C_3$  photosynthetic pathway of Yellowstone plants. Consumption also is higher in the Serengeti (average =  $7737 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , SE = 911) than in Yellowstone (average =  $1332 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , SE = 406), as is the percentage of production consumed,

Table 1. Properties of the Serengeti ecosystem and Yellowstone National Park (YNP).

| Property                                | Serengeti             | YNP                                   |
|---|-----------------------|---------------------------------------|
| Size (km <sup>2</sup> )                 | 26,000                | 9018                                  |
| Ungulate species                        | 31                    | 8                                     |
| Ungulate number                         | 2,137,000             | 40,600                                |
| Vegetation structure                    | Savanna and grassland | Coniferous forest and shrub-grassland |
| Photosynthetic pathway of grass species | $C_4$                 | $C_3$                                 |

65% (SE = 4) versus 40% (SE = 5).

There are two caveats to our interpretation of these findings. The first is that tropical forest habitat cannot be confidently classified with a single sample. The second is that our analysis does not include combined production-consumption data for tundra grazed by herds of caribou or reindeer (*Rangifer tarandus*). The two high-consumption tundra samples in Figure 3 were from sites experiencing rodent outbreaks, indicating that tundra can support high episodic rates of herbivory. However, whether ungulate-grazed tundra supports the chronic high levels of herbivory characteristic of grazing ecosystems is unknown.

Because of their higher rates of primary productivity and greater proportions of this production flowing to consumers, tropical grazing ecosystems support greater ungulate biomass than temperate grazing ecosystems per unit area. Using the most recent estimates of animal populations for the Serengeti ecosystem and YNP (Houston 1979, Singer and Mack 1993, Dublin 1995, YNP 1997) and mean adult biomass values for each of the ungulate species (Houston 1979, 1982), and assuming that elk (*Cervus elaphus*), bison, and pronghorn (*Antilocarpa americana*) are the predominant grazers of YNP grassland, we calculated that 1 ha of grassland supports 94 kg of ungulate biomass in the Serengeti and 37 kg of ungulate biomass in YNP. The finding that the 5.8-fold greater rate of consumption in the Serengeti results in only a 2.5-fold greater ungulate biomass indicates that conversion of plant material to ungulate biomass is more efficient in Yellowstone (360,000 kJ forage/kg grazer) than in the Serengeti (823,085 kJ forage/kg grazer). This difference may in part reflect the smaller average size of grazers in the Serengeti (116 kg) than in Yellowstone (255 kg), which results in a higher specific metabolic rate per unit of grazer biomass in the Serengeti (Peters 1983).

### Seasonal migrations

Animal biomass in grazing ecosystems is dominated by migratory herbivores (Fryxell et al. 1988). These animals face the problem of meeting

energy and nutritional requirements in grasslands, in which the quantity and quality of forage varies dramatically in space and time. Ungulates solve this dietary problem with a series of hierarchical foraging decisions that include which plant part or species to bite each second, which sward in a landscape to graze each hour, and which region to migrate to each season (Senft et al. 1987, McNaughton 1989).

Green waves and nutrition-rich diets. In the Serengeti, spatiotemporal variation in forage at the regional (spatial) and seasonal (temporal) scales is determined primarily by the pattern of precipitation across that ecosystem (Figure 1). Each year at the beginning of the wet season, millions of wildebeest (Figure 4), zebra, and eland (*Taurotragus oryx*) set out on a long-distance migration from the northwest corner of the Serengeti ecosystem, where they graze tall grasses of open woodlands during the dry season, to the southeast section, where they graze shortgrass plains in the wet season (Grzimek and Grzimek 1960, Talbot and Talbot 1963, McNaughton 1979). This migration represents movement against a gradient of mean annual rainfall and from heavily weathered, infertile (dystrophic) grassland in the dry season to volcanic, fertile (eutrophic) grassland in the wet season. Aerial surveys (McNaughton 1979) indicate that this migration

coincides with a "green wave" of plant production that is initiated in the western corridor (Figure 1) at the beginning of the wet season and sweeps eastward to the Serengeti plains as the season progresses.

In addition to the general pattern of green biomass spreading across the ecosystem through time, plant production is randomly distributed throughout the western corridor and the Serengeti plains early in the wet season because of stochastic rainfall events; grazers exhibit an uncanny ability to locate patches of plant growth (McNaughton 1979, 1985). At the end of the wet season, animals reverse their movements, eventually arriving in the northwest corner by the end of the dry season, which is often the only area supporting plant biomass at that time of year (McNaughton 1979, 1985).

The wet season migration to the Serengeti plains has been attributed to avoidance of sticky, muddy soil and predators rather than to the search for food because during the migration much of the Serengeti supports abundant forage biomass (Sinclair 1995). However, an analysis of 16 minerals required by grazers, and of two elemental ratios that affect mineral availability, in young grass leaves collected during the wet season from several locations representing wet, dry, and transitional season ranges, respectively—the Serengeti plains (where most of the animals were located), the north-

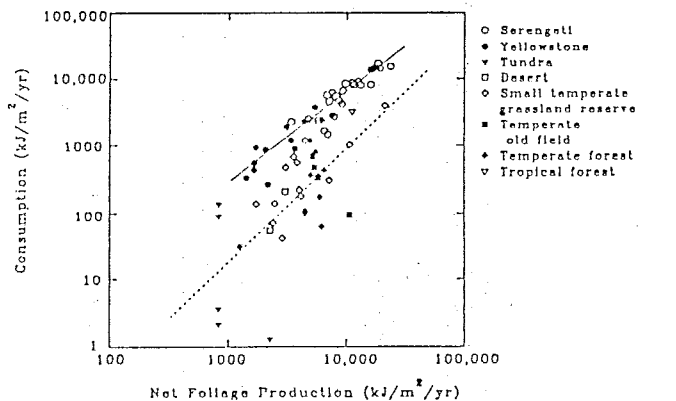


Figure 3. Relationship between herbivore consumption (C) and net foliage production (NFP) for terrestrial ecosystems. The solid line shows the relationship for the Serengeti and Yellowstone ecosystems ( $\log C = 1.42(\log NFP) - 1.90$ ;  $r^2 = 0.90$ ;  $df = 38$ ;  $P < 0.0001$ ); the dashed line shows the relationship for other terrestrial ecosystems ( $\log C = 1.62(\log NFP) - 3.55$ ;  $r^2 = 0.47$ ;  $df = 39$ ;  $P < 0.0001$ ). Serengeti and Yellowstone measurements were determined by the authors (McNaughton 1985, Frank and McNaughton 1992, Tracy 1996), and data from the other ecosystems were compiled from the literature (see McNaughton et al. 1989, 1991 for references).

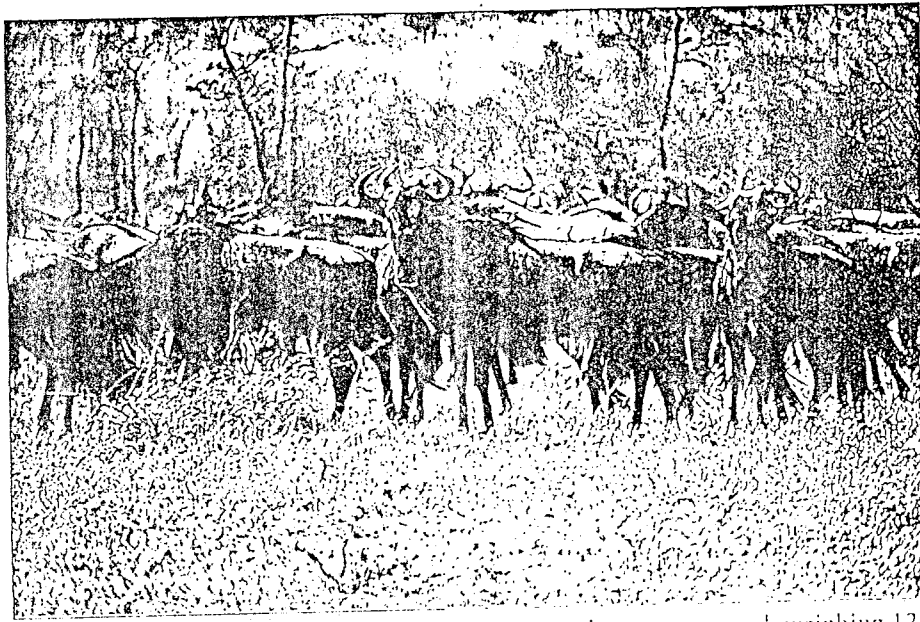


Figure 4. The 1.5 million wildebeest of the Serengeti ecosystem, each weighing 125 kg, dominate animal biomass in the system, contributing over 60%.

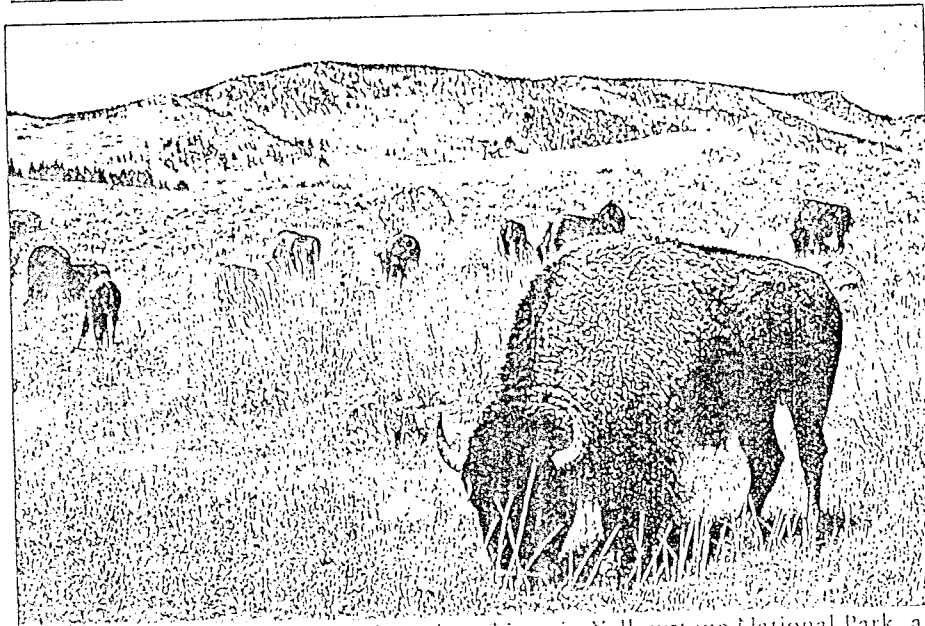


Figure 5. Large herbivores, such as these bison in Yellowstone National Park, are important regulators of grazing ecosystem processes.

west corner of the Serengeti, and the western corridor—showed that the seasonal movements are associated with the mineral content of the grasses that different regions of the ecosystem support (McNaughton 1990). Wet season forages were enriched in nine minerals (B, Ca, Co, Cu, Fe, Mg, N, Na, and P) compared with dry season forages, with transitional grasses displaying intermediate concentrations of many elements (McNaughton 1990).

Mineralogical analysis of the top 10 cm of soil collected directly beneath sampled grasses revealed that for all elements except Mg, plant concentrations were significantly related to soil concentrations. Thus, patterns of forage quality across the Serengeti are spatially linked to a gradient of soil fertility that is defined at one end by the heavily weathered soils of the dystrophic northwest corner and at the other by the volcanic soils of the eutrophic Serengeti plains

(McNaughton 1990).

In Yellowstone, ungulates undergo a seasonal migration that is functionally similar to that of the Serengeti, although it is driven by radically different environmental factors. Yellowstone ungulates migrate along an elevational gradient, between low-elevation winter habitat and high-elevation summer habitat (Figure 1; Meagher 1973, Houston 1982, Frank and McNaughton 1992). Elk and bison (Figure 5) migrating to their summer range track a wave of green biomass as it sweeps up the elevation gradient through the growing season (Frank and McNaughton 1992). These ungulates intensively graze grassland sites for the first month or two after snowmelt, a period of high plant productivity, and then move progressively upslope to phenologically younger vegetation. They reverse that movement during the fall, returning to valley bottoms, which accumulate low amounts of snow and support the greatest obtainable forage biomass in the ecosystem during the winter (Figure 6; Meagher 1973, Houston 1982).

To examine forage mineral content during the migration to summer range and the effect of plant phenology on elemental levels of forages, we collected whole-plant samples of dominant grass species each month through the growing season from summer, transitional, and winter range sites. Forages were analyzed for the same essential minerals and elemental ratios as the Serengeti samples (Table 2). N, P, and Na content was highest during the first month of the growing season, and K was highest during the first two months. In addition, the Ca/P ratio increased through the growing season, suggesting greater Ca interference of P absorption after the first month of plant growth. These results indicate that ungulates in YNP track mineral-rich forage as it sweeps upslope through the growing season.

Together, the findings from both ecosystems indicate that one key property of grazing ecosystems is the high spatiotemporal variation in forages; another is the close association between ungulates and the spatial pattern of high-quality forage, a pattern that is determined by environmental factors specific to each graz-

ing ecosystem. Forage quality varies more among seasonal ranges in the Serengeti than over the growing season in YNP, reflecting the fact that the edaphic effect on plant mineral content in the Serengeti is stronger than the phenological effect on plant mineral content in YNP.

Grassland structure and grazing efficiency. Foraging decisions influence not only diet quality but also consumption efficiency. This efficiency is important to migratory herbivores, which must balance time invested in energy and nutrient intake with nonfeeding activities, such as rest, reproduction, and travel (McNaughton 1984, Spalinger and Hobbs 1992). Forage yield per bite for cattle (Ludlow et al. 1982) and African buffalo (*Syncerus caffer*; Prins 1996) is positively correlated with plant biomass per unit volume (i.e., with biomass concentration). When forage biomass concentration is below critical levels, herbivores may be unable to acquire sufficient energy and nutrients to maintain themselves (Chacon et al. 1978).

To examine how grazer movements are associated with foraging efficiency, we measured plant biomass concentration throughout the seasonal ranges of migrating animals in both the Serengeti and YNP. In both ecosystems, forage biomass concentration was determined by dividing plant standing crop by canopy height, estimated as the resting height of a Styrofoam sheet placed on top of the vegetation (McNaughton 1985, Frank and McNaughton 1992). In the Serengeti, the maximum biomass concentration during the wet season was dramatically higher on shortgrass plains (average = 4.3 mg/cm<sup>3</sup>), where the animals were concentrated at the time of sampling, than in midgrass (average = 1.2 mg/cm<sup>3</sup>) or tallgrass (average = 1.9 mg/cm<sup>3</sup>) areas (see Figure 7a for the grazed grassland values; McNaughton 1984). Forage biomass concentration was similarly greatest in YNP grassland early in the growing season at precisely the time that herbivores were present (Figure 8).

Benefits conferred to herbivores by grazing highly concentrated, phenologically young vegetation in YNP are even greater when considering

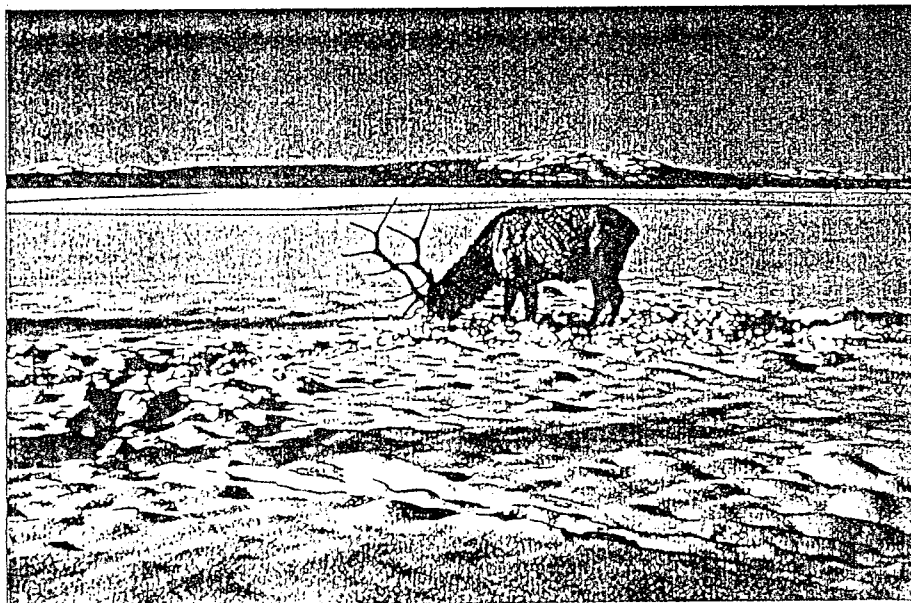


Figure 6. Snow cover severely limits access to food for elk and other ungulates in Yellowstone National Park during the winter. Photo: National Park Service.

only the green biomass, which represents relatively high-quality forage. Comparing maximum forage concentrations of up to 11 mg/cm<sup>3</sup> in the Serengeti (see Figure 7a for the grazed grassland values) with those of YNP (less than 1.5 mg/cm<sup>3</sup>; Figure 8) suggests that foraging efficiencies are substantially greater in tropical than in temperate grazing ecosystems. Our

findings for the two ecosystems thus indicate that the seasonal migrations in grazing ecosystems allow animals to simultaneously maximize diet mineral content and forage biomass obtained per bite.

Positive feedback on grazing efficiency. In addition to enhancing biomass yield per bite by responding to

Table 2. Mean mineral concentrations (in µg/g) and elemental ratios of grasses collected during different months after snowmelt at sites on the winter, transitional, and summer ranges in Yellowstone National Park.

| Element or ratio <sup>a</sup> | Month after snowmelt |         |         |          |         |
|-------------------------------|----------------------|---------|---------|----------|---------|
|                               | 1                    | 2       | 3       | 4        | 5       |
| Mineral                       |                      |         |         |          |         |
| B                             | 7.93ab <sup>b</sup>  | 5.85a   | 7.20ab  | 8.79b    | 10.1b   |
| Ca                            | 3187a                | 3272a   | 3691ab  | 4267b    | 4562b   |
| Co                            | 0.43a                | 0.37a   | 0.12a   | 0.52a    | 0.35a   |
| Cu                            | 7.17c                | 5.47ab  | 6.16bc  | 4.37a    | 5.68abc |
| Fe                            | 83.4a                | 81.3a   | 112.9a  | 100.1a   | 61.9a   |
| K                             | 22,380c              | 20,033c | 14174b  | 10,446ab | 7908a   |
| Mg                            | 1415a                | 1265a   | 1436a   | 1509a    | 1670a   |
| Mn                            | 58.4a                | 64.6a   | 75.9a   | 83.3a    | 92.0a   |
| Mo                            | 0.88a                | 0.82a   | 0.95a   | 0.89a    | 0.83a   |
| N                             | 33,997d              | 22512c  | 17,866b | 13,033a  | 9855a   |
| Na                            | 168c                 | 123b    | 94a     | 100ab    | 82a     |
| Ni                            | 1.64ab               | 2.29bc  | 2.87c   | 1.14a    | 1.28ab  |
| P                             | 2709d                | 1643c   | 1242b   | 885a     | 665a    |
| Se                            | 1.67b                | 0.46a   | 1.51b   | 1.89b    | 2.29b   |
| V                             | 0.93ab               | 0.72a   | 0.82ab  | 1.05b    | 1.03b   |
| Zn                            | 35.6a                | 26.2a   | 29.2a   | 27.7a    | 35.1a   |
| Ratio                         |                      |         |         |          |         |
| Ca/P                          | 1.19a                | 2.12ab  | 3.27b   | 5.54c    | 7.96d   |
| Cu/Mo                         | 8.33a                | 7.71a   | 7.49a   | 6.57a    | 8.29a   |

<sup>a</sup>B, boron; Ca, calcium; Co, cobalt; Cu, copper; Fe, iron; K, potassium; Mg, magnesium; Mn, manganese; Mo, molybdenum; N, nitrogen; Na, sodium; Ni, nickel; P, phosphorus; Se, selenium; V, vanadium; Zn, zinc.

<sup>b</sup>Values with different letters are statistically different from one another ( $\alpha = 0.05$ ).

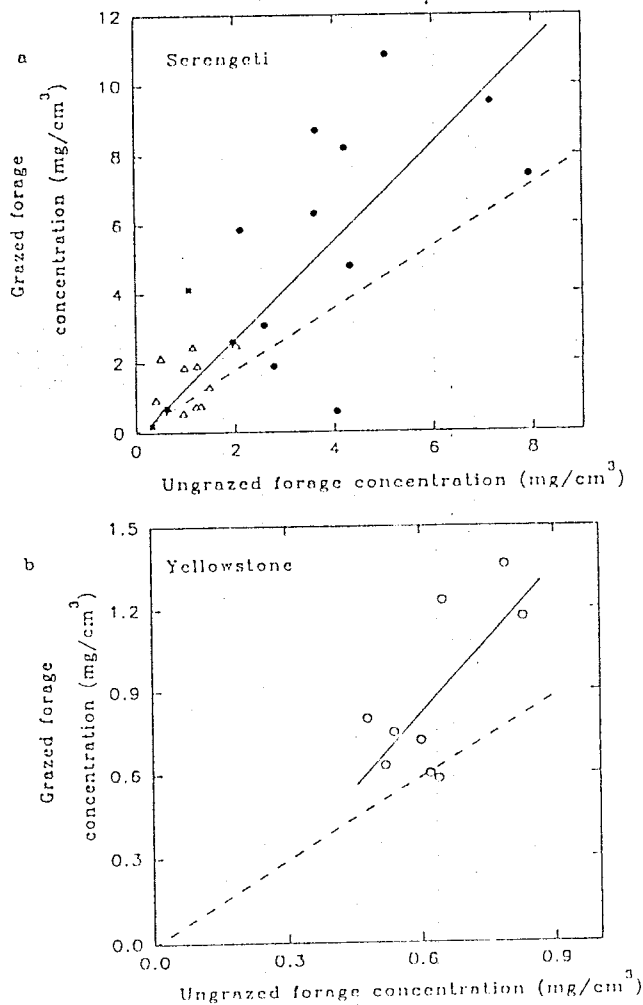


Figure 7. Forage concentration of grazed and ungrazed grasslands. (a) Serengeti sites include shortgrass (circles), midgrass (triangles), and tallgrass (squares). Redrawn from McNaughton (1984). (b) Yellowstone. Dotted lines denote equality (1:1). Solid lines are least-square fits; for the Serengeti,  $r^2 = 0.646$ ,  $P < 0.009$ ; for YNP,  $r^2 = 0.50$ ,  $P < 0.03$ .

tems, the positive relationship between forage mineral content and forage biomass concentration averts the potential difficulty of simultaneously optimizing forage quality and foraging efficiency. Seasonal animal movements allow forage to accumulate on ranges occupied by herbivores during "bottleneck" seasons when low or no forage production occurs—that is, the dry season in the tropical Serengeti and winter in the temperate YNP. Furthermore, ungulates in grazing ecosystems do not simply respond passively to ecosystem gradients of forage characteristics; they actually modify vegetation structure, with the result that herbivores increase their own foraging efficiency.

### Grazer regulation of plant aboveground production

Grazers have important indirect effects on grassland energy and nutrient flows in addition to their direct consumption of plant biomass. For example, as described above, defoliation promotes shoot growth (Caldwell et al. 1981, McNaughton 1984, Coughenour 1985). Grazing removes phenologically older, less productive tissue, which increases light absorption by younger, more photosynthetically active tissue (Caldwell et al. 1981, Wallace 1990) and improves both soil moisture status and plant water-use efficiency (McNaughton 1985). Grazers enhance mineral availability by increasing nutrient cycling within patches of their waste (McNaughton et al. 1988, Day and Detling 1990, Holland et al. 1992). In addition, grazing decreases microbial immobilization of nitrogen, resulting in greater rates of net nitrogen mineralization and nitrogen availability to plants (Holland et al. 1992). Consequently, ungulates stimulate allocation to shoot growth while simultaneously enhancing light levels, soil moisture, and nutrient availability.

The effect of large herbivores on aboveground production in the Serengeti and Yellowstone was examined by comparing productivity of grazed grassland with that of ungrazed grassland that had been fenced off for 1–2 years (McNaughton 1985, Frank and McNaughton

associated with forage concentration of the fenced controls, indicating that the densest ungrazed vegetation had the greatest capacity to increase in concentration in response to grazing.

Herbivores make forage more concentrated by reducing canopy height more than aboveground biomass (McNaughton 1984). Grazing stimulates regrowth from intercalary meristems located at the base of defoliated

shoots and from new stems (i.e., tillers) that develop at the ground surface, producing a short, uniform, highly concentrated canopy (McNaughton 1984). This phenologically young plant tissue is relatively nutritious, so grazers increase the nutrient content of their forage at the same time as they stimulate increased yield per bite (McNaughton 1976, 1979, McNaughton et al. 1982, Detling and Painter 1983).

We have already noted that ungulates in grazing ecosystems increase nutrient intake by tracking spatiotemporal waves of highly nutritious and concentrated forage sweeping across vast landscapes. In the Serengeti, spatiotemporal variation in forage quality results from the interaction of precipitation and soil fertility gradients. In YNP, forage variation results from an elevation gradient that controls when sites become snow free. In both ecosys-

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1993, McNaughton et al. 1996): Herbivores increased aboveground production by an average of 102% in Serengeti grasslands and 43% in Yellowstone grasslands (Figure 9); thus, they dramatically promoted energy capture in both ecosystems. Grazers had more variable effects on production in the Serengeti, where the effects ranged from 8% inhibition to 344% enhancement, than in YNP, where production was stimulated from 12% to 85%. Grassland sites in the Serengeti encompass broader climatic, edaphic, and consumption gradients than those in YNP, and this difference may explain the greater variability of grazer effects in the Serengeti. Thus, in contrast to most terrestrial habitats, where climate is the preeminent factor determining primary production and ecosystem energy flow, ungulates play a major role in regulating these processes in grazing ecosystems.

### The sustainability of grazing ecosystems

Grasslands and wild ungulates have coexisted for tens of millions of years. Their simultaneous emergence during the Late Mesozoic (Stebbins 1981, Gould and Shaw 1983, Archibald 1996) and concurrent adaptive radiations during the Miocene are among the most thoroughly documented evolutionary patterns in the fossil record (Love 1972, Morton 1972, Stebbins 1981, McNaughton 1991). The long coevolutionary history between grasslands and ungulates is testimony to the high sustainability of the grazing ecosystem. Key stabilizing elements of this habitat are the large spatial and temporal variation in mineral-rich forage; the migratory behavior of ungulates, which track high-quality forage across a large region; and the intercalary meristem of grasses, which allows defoliated plants to regrow.

Because animals are continually on the move, grazing at any site, although often intense, never lasts long. Furthermore, because ungulates tend to graze grasslands early in the growing season, when forage is the most rich in minerals, and then migrate off sites while conditions are still favorable for plant growth, de-

Figure 8. Relationship between forage concentration and number of days after snowmelt in Yellowstone. Solid triangles, all forage; open squares, green forage only; dashed line, least-squares best fit for all forage ( $r^2 = 0.27$ ,  $P < 0.0001$ ); solid line, least-squares best fit for green forage ( $r^2 = 0.47$ ,  $P < 0.0001$ ).

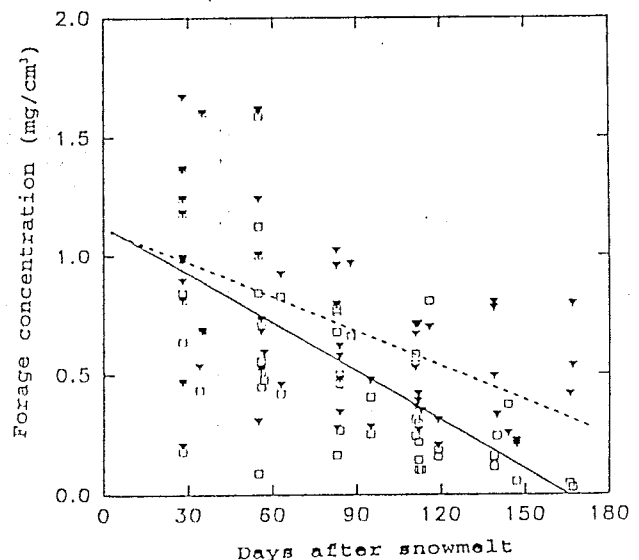
foliated plants are provided with both sufficient time and suitable conditions to regrow. Thus, the spatiotemporal dynamics of grazing ecosystems promote sustainability despite the high chronic herbivory that these habitats experience.

### Human transformation of grazing ecosystems

The grazing ecosystems of prehistory have largely been converted to food-producing regions for the earth's human population. Cultivation has claimed approximately 20% of the earth's grasslands (Graetz 1994), whereas much of the rest of the grassland habitat has been transformed into pasture and open rangeland supporting domesticated ungulates. These pastures and rangelands differ from grasslands grazed by wild ungulates in several important ways.

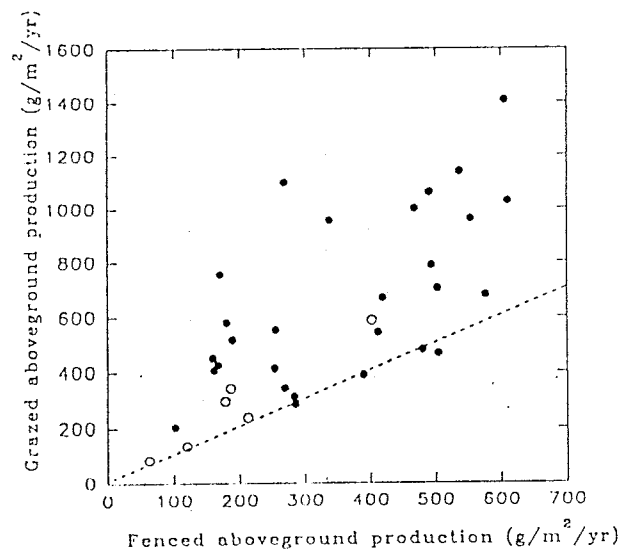
First, the management intent of animal husbandry is to maximize the production of ungulate biomass through veterinary care, predator control, and supplemental water,

Figure 9. Relationship between rates of aboveground production in grazed and fenced areas of the Serengeti (solid circles) and Yellowstone National Park (white circles). Grazers substantially increase aboveground production in both ecosystems. Dotted line reflects equality.



mineral nutrients, and feed. As a result, domesticated ungulate biomass on pasture and rangeland tends to be higher than wild ungulate biomass in grazing ecosystems (Oesterheld et al. 1992). Second, herding of domesticated ungulates by humans does not mirror the movements of wild ungulates. The invention of the windmill-driven water pump and barbed-wire fencing transformed grasslands throughout Earth, leading to more sedentary and concentrated animal use (McNaughton 1993).

Therefore, not only are the densities of domesticated ungulates often higher than those of wild ungulates, but also the spatiotemporal pattern of grazing, which may play an important role in the recovery of defo-





liated grasses, has been disrupted on rangelands grazed by domesticated herbivores. These differences between systems grazed by wild and domesticated ungulates help explain the discrepancy between the positive feedbacks of wild ungulates on forage properties versus the neutral or negative influences of domesticated herbivores on forage (Westoby 1985, Oesterheld et al. 1992, Milchunas and Laurenroth 1993).

### The conservation of grazing ecosystems

Wild ungulates are an inextricable component of the web of energy and nutrient flows in grazing ecosystems. When ungulates are removed from grasslands, the functional character of the system is altered, transforming a consumer-controlled, rapidly cycling ecosystem into one that is detritivore based and slowly cycling. Recent evidence suggests that eliminating processes, such as fire, that occur at large spatial scales disrupts the long-term structural integrity and biodiversity of grassland fragments (Leach and Givnish 1996). Eliminating grazers that migrate over vast, spatially heterogeneous environments by fragmenting grazing ecosystems into grassland remnants similarly alters the fundamental ecological character of those fragmented habitats.

The world's few extant grazing ecosystems face large and growing threats. As human populations continue to increase around the boundaries of these systems, animal movements in and out of grassland reserves are becoming increasingly limited (Western and Pearl 1989, Arcese and Sinclair 1997). In addition, diseases transmitted from the outside threaten some wildlife populations in reserves, such as that of the African wild dog (*Lycan pictus*) in the Serengeti (Burrows 1995). Fear of diseases being transmitted from ungulates migrating out of reserves to livestock has led to animals, such as bison in YNP, being slaughtered at the wilderness boundary (Meagher and Meyer 1994). The fundamental problem with respect to the conservation of grazing ecosystems is that these habitats are incompletely protected. This difficulty can be lessened by identifying and protecting important areas

of high ungulate use outside of reserves and by promoting incentives, such as ecotourism and indemnities, for landholders surrounding reserves to preserve animal migration routes. However, completely eliminating threats to the integrity of grazing ecosystems will be problematic so long as human settlements occur within the boundaries of the annual movements of migrating large herbivores.

### Conclusions

Studies of the Serengeti ecosystem and the Yellowstone ecosystem document many common ecological properties of grazing ecosystems. Broad abiotic gradients result in high spatiotemporal heterogeneity of forages. Migratory grazers track these spatiotemporal patterns to increase their diet quality and grazing efficiency. Indeed, environmental gradients producing spatial variability in forages may be a necessary feature of grazing ecosystems that contributes to the characteristically high grazer biomass of these habitats (by increasing the availability of high-quality forage to mobile animals) as well as to ecosystem sustainability (by ensuring a natural rhythm of vegetation defoliation-regrowth at any particular site).

A continuum exists among grazing ecosystems, from relatively less productive and moderately grazed temperate grassland (e.g., Yellowstone) to highly productive and heavily grazed tropical grassland (e.g., the Serengeti). Because of feedback mechanisms in which herbivores promote plant growth, grazers are important regulators of ecosystem processes in grazing ecosystems. Stronger feedbacks in the Serengeti, including larger ungulate effects on grazing efficiency and aboveground primary production, suggest that herbivores and other ecosystem components are more tightly linked in tropical grazing ecosystems than in temperate grazing ecosystems.

The grazing ecosystem is among Earth's most endangered terrestrial habitats. The region-size reserves required to support the unique ecological processes of these systems make acquisition of sufficient ranch land and cropland to restore grazing ecosystems prohibitively expensive.

Instead, protection of the few grazing ecosystems that remain is the only feasible option for preserving this rare habitat. As threats to these ecosystems intensify, it becomes increasingly important to develop measures for their preservation.

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