observed, whereas in the q_y-q_z plane two strong and narrow scattering peaks along q_z are detected. This result is expected for lamellae oriented parallel to the film surface. It demonstrates that the solvent-cast technique is capable of inducing macroscopically aligned samples for the present lamellar silica-type mesostructures. Because the film thickness of these materials is considerable (~1 mm), surface-induced morphological transitions and related effects observed for very thin films (*23*) can be neglected.

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Promotion of the Cycling of Diet-Enhancing Nutrients by African Grazers

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Experiments in Serengeti National Park, Tanzania, provide direct evidence that large, free-ranging mammalian grazers accelerate nutrient cycling in a natural ecosystem in a way that enhances their own carrying capacity. Both nitrogen and sodium were at considerably higher plant-available levels in soils of highly grazed sites than in soils of nearby areas where animal density is sparse. Fencing that uncoupled grazers and soils indicated that the animals promote nitrogen availability on soils of inherently similar fertility and select sites of higher sodium availability as well as enhancing that availability.

There is a growing recognition in ecology that organisms can modify their environments in ways beneficial to themselves, rather than inevitably causing environmental deterioration (*1*), and it is a maxim of grassland ecology that nutrient recycling by grazers contributes to plant regrowth potential (*2*). However, direct evidence of the effect of large wild mammals on nutrient recycling is meager (*3*), and studies in boreal forests (*4*) indicate that moose (*Alces alces*) browsing indirectly diminishes soil mineralization rate by shifting the composition of vegetation species to less palatable and less decomposable plants.

The distribution and abundance of large grazing mammals in Serengeti National Park, Tanzania, are influenced by the occurrence of nutritionally sufficient forages (*5*) and the spatiotemporal variation of vegetation productivity due to pronounced geographic rainfall gradients and production seasonality (*6*). Grazers preferentially forage on swards enriched in minerals that are important in late-stage pregnancy, lactation, and the growth of young animals (*5*). There are two plausible explanations for this phenomenon: Animals forage on vegetation supported by soils of innately greater nutrient availability, or animal activities augment nutrient availability. Identification of the correct explanation has implications for conservation policy and management (through an understanding of the habitat requirements of endangered wild grazing mammals) and for ecological theory (by documenting how grazing mammals are mechanistically coupled with their habitats). Regional edaphic differences affect the mineral contents of forages and thereby influence seasonal movements of migratory grazers in the Serengeti, but no evidence of general soil differences was found in landscape-level studies of resident grazers (*5*), which are those that do not migrate but occupy discrete home ranges. Here we present evidence concerning the mechanisms associated with higher nutrient availability at sites preferred by resident grazers.

Mineralization of two elements—nitrogen (N), which is essential to both plants

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and animals, and sodium (Na), which is essential to animals but is generally inessential or required in very small concentrations by plants—was studied for 2 years in two areas where resident ungulates concentrate during the wet season and in two paired nearby (2 to 3 km away) unoccupied areas consistently identified by over 20 years of observation (5). One pair of stands was in the northwest and the other was in the north-central portion of the ecosystem. The principal animal species are Thomson's (*Gazella thomsoni*) and Grant's (*G. granti*) gazelles, topi (*Damaliscus korrigum*), and kongoni (*Alcelaphus buselaphus*). They occur in the hundreds on concentration areas and are rarely seen on reference sites. The principal plant species on both types of sites are red oat grass (*Themeda triandra*), colorful panic grass (*Panicum coloratum*), and dropseeds [soda (*Sporobolus ioclados*) and pyramid (*S. pyradmidalis*)], with the red oat grass always making up more than 50% of the total above-ground plant biomass (6). Net microbial mineralization was measured with polyvinyl chloride mineralization tubes measuring 5 cm (inside diameter) by 20 cm (7). Soil cores extracted at T0 were collected when tubes were loaded; those extracted at TX were collected after an incubation period of x days (30 days during periods of heavy rain; 60 days otherwise). TX – T0 is net mineralization for period x (7). Animals and soils were uncoupled with fencing (6), and fenced and unfenced plots were compared for the 2-year study period to separate intrinsic soil process differences from those associated with animal activity. For the two study years, annual rainfalls at nearby rain gauges were 922 and 1013 mm at one site and 1104 and 997 mm at the other site.

Standing stocks of extractable N at T0 were indistinguishable ($F_{1,242} = 0.2$, $P > 0.6$) in the soils of sites of high herbivore density (5.6 mg kg^{-1}) and low herbivore density (5.3 mg kg^{-1}). However, net rates of N mineralization in control grassland soils (Fig. 1A) were consistently below the levels of N in soils of animal concentration areas (Fig. 1B). Averaged over the 2 years and four sites, annual N mineralization rate ($F_{1,354} = 13.01$, $P < 0.0001$) was 3.34 g of N m^{-2} $year^{-1}$ in control grassland soils and 7.09 g of N m^{-2} $year^{-1}$ in animal concentration areas, both measurements made to a depth of 20 cm. Therefore, the net N mineralization rate in soils supporting dense resident animal populations was over twice that of areas where animals are uncommon. There was no evidence that the short-term interruption of grazing caused by erecting fences for 2 years affected N mineralization rates ($F_{1,354} = 0.8$).

Standing stocks of extractable Na concentrations (Fig. 2) were universally, and substantially, higher in soils of animal concentration areas. In addition, fencing conspicuously decreased Na availability during the wet season (November to May) in animal concentration areas, whereas there was no significant difference between fenced and unfenced plots in those areas during the dry season or at any time in grasslands with low herbivore density ($F_{7,354} = 2.10$, $P < 0.05$ for the interaction; site x fencing x month). Averaged over study years, the annual difference between extractable Na in grazed and fenced plots to a depth of 20 cm was 5.14 g of Na m^{-2} $year^{-1}$ in reference grassland soils and 52.5 g of Na m^{-2} $year^{-1}$ in soils supporting vegetation where animals congregate ($F_{1,354} = 7.028$, $P < 0.0001$). On average, then, grazing increased the Na supply from Serengeti soils by an order of magnitude.

Increased stomatal conductance and transpiration of defoliated grasses (8) could lead to moderate Na accumulation in surface soil layers, by a process analogous to the salinization of agricultural soils in irrigated arid lands (9). Grazing also commonly leads to increased leaf N concentration (8) and therefore to litter of greater decomposability (10). In addition, urination enriches soil with N from urea, leading to a burst of organic matter mineralization that produces greater available mineral N in the soil than is added as urea (11). These mechanisms, which are due directly to the presence of abundant grazers, probably account for the patterns of mineral availability documented here.

Scant data are available that directly measure the effect of wild herbivores on nutrient cycling in terrestrial ecosystems (3), and, to our knowledge, only one set of comparative data on different habitats is available. The effect of mammalian grazers on nutrient cycling in Serengeti tropical savanna grasslands documented here is in marked contrast to the effect of moose browsing in boreal forest (4). Moose inhibit mineralization rate by converting forest species composition from broadleaf trees with readily decomposable litter to coniferous trees with much more recalcitrant litter. The moose effect is a long-term one, however, with the mechanism being considerable change in plant community composition, in contrast to the Serengeti grasslands, which are composed of species that are similar to each other (5, 6).

It has generally been recognized that mammalian grazers should accelerate grassland nutrient cycling (2, 3), although we know of no data directly documenting that

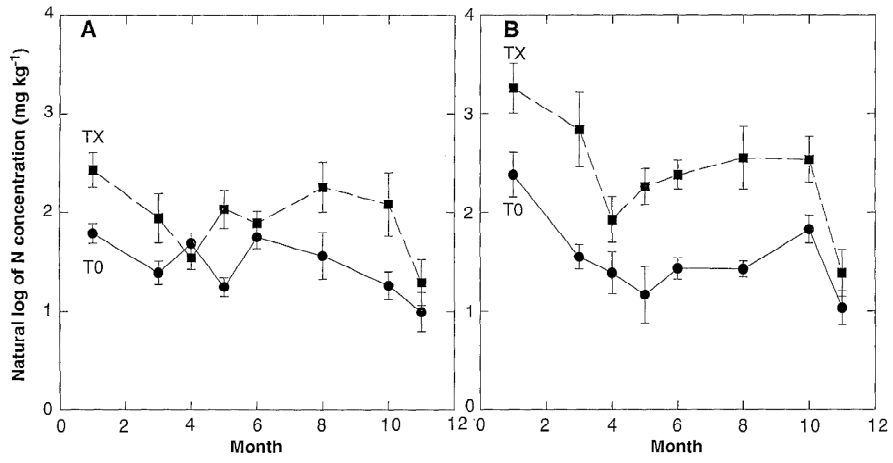


Fig. 1. Extractable N in situ at sites (**A**) lacking and (**B**) supporting dense resident grazing mammal populations in Serengeti National Park, Tanzania. TX is the extractable N at the end of an incubation period; T0 is that value at the beginning of the incubation period. TX – T0 = net N mineralization for period x. Vertical bars indicate 0.95 confidence intervals.

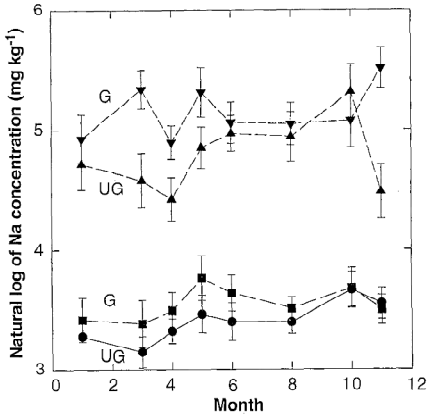


Fig. 2. Extractable Na in situ at sites (upper traces) supporting and (lower traces) lacking dense resident grazing mammal populations. G, samples incubated outside fences; UG, samples incubated inside fences. Vertical bars indicate 0.95 confidence intervals.

supposition in a native ecosystem. The data presented here demonstrating that herbivory by Serengeti grazers tangibly accelerates the mineralization of two minerals of considerable importance in animal nutrition are consistent with simulation results from grassland ecosystem models (*3*). In addition, they indicate that the accelerated recycling of plant-available Na is probably the mechanism leading to levels of that animal nutrient in grazer-exploited Serengeti grasslands that are sufficient to alleviate nutritional shortage in the grazers, particularly reproductive females and growing young (*5*).

Mammalian herbivores have been pervasive in grasslands through evolutionary time (*12*), their levels of forage consumption are considerable (*6*, *13*), and the animals accelerate rather than retard nutrient cycling. The intensity of the plant-herbivore interaction in grasslands, and its evolutionary antiquity, may have attenuated detrimental interaction effects through coevolution (*1*). Overgrazing of grasslands, on the other hand, which is commonly associated with the replacement of free-ranging wild herbivores with livestock and the resulting higher animal densities (*14*), often causes the replacement of highly palatable forages (*15*) that produce easily decomposable litter (*10*) with other plant species of lower nutritional quality and decomposability.

These data provide evidence that a terrestrial grazer can modify ecosystem processes in such a way as to alleviate nutritional deficiencies and, therefore, plausibly to elevate the carrying capacity of the ecosystem. The data also identify accelerated nutrient cycling as an important property of habitats that are critical to large mammal conservation (*16*). The coupling of animal site preference with nutritional effects could provide a guide for identifying sites essential for planning large mammal conservation in natural ecosystems. In addition, the presence of such sites, and the role of mammals in maintaining them, provide clear evidence that habitat deterioration is not an inescapable consequence of increased density of organisms (*1*).

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Hyaluronan Synthase of Chlorella Virus PBCV-1

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Sequence analysis of the 330-kilobase genome of the virus PBCV-1 that infects a chlorella-like green algae revealed an open reading frame, A98R, with similarity to several hyaluronan synthases. Hyaluronan is an essential polysaccharide found in higher animals as well as in a few pathogenic bacteria. Expression of the *A98R* gene product in *Escherichia coli* indicated that the recombinant protein is an authentic hyaluronan synthase. *A98R* is expressed early in PBCV-1 infection and hyaluronan is produced in infected algae. These results demonstrate that a virus can encode an enzyme capable of synthesizing a carbohydrate polymer and that hyaluronan exists outside of animals and their pathogens.

Hyaluronan or hyaluronic acid (HA), a member of the glycosaminoglycan family that also includes heparin and chondroitan, is a linear polysaccharide composed of alternating β1,4-glucuronic acid (β1,4-GlcA) and β1,3-*N*-acetylglucosamine (β1,3-GlcNAc) groups. Typically the full-length polymer chains are composed of 10^3 to 10^4 monosaccharides (10^6 to 10^7 daltons). HA is an important structural element in the vitreous humor of eye, synovial fluid, and skin of vertebrates (*1*). Furthermore, HA interacts with proteins such as CD44, RHAMM, and fibrinogen, thereby influencing many natural processes such as angiogenesis, cancer, cell motility, wound healing, and cell adhesion (*2*). HA also constitutes the extracellular capsules of certain bacterial pathogens such as group A and C *Streptococcus* and *Pasteurella multocida* type A (*3*, *4*). These capsules act as virulence factors that protect the microbes from phagocytosis and complement during infection (*5*, *6*). Because HA, a component of the host tissues, is not normally immunogenic, the capsule serves as molecular camouflage (*7*).

HA synthases (HASs) are integral mem-

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