# Large Animals and System-Level Characteristics in River Corridors

## Implications for river management

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Processes structuring riparian corridors can be viewed as a hierarchy, in which primary factors (such as matter, energy, and water) create a spatially extensive and temporally variable physical environment, which becomes habitat for plants and animals. The habitat is further modified by the activities of large animals as they selectively eat vegetation, burrow and wallow in soils, and build dams on streams, among other activities. As a result, the variety of habitats, or "patches," is increased. The vegetation and microorganisms living on the increased variety of habitat patches largely determine the eventual distribution and cycling rates of elements (e.g., nitrogen and phosphorus) as basic population and community processes are carried out (Table 1).

In general, ecologists understand how interactions among water, energy, and matter shape the physical characteristics and habitat patches of river corridors, and how vegetation and microbes cycle elements, grow, reproduce, compete, and otherwise function. However, there has been little recognition of the equal importance of large animals in shap-

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### Large animals can significantly modify the structure and function of river corridors

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ing the character of riverine corridors. This omission is especially surprising, considering that their influence on the habitat mosaic of rivers is second only to the primary factors of matter, energy, and water (Table 1). By eating plants, moving soil, and dispersing seeds, larger animals (such as mammals, reptiles, and birds) alter vegetative structure, modify channel morphology, and assist in developing microtopography. The ecosystem-level consequences of these physical and trophic activities go far beyond supplying individuals with food and habitat (Johnston 1995, Jones and Lawton 1995, McNaughton et al. 1988, Naiman 1988).

Many ecologists and managers tend to treat the role and effects of each species on river corridors individually. For example, in North America, beaver (*Castor canadensis*) and moose (*Alces alces*) are traditionally studied and managed separately, as are hippopotamus (*Hippopotamus amphibius*), crocodile (*Crocodylus niloticus*), and elephant (*Loxodonta africana*) in southern Africa. However, this focus on individual species often results in the failure to recognize fundamental, synergistic forces that result from interactions among large animals in river corridors. As we show in this article, community interactions among species have long-term, complex ecosystem-level consequences (Johnston et al. 1993, McNaughton 1985).

## The integrity of river corridors

Recent research indicates that large animals can significantly modify the structure (channel geomorphology, vegetative characteristics, and biodiversity) and function (productivity, connectivity, and resistance and resilience to disturbance) of river corridors and that management of population demography may have long-term ecosystem-level consequences (Butler 1995, Johnston 1995, Naiman 1988). Viewing the activities of large animals in the context of habitat patch dynamics may also provide a useful framework in which to analyze their effects on the environment, and to improve conservation management of riverine corridors.

Animal populations and, consequently, their effects on ecosystems vary widely in time and space (Egerton 1973, Elton 1930, Turner et al. 1995). Population sizes often fluctuate over years to decades; animal distribution patterns often track vegetation change from decades to centuries, and the relative mix of species in the community responds to competition, predation, disease, and other environmental influences. River and riparian corridor management could be improved by shifting

Table 1. Hierarchical influences on the structure and dynamics of riparian corridors.

| Level of influence | Factors | Actions | Consequences | Approximate scales | |
| --- | --- | --- | --- | --- | --- |
| | | | | Spatial (km²) | Temporal (years) |
| First-level | Matter, energy, water, gravity, fire | Erosion, deposition, slope, aspect, altitude | Soil formation, macroclimate, geomorphology | $10^6$–$10^8$ | $10^6$–$10^8$ |
| Second-level | Biophysical alterations: habitat modification | Dam building, wallows, herbivory, burrowing | Conversion of habitat from macropatches to mesopatches | $10^{-1}$–$10^3$ | $10^{-}$–$10^4$ |
| Third-level | Elemental distribution and cycling by biota | Metabolism, nutrient cycling, formation of specialized chemicals | Productivity, succession, biotic distribution, formation of meso- and micropatches | $10^1$–$10^2$ | $10^{-}$–$10^3$ |
| Fourth-level | Biotic interactions (including disease) | Life history strategies, population and community processes, trophic pathways, epidemics | Competition, mutualism, abundance, micropatch distribution | $10^{-2}$–$10^1$ | $10^{-2}$–$10^1$ |
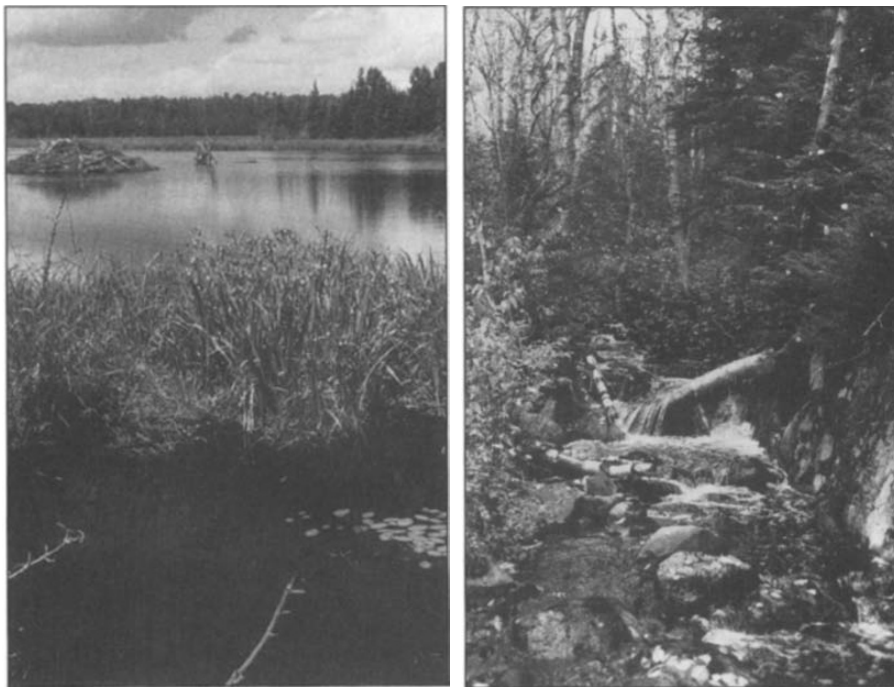


Figure 1. The presence of beaver in streams in North America has significantly influenced aquatic ecosystems. The biological communities and ecological characteristics of streams with beaver ponds (left) are unlike those of free-flowing streams (right).

management of individual species for stable populations to managing them for variability as well as for their interactive roles in the ecosystem. Focusing on a particular species is not sufficient to maintain biodiversity and other ecosystem-scale attributes for the long term.

An emphasis on management for variability and interaction is especially appropriate for river corridors, where ecological integrity and long-term vitality are created and main-tained by sustained spatial and temporal variability and by strong interactions among environmental components (Naiman et al. 1992). In river corridors, the numbers of animals and the abundance (and quality) of food vary constantly, and the variations are irregular, both spatiotemporally and in amplitude. Variations in the abundance of one species have direct and indirect effects on the abundance of others, which themselves also vary somewhat independently in abundance (Elton 1930). Unfortunately, these basic principles of ecology are all too often violated by the philosophies and strategies of resource management programs, which tend to focus on stability and populations (Botkin 1990).

Many management strategies inadvertently simplify river corridors by not being attentive to basic principles governing large animals in highly variable environments. The result of such strategies is a reduction in compositional, structural, and functional biodiversity that goes far beyond the effects of modifying the population dynamics of a single species. Examples are the long-term consequences of beaver and elephant control programs and the removal of hippopotamus from rivers. The large-scale elimination of beaver in North America substantially altered the vitality of drainage networks (Figure 1). Similarly, the exclusion or removal of elephant and hippopotamus from river corridors in Africa has led to pools filling with sediment, to the closure of riparian forest canopies, and to altered species composition (Hatton and Smart 1984, Laws 1970, Owen-Smith 1988).

The issue of system simplification is conceptualized in Figure 2. In highly managed rivers with constrained channels and with large animals removed, the river's influence on the riparian habitat structure is similar to that of the littoral zone of static water bodies, which are characterized by linear zones of vegetation

(Figure 2a). In moderately managed rivers, the natural lateral movement of the channel modifies the physical environment and provides greater patchiness to the zones (Figure 2b). The full diversity and dynamics of the habitat patches will, however, be realized only when the influences of large animals become an integral part of the management strategy (Figure 2c).

To illustrate the importance of the activities of large animals for the long-term integrity of river corridors, we begin by examining the concept of functional groupings, which categorize often dissimilar species into units that share similar environmental functions. We then provide examples of functional similarities among animals from two contrasting regions, North America and southern Africa. Even though the two regions have fundamentally different animal assemblages, animals in both regions have similar or complementary effects on ecosystem processes and structure. Accepting



Low Disturbance Few Animals    Moderate Hydrologic Disturbance    Hydrologic and Animal Disturbances
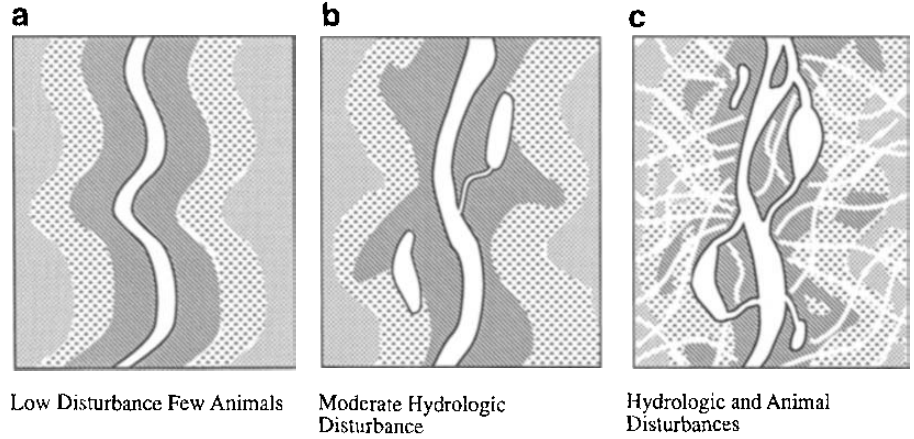
Figure 2. Human modifications have fundamental impacts on the vegetative patch structure of river corridors. When channel processes are constrained by management, the vegetation mosaic becomes a simple linear zone (a). Under the influence of natural hydrology and channel processes, the heterogeneity is improved (b), but only with the feeding and movements of large animals is the patch heterogeneity optimized for riparian vegetation. Vegetative patches are smaller, more numerous, and more spatially dispersed under the influence of animals (c).

the idea that biodiversity has structural, functional, and compositional components, we illustrate commonalities, and thus ubiquity, in the activities of large animals, eventually concluding that management strategies need to balance the emphasis on species composition with an emphasis on structural and functional aspects of river corridors.

| Basic Life Requirements | Primary Activity | Characteristic Animals | | Specific Patch-Level Effects | Patch-Level Consequences | | Ecosystem Properties |
|---|---|---|---|---|---|---|---|
| | | North America | Southern Africa | | | | |
| Habitat | Ponding | Beaver | Elephant, Ungulates, Hippopotamus | Modifies morphology and local hydrology. Affects pool depth and size, channel morphology. | | | 1. High internal biodiversity (species, land forms, habitats) |
| | Burrowing | Fossorial Rodents | Crocodile | Affects bank stability. | | | |
| | Trampling | Moose, Elk, Beaver, Brown Bear | Hippopotamus, Elephant, Buffalo | Creates paths - increases patch connectivity. Modifies microtopography. | Structures physical template; spatial and temporal heterogeneity | | 2. Dynamic heterogeneous patch mosaic |
| | Movement | Deer, Beaver, Elk, Birds | Hippopotamus, Elephant, Ungulates, Birds | Disperses resources within and between patches and into and out of system. | | | |
| | Digging | Brown Bear | Warthog, Elephant | Increases spatial and temporal heterogeneity of microtopography. | | | 3. Nutrient retention (i.e. standing crops), rapid and efficient cycling, high productivity |
| Feeding | Selective Grazing | Lesser Snowgeese, Prairie Dog | Spur-winged Geese, Waterbuck, Reedbuck | Modifies plant species competition. | | | |
| | Bulk Grazing | | Hippopotamus, Buffalo | Reduces the role of competition and enhances patch contrast. | Determines physiognomy, resource distribution and process rates | | 4. High internal patch connectivity |
| | Selective Browsing | Elk | Kudu, Giraffe, Bushbuck | Modifies competition. | | | |
| | Bulk Browsing | Moose | Elephant | Modifies vegetation physiognomy and patch structure. | | Species and community scale responses to the physical template. | 5. High resilience and resistance to disturbance |
| | Frugivory | Bats, Birds | Monkey, Birds, Baboon | Seed dispersal | | | |
| | Granivory | Birds, Rodents | Birds, Rodents | Modifies propagule distribution and number. | Influences propagule availability and dispersal | | 6. Large contribution to landscape diversity |
| | Predation | Wolf, Otter, Coyote, Kingfisher, Dipper | Crocodile, Leopard, Lion, Kingfisher, Heron, Cormorant | Modifies population dynamics and interspecies competition. | | | |

Figure 3. The basic life requirements of large animals are carried out through a set of primary activities that have both specific patch-level effects and ecosystem-scale consequences. Examples are provided from a few characteristic animals for North America and southern Africa.

**Figure 4.** In southern Africa, wallowing by Cape buffalo, elephant, hippopotamus, and other large animals over long periods of time increases the size of natural depressions (i.e., pools), allowing a greater volume of water to accumulate during the wet season.

## Functional groupings

The concept of functional groupings organizes animals around primary activities (e.g., ponding water, trampling, selective grazing, and browsing) that affect habitat-level structural characteristics and functional processes (Figure 3). Functional grouping by activity illustrates a range of patch-level effects, which collectively have strong influences on ecosystem-level properties. In the case of rivers, these ecosystem properties include high biodiversity, which is maintained through a mosaic of constantly changing habitat patches; increased productivity, which is maintained through nutrient retention and rapid recycling; high connectivity between different parts of the drainage network, which is maintained through the movement of organisms and materials; and a strong resistance and resilience to disturbances at the catchment scale, which is maintained by the existence of a diversity of habitat and resources.

Functional groupings differ from functional feeding groups (Merritt and Cummins 1978), which are a more familiar way to organize animals, in two respects: they are defined by habitat modification as well as by feeding, and they explicitly incorporate the effects and consequences of modifying habitat and procuring food. For example, many animals influence the geomorphology of rivers and the associated riparian forest by ponding water, digging soils, trampling, or moving materials, whereas others influence the riverine system by altering the vegetation through various types of feeding activities (Figure 3). Both beaver and hippopotamus pond water, beaver by building dams and hippopotamus by wallowing in channels. Similarly, elephant, gemsbok (*Oryse gazella*), and baboon (*Papio* sp.) dig holes in temporary stream beds to procure water, indirectly providing refuge for fish and amphibians. The specific effects and ecological consequences of all of these activities are conceptually the same: They modify both the riverine environment, by increasing the number, depth, and size of pools, and the local hydrology, by retaining water for longer periods (Figure 4). The result is a physical environment with a greater diversity of habitat.

In an analogous way, browsing by elk (*Cervus canadensis*) and moose in the riparian forests of North America has similar effects and ecological consequences to browsing by kudu (*Tragelaphus strepsicerous*), giraffe (*Giraffa camelopardalis*), bushbuck (*Tragelaphus scriptus*), and elephant in southern Africa. Browsing modifies vegetative competition, enhances contrast among vegetative patches, and alters plant physiognomy. These activities produce a community structure that is significantly modified from that which would arise in response to the physical environment alone. This new vegetative community, in turn, has consequences for populations of other animals. Perhaps this influence is not surprising to some wildlife managers, but it has frequently been ignored. For example, in Travo National Park in East Africa, feeding by elephant created gaps in the savannah and riparian thickets, causing major changes in ungulate species composition. Over a 20-year period (1963–1982), the population of lesser kudu (*Tragelaphus inbergis*) decreased by 90%, of gerenuk (*Litocramius walleri*) by 80%, and of giraffe by 40%; the black rhinoceros (*Diceros bicornis*) declined to "very low numbers" (Parker 1983).

To develop effective management strategies for riverine environments, it is necessary to consider not only similarities among functional groupings among different ecoregions but also inherent differences in the ecological histories and physical environments of these regions (e.g., Belsky and Canham 1994). In temperate North America, there are no animals that maintain pools by wallowing, and in semiarid regions of southern Africa, there are no animals that maintain pools by building dams. Why? One explanation for these differences may be that the water in North America is too cold for large amphibious mammals to use it as a refuge. And in southern Africa, where termites are a dominant ecological force (Scholes and Walker 1993) and where the low vegetative cover on uplands and intense precipitation result in an unusually rapid and powerful runoff (Gordon et al. 1992), dam building simply would not be adaptive. That is, termites and the rapidity and power of runoff preclude the widespread use of wooden dams in southern Africa.

The food preferences of grazers provide another example of how differences in ecoregions lead to differences in the members of functional groupings. In temperate North America, most grazers and browsers (such as deer, elk, and moose) are

generalists that forage on many types of riparian plants. In southern Africa, with its rich diversity of plants and animals, many grazers are more specialized. For example, waterbuck (*Kobus ellipsiprymnus*) and reedbuck (*Redunca arundinum*) are selective grazers of riparian and terrestrial grasses, whereas hippopotamus and Cape buffalo (*Syncerus caffer*) are bulk grazers and, thus, much less specific in their diet. Kudu, giraffe, and bushbuck selectively browse woody shoot tips and leaves, whereas elephant destructively browse a wide variety of shrubs and trees over large areas. Thus, the pattern and intensity of disturbance covered by individual species is different, but at the system level these contrasts are evened out because the effects of many specialists produce similar consequences to those of a few generalists.

The fundamental reason for establishing functional groupings is to visualize how animals act to modify and shape ecosystems (Jones et al. 1993, Rogers 1997a). There is a growing realization that to move toward a more holistic, ecosystem-based approach to management it is necessary to turn the focus from species as compositional components of ecosystems to species as functional components. In the past, functionality was seen largely as trophic dynamics, competition, or other aspects of species–species interactions. Here we focus on a different but equally important aspect—how large animals modify ecosystem structure by "engineering" the environment and, in the process, create a dynamic collection of resource patches.

## Case studies of functional similarities

Functional similarities in habitat modification and food procurement among ecoregions (in this case, North America and southern Africa) are numerous. Although many animals and activities could provide examples of these similarities, we have limited our discussion to the few characteristic animals for which reliable data or observations are available.

**Habitat modification.** In temperate North America, the beaver is the only mammal that actively modifies



Figure 5. In the process of making nightly feeding forays between rivers and surrounding riparian zones, hippopotamus create a maze of trails and canals that serve as corridors for the movements of many other species. (left) Hippopotamus trail leading to riparian feeding sites. (right) Hippopotamus canal between sites within a large wetland adjacent to Lake Kariba, Zimbabwe.

channel geomorphology and hydraulic conditions (Naiman et al. 1986, 1988, 1994). Beaver normally build dams in the main channels of second- to fourth-order streams and in the secondary channels and floodplains of larger streams (Figure 1). Suitable habitat may have 8–16 dams per km. The dams retain not only water but also large volumes (up to 20,000 m³) of sediment that would normally erode downstream. The ponding of water and the storage of wetted sediments has profound long-term consequences for the entire drainage network. This activity creates and maintains physically diverse wetlands, modifies biogeochemical cycles, alters the vegetative composition of in-channel and riparian communities, and influences the character of water and material transported downstream (Naiman et al. 1994, Pollock et al. 1995). The result is a mosaic of temporally and spatially variable habitat patches with strong, long-term influences on watershed-level features.

In southern Africa, hippopotamus are the main animals responsible for modifying the physical environment and, thus, local hydraulic conditions—

although, as mentioned earlier, other large animals (i.e., rhinoceros, baboon, and elephant) also can have a significant effect. Two types of hippopotamus activity are related to habitat modification: daytime wallowing in pools, and nighttime movements to and from feeding grounds (Figure 5). During the day, hippopotamus gather in deep waters, where their general movements stir up sediments that are either carried downstream or moved laterally to shallow depositional areas. The result is that pools are deeper, thereby providing habitat not only for hippopotamus, but also for crocodile and larger fish. In addition, the deeper pools reduce evaporation, allowing water to persist longer during dry periods and providing essential habitat and refuge during droughts or in nonpermanently flowing streams (Allanson et al. 1990). During the night, hippopotamus persistently follow the same paths to, from, and among pools and the terrestrial grazing areas. This activity keeps existing channels free of vegetation and sedimentation and creates new channels.

Thus, in floodplains, hippopotamus maintain connectivity between

habitat patches. This connectivity promotes movement of other species (such as fish and amphibians) among populations and resource patches as well as the movement of water and nutrients. Connectivity is especially evident in the 16,000 km² Okavango Delta, Botswana (Rogers 1997b), where hippopotamus movements change the mosaic of habitat patches in the same way that beaver does at the watershed scale.

Burrowing, trampling, migrating, and digging provide additional examples of geomorphic modification of rivers by large animals that have similar consequences in North America and southern Africa. Trails created and maintained by beaver, moose, elk, brown bear (*Ursus middendorff*), and other animals occur approximately every 10 m along riverbanks in North America (Naiman et al. 1986) and create a maze of trampled paths in temperate riparian forests (Figure 2c). The same sort of mosaic is produced by elephant, hippopotamus, and antelope in southern Africa. An interesting aspect of this mosaic relates to the permeability of riparian boundaries to the movement of materials from uplands. In recent years, the ability of riparian forests to filter, retain, and transform nutrients that are flowing off the surrounding landscape has been recognized (Pinay et al. 1990), but there has been scant recognition of the fact that large animals act as significant agents for the movement of materials across riparian boundaries. This oversight may be due to the fact that most nutrient retention studies have been conducted in highly managed or unnatural environments, where the riparian patch structure responds primarily to the physical environment rather than to animal influence (Figures 2a and 2b).

Burrowing and digging also have similar consequences in both regions. For example, in North American uplands, free-living gopher (*Thomomys*



Figure 6. Warthog are important in structuring riparian vegetation in southern Africa. (top) Warthog feeding on the shoots of riparian grasses at the end of the wet season. (bottom) Warthog plow extensive areas in their search for tubers, rhizome, and other underground storage organs.

and *Geomys*) and ground squirrel (*Citellus* spp.) move 10,000–90,000 kg · ha⁻¹ · yr⁻¹ of subsurface soil to the surface (Andersen 1987a), where the physical mixing of nutrients results in altered species composition and productive plant communities (Huntly and Inouye 1988). If the numerous mice, voles, and shrews inhabiting North American riparian forests move even a fraction of this amount of soil, then the environmental effects would be significant. In southern Africa, a major mover of soil is the warthog (*Phacochoerus aethiopicus*), which uses its snout to dig for grass rhizomes, tubers, and other underground plant storage organs in riparian wetlands (Rickard 1993). Individual feeding patches are usually 1–2 m in diameter and 10–15 cm deep, with soil and plant litter piled around the circumference another 10–15 cm high (Figure 6). When flooded, these patches form pools with distinctive plant and invertebrate communities that attract wad-

ing birds. During the dry season, this activity results in extensive areas (up to tens of hectares) resembling a plowed field (Figure 6) and a complete change in plant species dominance, as perennial rhizomatous grasses are replaced by annual grasses and forbs (Rickard 1993). Although the specific consequences of burning and digging differ between the two regions because of specific site conditions, in both regions the digging activities modify soil, microtopography, and vegetation.

Feeding strategies. Depending on the season, herbivores may act as predators (by removing plants or seeds) or as parasites (by partially reducing plant biomass), or they may promote some form of mutualistic association (by distributing seed and plant fragments to favorable growth environments; Crawley 1983). In both temperate North America and subtropical southern Africa, food preferences, feeding method, and seasonal variations in food chemistry all strongly influence riparian community structure, plant physiognomy, competition, soil development, and propagule dispersal (Figure 3). The influence of herbivores on plants should seem self-evident because the ecological effects and consequences of feeding on the plant community itself are well known, but the effects of feeding on the ecosystem as a whole are less well understood (e.g., Andersen 1987b, Crawley 1983, DeAngelis et al. 1989, Huntly 1991, Jefferies 1988). However, with the exception of a few comprehensive studies (e.g., Carpenter and Kitchell 1988, McNaughton 1985, Pastor et al. 1993), much less is known about the ecosystem-scale consequences of feeding.

Moose provide an excellent example of ecosystem-scale browsing effects and their consequences for temperate North American riparian forests (McInnes et al. 1992, Pastor et al. 1988, 1993). Moose consume approximately 5–6 metric tons of

aquatic, riparian, and upland plant biomass annually, returning approximately 60% of this biomass to the soil. Moose prefer to forage on aquatic macrophytes and early successional riparian plants, such as willow (*Salix*) and poplar (*Populus*), which grow rapidly and produce easily decomposable, nitrogen-rich litter. Moderate to heavy moose browsing prevents saplings of preferred food species from growing into the tree canopy, increases the abundance of species not browsed (e.g., white spruce, *Picea glauca*), and decreases the quality of litter returned to the soil, thereby controlling the nitrogen cycle and the long-term productivity of the plant community (Figure 7). Clearly, the indirect effects of moose browsing on decomposers through changes in the quality of litterfall has serious long-term consequences for riparian forests (McInnes et al. 1992, Pastor et al. 1993).

In subtropical southern Africa, bulk grazing by hippopotamus; selective browsing by kudu, giraffe, and bushbuck; and bulk browsing by elephant all have similar effects on the riparian corridor. For example, hippopotamus feed on floodplain and terrestrial grasses by night and return to water by day. Each hippopotamus consumes approximately 135 kg of grass daily (Owen-Smith 1988) and transfers approximately 9 metric tons dry mass of feces to the aquatic system annually (Heeg and Breen 1982). Under natural conditions, it is not uncommon to find hippopotamus in water at densities exceeding 0.1/ha, which means that detritus (largely of terrestrial origin) in the amount of approximately 1 metric ton/ha is added to the water body annually. In addition, because hippopotamus are area-selective bulk grazers, they reduce patches of tall grass to short grass, thus enhancing contrast with surrounding vegetative patches but re-



Figure 7. In southern Africa, as in North America, there is a close association between soil properties and grazing. At Nylsvley Nature Reserve in South Africa, soil characteristics influence the grazing rate. (top) Riparian areas high in sodium (an essential dietary nutrient) are heavily grazed, whereas areas low in sodium (bottom) are lightly grazed.

ducing species diversity within the feeding patches (Figure 7; Owen-Smith 1988). When considering their feeding effects in combination with their ponding activities, it becomes apparent that hippopotamus play a similar role to beaver—that is, even though the individual activities of these animals are different, both modify habitat patch structure, nutrient retention and productivity.

Other feeding strategies, such as selective grazing, frugivory, granivory, and predation, also have similar effects and ecosystem-scale consequences in North America and southern Africa. In temperate North America, grazing by lesser snow geese (*Chen caerulescens*) and prairie dog (*Cynomys* spp.) alter vegetative patch structure, nutrient cycling, and feeding site selection by other herbivores (Jefferies 1988, Whicker and Detling 1988). In addition, fruit-eating bats and a variety of seed-eating birds affect propagule distribution and

seedling abundance (Marks 1983). Moreover, large predators such as wolf (*Canus lupis*), river otter (*Lutra canadensis*), and kingfisher (Alcedinidae) directly affect the abundance and distribution of other riverine species and indirectly affect many ecosystem-scale processes by modifying the food web. In subtropical southern Africa, the spur-winged goose (*Plectropterus gambensis*) is the functional equivalent of the snow goose (Rogers 1997b). Riverine corridors are also habitat for monkey, baboon, fruit bats, and hundreds of bird species, such as green pigeon (*Treron calva*) and purple crested lourie (*Tauraco porphyreolophus*), all of which play important roles in shaping the character of the riparian system by selective feeding and movement of plant propagules.

## Wildlife management and river corridors

In this article, we have shown that large animals greatly influence habitat creation and maintenance. We have also provided a conceptual framework in the form of functional groupings, using case studies from North America and southern Africa, to support our assertion that animals are key elements in the structure and function of riverine ecosystems. If, as we have already stated, management of rivers for long-term ecological integrity must recognize the consequences of animal activities, then how could wildlife management be better integrated with river management?

Wildlife, water, and vegetation (as well as the habitat patches that their interactions create) need to be thought of as an integrated system that is constantly changing over space and time. We propose that principles for wildlife management in river corridors adhere to the guidelines that were recently proposed for ecosystem management (Christensen et al. 1996, Grumbine 1994). These guidelines recommend maintaining viable populations of all species across their natural range of variation, manag-

**Table 2.** Wildlife management strategies to create and maintain the ecosystem-level characteristics and integrity of river corridors in temperate North America and subtropical southern Africa.

| Ecosystem characteristic or process | Strategies | Examples |
| --- | --- | --- |
| Nutrient flux across boundaries | Allow a wide variety of browsing; establish roosting sites for for bird and bats; maintain terrestrial populations consuming aquatic organisms (i.e., bear, mink, otter, kingfisher). | Allow unrestricted tree cutting by beaver; maintain or reintroduce hippopotamus for terrestrial grazing. |
| Nutrient retention | Maintain ponded waterbodies; encourage animals feeding on aquatic organisms. | Maintain viable populations of crocodile otter, bear, and others feeding on fish; encourage dam building and wallowing. |
| Spatial heterogeneity | Maintain ponded waterbodies; encourage spatially diverse browsing and grazing; allow population cycles by fossorial rodents. Develop management plans that emphasize decades rather than years. | Create opportunities for dam building by beaver and for wallowing by a variety of animals. |
| Temporal heterogeneity (dynamic habitat patches) | Manage animal populations for variability over time and for variable ratios between species. | Allow population cycles and natural activities of browsers, grazers, and predators. |
| Connectivity | Allow contagion for the movement of information, nutrients, propagules, and organisms maintained by an ecologically diverse but dynamic community for an array of mechanisms that transcend patch boundaries. | Allow hippopotamus to create channels or or keep existing channels open. Develop a regional network of well-functioning systems to allow for uncertainties. |
| Biodiversity | Combine strategies and examples for spatial and temporal heterogeneity to provide suitable environmental conditions for maintaining biodiversity. | Specific management strategies are given above but in combination have broader outcomes. |
| Productivity | Combine strategies and examples given for nutrient flux and retention and for spatial and temporal heterogeneity to provide suitable environmental conditions for maintaining productivity. Exceptions would be high and grazing populations for long periods. | Specific management strategies are given above but in combination have broader outcomes. |
| Biotic disturbance regime | Maintain dynamic population cycles and demographic patterns to create conditions that impart resistance and resilience within the system to external disturbances. | Specific management strategies are given above but in combination have broader outcomes. |

ing over time periods that are long enough to maintain the evolutionary and ecological potential of species and ecosystems, and accommodating human use and occupancy within these constraints. We support both Grumbine's and Christensen et al.'s perspective because the biodiversity and ecological integrity of river corridors continue to decline globally in response to ineffective policies that emphasize piecemeal approaches to management rather than the comprehensive approaches that are needed to protect the integrity of ecological systems (Angermeier and Karr 1994).

How can wildlife resources be managed to provide ecosystem-level integrity for rivers? We offer some recommendations, whose effectiveness will, of course, depend on specific regional characteristics (Table 2). For example, to maintain nutrient fluxes across boundaries between the river channel, the riparian forest, and the uplands, it is necessary to allow animals such as beaver, hippo-

potamus, and various ungulates freedom of movement; to ensure roosting sites for bats and birds; to encourage colonization of riparian zones; and to maintain viable populations of large animals (e.g., brown bear, otter, heron, and kingfisher) that consume aquatic animals and plants but defecate in terrestrial environments or the converse. The recommendations in Table 2 are not exhaustive for each ecosystem-level characteristic, but their implementation should move the ecological system toward more complex and synergistic interactions, maintaining the long-term integrity and vitality of river systems.

## Developing a new perspective

In the past, species-focused management was dominated by concepts such as "carrying capacity," which estimates the optimal number of large animals for an area and implies a "balance of nature" viewpoint. By contrast, ecosystem management, as dis-

cussed in this article, focuses on managing for spatiotemporal variability (i.e., a "flux of nature" concept). The former approach dampens extreme population and community changes, as well as ecosystem resilience, whereas the latter generates complexity and heterogeneity, which increase ecosystem resilience to disturbances.

The perspective outlined in this article provides a basic step in developing a holistic understanding of river ecosystems. Although the influence of large mammals in terrestrial systems is well recognized, it is not so within riparian corridors. Moreover, even in terrestrial systems, large mammals are seldom managed for the effects they have on physical habitat conditions. We suggest that viewing animal effects in riparian corridors in the context of patch dynamics has value for scientists and managers for two reasons: riparian corridors are inherently disturbance-driven systems, and functional groupings provide a valuable framework for translating detailed

ecological knowledge into resource plans. As interactions intensify among cultural values, societal behavior, and the environment, it will become increasingly important that ecosystem management be based on sound ecological principles. We suggest that the importance of large animals in creating and maintaining the character of river corridors is one of those principles.

## Acknowledgments

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