THE ROLE OF MAMMALS AS ECOSYSTEM LANDSCAPERS

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ABSTRACT: The role of mammals in ecosystems is to modify vegetation structure, alter pathways of nutrients, and thereby change species composition. Their large-scale structuring effects make large mammals 'ecological landscapers'. Through this they influence ecosystem function and biodiversity. Landscaping effects occur when mammals are regulated by food, rather than by predators. This condition is constrained by four factors: when (1) body size is large enough to avoid predators; (2) populations adopt large scale migration behaviour because predators are unable to follow them; (3) in multispecies communities (savanna, grasslands) with a range of predator and prey sizes, only the largest species can avoid predation because they subsidize predators that regulate smaller prey species; and (4) in single predator-prey systems (tundra, desert, boreal, and temperate forests), ecological conditions determine whether or not predators regulate prey. The structuring role of mammals in maintaining species diversity is evident not just in vegetation, but also in birds, other mammals, and invertebrates. This role makes them prime candidates as 'umbrella species' for conservation. Protection of large mammal species and their habitats also conserves a large part of the remaining community. It also means that such mammals become the 'indicator species' for the health of the ecosystem.

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In terrestrial ecosystems, plants form the basis of all communities, in terms of both structure and function. The abiotic environment sets the particular form of structure, with cold and dry climates having slow and intermittent flow of resources. The structure moves from single layer lichens in the Antarctic through arctic tundra to complex rainforests of the tropics. Thus, plants determine the niche possibilities of animals.

To what extent do mammals alter the basic structure of communities set by plants? Because all animals in terrestrial systems depend directly or indirectly on plants, they must to some degree alter plant structure, rates of flow, and species composition. Mammals, even at their most abundant, are numerically insignificant in comparison to such groups as birds and reptiles, not to mention insects, protozoa, and protists. Nevertheless, mammals impact plant structure and function to a greater extent, relative to their abundance, than any other animal group. Mammals are "ecological landscapers".

Because mammals change the physical and biotic landscape, they can affect ecosystem function (Hurlbert 1997, Paine 2000). This impact leads naturally to the conservation issues of umbrella species and indicator species (Landres et al. 1988). Can mammals act as umbrella species purely because of their large scale structuring and functional effects so that in protecting them they also protect most other species? Can they also act as surrogates for other groups so that easily detectable trends in mammals reflect similar trends in other less obvious groups?

MAMMALS AS ECOLOGICAL LANDSCAPERS

'Ecological engineers' are species that change the physical state of the biotic or abiotic environment in which they live, and thereby, alter the flow of resources to other species (Jones et al. 1994, 1997). Thus, in marine environments corals create their own local environment as well as large-scale habitats for other species. Perhaps, termites create similar households on a local scale in terrestrial systems.

However, such 'engineering' operates on relatively local scales. There are also processes that take place on much larger scales (landscapes, watersheds, biomes) and determine not only physical structure, but also function and species composition of whole ecosystems. An example of one such process is fire, which in savanna biomes of Africa, Australia, and South America changes plant succession from a 'fireless climax' to a 'fire disclimax'. In savanna, fire typically impedes the succession of trees and promotes grassland and fire tolerant herbs (Frost 1985a). Fire operates as a probability function on a biome scale, while individual fire events occur at least at landscape scales.

Mammals can have analogous effects to fire in savanna systems (Hobbs 1996, Sala et al. 1996). One could even describe a 'mammal disclimax' where plant succession is held in a different state as a result of the restructuring imposed by mammals. Thus, mammals act as ecological landscapers. Such impacts are evident in most terrestrial biomes where mammals are abundant.

Boreal and Taiga Forests

The boreal forests of Canada are dominated by a few species of conifer trees, in particular the white spruce (*Picea glauca*). The dominant mammal there is the snowshoe hare (*Lepus americanus*) that depends largely on woody shrubs such as willow (*Salix* spp.) and birch (*Betula* spp.) during winter. Every 10 years hares reach high numbers and at those times they eat all of the terminal shoots of small white spruce within their reach (usually up to 120 cm) (Fig. 1). The slow growing spruce then take about 10 years to recover from this brows-

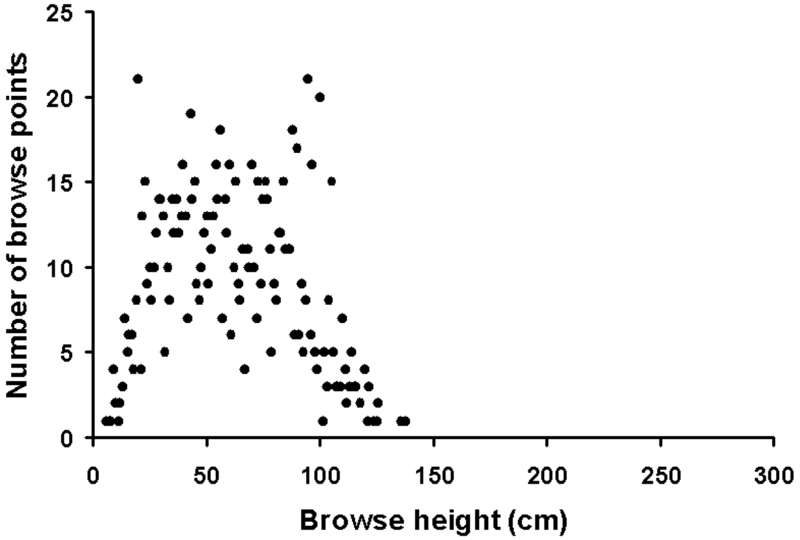

Fig. 1. The frequency of snowshoe hare browse heights on terminal shoots of small white spruce, Yukon, Canada. Hares can prevent trees from growing above about 1 m for several decades.

ing, develop a new shoot, and add another 10 cm in height, only to have this browsed off at the next peak. Thus, a tree, 50 cm high, may take 50-80 years to reach the escape height, and some of them never do so and die. In contrast, trees protected from browsing grow at an accelerating rate and can escape within 10 years. The boreal forest is subject to fires from lightening strikes and so a mosaic is formed of patches at different ages since a fire occurred. The effect of hares is to keep these patches in an open state for a century or more, creating a landscape suitable for other plants that like open areas (many herbs and shrubs) and indirectly promoting their own food supply (Krebs et al. 2001.). Furthermore, experiments have shown that hare numbers decline because of a combination of lack of food and an increase in predators. Experimental increase in rate of food supply plus removal of predators kept hare numbers high for an extended period. The inference is that under these conditions hares could prevent forest regeneration altogether. There are similar browsing effects by moose (*Alces alces*) on aspen and other species at Isle Royale, U.S.A. (Risenhoover and Maass 1987, Pastor et al. 1988, McInnes et al. 1992, Pastor and Naiman 1992), and on birch in Scandinavia (Danell et al. 1985, Danell and Bergstrom 1989, Danell et al. 1994). Moose abundance influences the density of trees and hence composition of the habitats, but these effects also depend on the abiotic conditions and composition of other vegetation. In general, a forest with many moose is different structurally from one without them.

In both Banff National Park, Canada, and Yellowstone National Park, USA, elk (*Cervus elaphus*) browsed juvenile trees of aspen and willow (*Salix* spp.) so intensively that they changed the landscape from a dense conifer and aspen woodland to an open parkland (grassland with scattered mature trees), and maintained it thus for 40 years (Houston 1982,White 2001).

Temperate Woodland

The deciduous hardwood forests of North America are the home of white-tailed deer *(Odocoileus virginianus*) (McShea et al. 1997). The preferred habitat of these deer is young forest, regenerating after fire (or logging). In these conditions deer can reach numbers that prevent forests from regenerating, holding them in an open shrub state (Schmitz and Sinclair 1997). Deer can maintain this state while inhibiting hemlock (*Tsuga canadensis*) regeneration and extirpating rare herbaceous plants (Alverson and Waller 1997). Without deer, forests proceed to dense hardwood forests with abundant infrastructure in the shrub layer that forms the nesting habitat for rare birds such as the Kentucky warbler (*Oporornis formosus*) (McShea and Rappole 1997). In essence, there are two woodland states and which state prevails is determined by the abundance of deer.

Tropical Forest

Tropical forests, at least in the Holocene, have been far less subject to major structuring forces of mammals. In both Africa and Asia, elephant species inhabit the forests but their large-scale impact (as opposed to local feeding effects) remains unknown. This is a subject that needs research for conservation reasons. I will refer later to the paleohistorical effects of megaherbivores in forests.

Mammals, however, do influence the distribution of trees in tropical forests and, thereby, the species diversity of tropical trees. In turn, the dispersion of trees influences the extraordinary diversity of insects that live in these trees (Janzen 1970). Mammals such as bush pig (*Potamochoerus porcus*) and duiker (*Cephalophus, Sylvicapra*) species in African lowland forest, and peccaries (*Pecari, Tayassu*), deer, pacas(*Agouti* spp.), agoutis (*Dasyprocta* spp.), and rats in New World tropical forests concentrate on fruit under parent trees, removing most of them, and transporting a few to other areas. We can see the effect of mammals by examining tree distributions in areas where mammals have been removed. Thus, in tropical forests of Costa Rica disturbed by agriculture, mammals are at low density from hunting. The undispersed seeds of the tree, *Cassia grandi,* are at high density and suffer unusually high mortality from bruchid beetles (Janzen 1971). Similarly, tropical islands often lack the large vertebrates found on the mainland, and tree population structure differs markedly. In Puerto Rican forests, trees such as *Trophis* (Moraceae) have dense stands of young trees under the canopy not seen in the Costa Rican mainland where seeds are removed by native rodents and birds (Janzen 1970).

Savanna

Savannas are grasslands with scattered trees in the tropics and subtropics, typical of Africa and Australia, but with some representation in southern Asia and South America. They intergrade with broad-leaved evergreen dry woodlands, particularly the 'mopane' woodland of southern Africa and eucalypt woodland of Australia. Large mammals in Africa impose substantial structural impacts in these biomes. In southern Africa, heavy grazing of grasses by ungulates (monocot feeders) alters the balance of water relations between the tree component and the herb layer so that trees and shrubs become dominant. In turn browsing ungulates (dicot feeders) such as impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and giraffe (*Giraffa cemlopardalis*) benefit and their numbers increase (Walker 1985, Owen-Smith 1988).

Fire is required to change the tree dominated vegetation state back to a grassland state. This was demonstrated in the *Acacia* savanna of the Serengeti-Mara ecosystem, East Africa (Norton-Griffiths 1979). Between 1890 and 1950 *Acacia* and related trees dominated the vegetation. A 20-year period (1950s, 1960s) of severe burning, where 80 % of the system was burnt each year, resulted in virtually no tree seedlings escaping fire. Eventually senescence of mature trees, expedited only to a minor degree by African elephants (*Loxodonta africana*), resulted in a grassland state. It is in this grassland state that elephants played their major structuring role (Dublin et al. 1990, Dublin 1995). Elephants, by systematically browsing tree seedlings, were able to prevent regeneration of the trees and so hold the vegetation in a grassland state. Later, in the 1980s, elephants were removed by poachers and trees regenerated in abundance forming dense thickets (fire having been reduced through grazing by wildebeest, *Connochaetes taurinus*; Sinclair 1995). Thus, it was the combination of browsing by elephants and grazing by wildebeest that determined which of the two vegetation states, savanna or grassland, persisted (Sinclair and Krebs 2002, Fig. 2). The return of savanna has resulted in an increase in impala.

Elephants as a structuring force were to be seen in another area of East Africa, the Tsavo National Park, Kenya. In the period 1850 – 1900, the ivory trade in East Africa decimated elephant populations and none were to be found in the Tsavo of the 1890s (Patterson 1907). Furthermore, the African tribe that lived around Tsavo, the Wakamba, were traditional elephant hunters and kept numbers low in their area during 1900 – 1949. The vegetation without elephants was dense shrubland with scattered trees. It was sufficiently dense that hunters had to crawl along tunnels made by

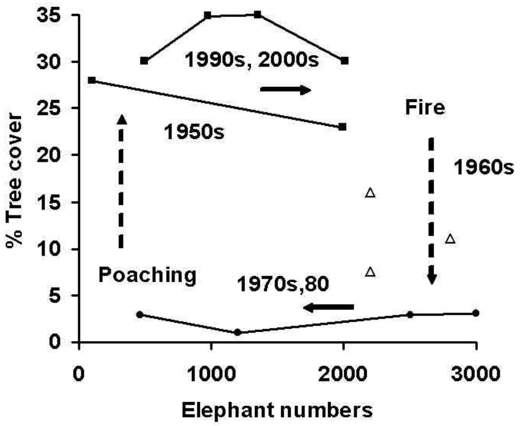

Fig.2. Savanna trees in Serengeti can exist in two states with the same density of elephants. A high tree density in the 1950s (squares) was reduced by fires in the 1960s (triangles) through the inhibition of seedlings. The resulting low tree density was maintained by elephant browsing of seedlings (circles). Only when elephants were removed by poaching (1980s) was the high tree density state restored (data from Dublin et al. 1990, Dublin 1995, personal observations. Redrawn from Sinclair and Krebs 2002).

black rhino (*Diceros bicornis*) (Patterson 1907). In 1949, Tsavo National Park was formed and it contained few elephants and dense vegetation. Elephants, now released from hunting, increased rapidly with the abundant food supply. They reduced the shrub and tree densities in inverse proportion to the distance from water. The population increase ceased with an initial die-off due to starvation (Corfield 1973) and has since stabilized. In the presence of elephants the landscape is a mosaic of open grassland, shrubland, and savanna. This change in vegetation structure led to declines of browsers such as gerenuck (*Litocranius walleri*), lesser kudu (*Tragelaphus imberbis*), and giraffe and an increase in grazers such as zebra (*Equus burchelli*) and buffalo (*Syncerus caffer*) (Parker 1983, Owen-Smith 1988).

Giraffe also structure savanna vegetation through two effects. One effect is by keeping small trees at a low height (1 – 2 m) through constant browsing (Pellew 1981, 1983). This height makes small trees vulnerable to fire, whose effects can reach up to 3 m. When a browsed tree in this height range experiences a hot fire, all its above ground biomass is killed, and it must regrow from the rootstock (Dublin 1986). Thus, giraffe indirectly reduce the density of trees and maintain a more open vegetation structure. Furthermore, abundant low level tree seedlings benefit other browsers such as greater kudu and impala (Owen-Smith 1988). The second effect of browsing is on mature trees that escape the fire window. These trees can be sculptured into a variety of shapes beginning with a ‘top’ shape, broad at the base and with a narrow central pole that giraffe cannot reach. This shape grows into an hourglass form as the central pole spreads out above the reach of giraffe. Eventually, the tree forms the characteristic flat top or umbrella top. This phenotype is the direct result of giraffe browsing, for in their absence we see trees with branches that droop down to the ground, forming dense thickets. These differences in tree morphology determine their suitability as nest sites for birds.

Grasslands

Mammals play a major role in structuring grasslands, especially wet grasslands and swamps, in temperate and tropical regions. The treeless eastern Serengeti plains are composed of short height grasses such as *Andropogon greenwayi* and *Sporobolus spicatus*. They also support a large number of small herbaceous dicots. The structure and species composition of these plains is maintained by near continuous grazing from the large herds of migratory wildebeest and zebra (McNaughton and Sabuni 1988). When wildebeest numbers were reduced to 20 % of the present day population, as a result of rinderpest mortality that persisted for some 70 years (1890-1963), these eastern grasslands changed in structure, becoming taller (1 m). Similar tall grasslands currently on the western Serengeti plains show that most dicot species become overshadowed and drop out. The impact of wildebeest grazing is demonstrated from the measurement of grass consumption on the short grass plains compared to the long grass plains (Fig. 3) (McNaughton 1984, McNaughton and Sabuni 1988, Augustine and McNaughton 1998). Furthermore, our studies reveal that the long grass structure provides the habitat for a wide range of grassland bird species including grass warblers (*Cisticola* spp.) and larks (Alaudidae). Long-term grazing results in a short-grass structure. This in turn provides the habitat for a different bird community, including species such as the red-capped lark (*Calandrella cinerea*), capped wheatear (*Oenanthe pileata*), and desert cisticola (*Cisticola aridulus*). Grasshopper species also change with grass structure. Thus, wildebeest grazing creates a niche for several different groups of species in the grassland community. Similar changes in the dicot herbs occurred with grazing in the flooded pampa grasslands of Argentina (Sala 1988).

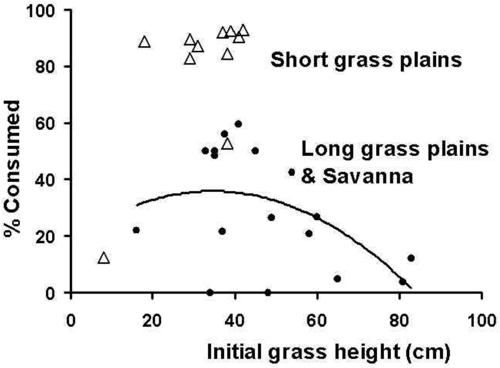

Fig. 3. Serengeti migrant herbivores maintain the short grasslands by consuming most of the growth (triangles), measured from small exclosure plots. In contrast, herbivores have less impact on the long grass plains and savannas as seen from the lower consumption rates (circles). The taller the grass the less is consumed (data from McNaughton and Sabuni 1988).

In tundra biomes caribou or reindeer (*Rangifer tarandus)* reduce lichen cover and promote crustose lichens and bryophytes (den Herder et al. 2003). Along the Arctic shoreline of Canada, geese rather than mammal herbivores are the major determinants of structure (Jefferies et al. 1994). However, the low impact of mammals is a recent event. I address the Pleistocene impacts below.

Swamps

Grazing by wildebeest, and their effect on grass structure, illustrates the process known as 'facilitation' whereby one species provides niches for other species. Elephants can facilitate the coexistence of other ungulates in swamp grasslands by breaking down, trampling, and feeding on very tall (3-5 m high) woody grasses. The young regenerating shoots of these grasses combined with other species that can grow in the openings provide the niche for African buffalo, topi (*Damaliscus korrigum*), and waterbuck (*Kobus defassa*), a sequence that was classically named the 'grazing succession' (Vesey-Fitzgerald 1960).

The Kafue flood plains in Zambia are annually flooded to depths varying from a few cm to several meters. Kafue lechwe (*Kobus leche*), a semi-aquatic antelope, occur at high density and impose considerable grazing pressure. The vegetation exhibits clear zonation determined by the degree of grazing, which in turn is determined by the degree of flooding and depth of water. In shallow zones, grazing is year round and grasses such as *Panicum repens* have evolved a leaf structure that remains under water and protected from grazing. In deep water, out of reach of grazers for part of the year, grasses like *Vossia cuspidate* have evolved a canopy that grows above the water surface (Ellenbrock and Werger 1988). It is likely that these different growth forms will support different animal communities.

Deserts

In Australia, burrowing bettongs (*Bettongia lesueur*), a small macropod marsupial the size of rabbits, now extinct on the mainland, were thought to structure the vegetation over large areas of *Acacia* shrubland (mulga) (Noble 1999, Noble et al. 2001). They formed large underground warrens from which they commuted several kilometres to feed on shrubs. Under certain fire frequencies they were apparently able to prevent shrub regeneration and maintain an open herbaceous structure. The removal of bettongs through invasion of exotic red fox predators (Short et al. 2000) changed the landscape to dense stands of *Acacia* shrubs. Incidentally, the pastoral value of these landscapes was probably much higher in the presence of bettongs than at present with the unutilized stands of shrubs.

The Chihuahuan deserts of Mexico are presently characterized by dense stands of cactus such as *Opuntia*. Currently, cattle open up these stands but bison (*Bison bison*), elk, and peccaries did so previously. Openings increase diversity of herbs that are redistributed by mammals (Janzen 1986).

MAMMALS AND ECOSYSTEM PROCESSES

Mammals influence the rates of nutrient cycling in addition to altering physical structure. In boreal forests moose decrease nitrogen mineralization of the soil by decreasing the return of high quality litter: their browsing on deciduous trees reduces their leaf fall while promoting low quality white spruce inputs (Pastor et al. 1988, 1993; Pastor and Danell 2003). In contrast, soil nitrogen cycling in Yellowstone and other prairie areas of the U.S.A. is increased by large mammal grazers (Hobbs 1996, Frank and Evans 1997).

The woodland-savanna biomes of Africa are dichotomous in terms of nutrients. Soils formed from old granitic rocks are sandy, heavily leached, and low in nutrients (dystrophic), particularly in calcium and phosphorus. These areas tend to be in the miombo woodlands of southern Africa. In contrast, soils formed from volcanic origins such as basalt are high in nutrients and are fine, clay types (eutrophic). These are more frequently found in East African *Acacia* savanna (Bell 1982, Frost 1985b, Naiman and Rogers 1997). However, superimposed on this pattern is an effect of large ungulates: high soil nutrients lead to high ungulate densities, rapid grazing/browsing offtake, and high fecal deposition. Nutrients in the feces are then returned rapidly to the soil to be used by forage plants. In essence, ungulates fertilize their own food, and thereby, create a positive feedback increasing their own density. These effects are observed in the medium rainfall range of 500-1000 mm per year (Botkin et al. 1981). In arid areas there is high soil nutrient but insufficient rain to promote recycling, whereas in very wet (forest) areas there is too much leaching and insufficient herb layer to support high densities of ungulates.

At a smaller scale within the Serengeti system, McNaughton et al. (1997) have found that concentrations of non-migratory ungulates occur at localities naturally high in sodium. These are similar to the ‘sodic’ sites found in Kruger National Park, South Africa, and at Yellowstone and prairie sites in North America (Tracy and McNaughton 1995). On the Serengeti sites the concentration of ungulates produces higher levels of soil nutrients and hence higher nitrogen mineralization rates. Such sites have been dubbed ‘hotspots’.

On the subarctic heathlands of Finland reindeer reduce lichen biomass, which allows a higher mineralization by soil microbes. Lichens are so efficient at removing nitrogen from rainwater that they reduce the amount reaching the soil (den Herder et al. 2003).

MAMMALS AND PLANT SPECIES COMPOSITION

Black-tailed prairie dogs (*Cynomys ludovicianus*) and pocket gophers (*Geomys bursarius*), rodents that live in large colonies on the prairies of North America, provide one of the classic examples of mammals that structure the landscape, alter the species composition of the vegetation, and so facilitate other herbivores (Huntly and Inouye 1988, Whicker and Detling 1988a,b). Miller et al. (1994) suggest that they act as 'keystone species' through their disproportionately large influence on vegetation composition. Studies at Wind Cave National Park show that prairie dogs graze grasses to a low level (a few cm) around their colonies. Constant grazing changes grass species composition to low growing forms and many dicot species survive due to reduced competition from grass. American plains bison preferentially graze these short grasses and pronghorn antelope (*Antilocapra americana*) feed on the dicots. Originally prairie dogs affected at least 20 % of the prairies (Coppock et al. 1983, Whicker and Detling 1988a,b). Exclusion of prairie dogs and bison returns the vegetation to long grass prairie (Cid et al. 1991).

Elk (*Cervus elephus*) maintain grass patches in the understory of old growth conifer forests of Olympic and Yellowstone National Parks, U.S.A. Exclusion of elk results in grass species being replaced by mosses, ferns, and shrubs (Schreiner et al. 1996, Augustine and McNaughton 1998).

Rabbits on the short grass chalk grasslands of Sussex, England (the South Downs), determine both their structure and plant composition. These effects were detected when marked vegetation changes took place after rabbits were removed through the epizootic myxomatosis in 1953 (Ross 1982). Short grasses and many dicots were replaced with tall tussock grasses, and there were subsequent changes in ants and lizards dependent on these plant forms.

On tundra and subarctic heathland, selective grazing by reindeer keeps the community in an early succession stage. They reduce the preferred and competitively dominant *Cladina* lichens, which allows other lichens, bryophytes, and dwarf shrubs to exist, but it also reduces regeneration of conifer seedlings (den Herder et al. 2003).

CONSTRAINTS ON THE ROLE OF MAMMALS AS ECOSYSTEM PROCESSORS

Fundamentally mammals restructure landscapes when they are food limited. Herbivore populations that are regulated by predators have only selective effects on vegetation, often in local (small-scale) predator-safe areas. What are the conditions, therefore, that determine when mammal herbivores are food limited? In essence there are 4 main conditions that affect the cause of regulation:

Body Size

Very large herbivores are simply too large for predators. Clearly elephants, rhinos, and hippos fall into this category despite a few newborn animals being killed occasionally. In addition, even animals the size of African buffalo and giraffe are large enough that predators have difficulty killing them. The consequence is that predation accounts for only 25 % of annual mortality in buffalo (Sinclair 1977, 1979). It appears that wood bison (*B. bison athabascae*) also falls in this category, since a population in the Mackenzie Bison Sanctuary of Canada continues to expand despite wolf predation of juveniles (Larter et al. 2000).

Migration

Predators cannot follow, on a year-round basis, animals that migrate. This general rule is evident in all mammal migration systems including those by caribou (*Rangifer tarandus*) in northern Canada, white-eared kob (*Kobus kob*), in Sudan, gazelles in Botswana, and wildebeest and gazelles in Serengeti (Sinclair 1983, Fryxell and Sinclair 1988). These species, therefore, escape from predator regulation. In addition, migration is an adaptation to access ephemeral, high-quality food resources not available to non-migrants. These two features of migration systems allow populations to become an order of magnitude greater in number compared to residents. Thus, migrant wildebeest in Serengeti occur at 50 animals/km^2 compared to a sympatric resident population at 5 animals/km^2. Such large populations have major structuring effects on the ecosystem.

Diversity of Herbivore and Carnivore Guilds

In some systems there is a high diversity of large mammal herbivores and carnivores. Nearly all are associated with tropical savanna and grassland. Whether a population of herbivores is limited by predators, and so has little structuring effect on vegetation, is determined by its place in the hierarchy of herbivores.

In African savanna there are as many as 10 co-existing canid or felid carnivores feeding on ungulates, lagomorphs, and rodents. They vary in size from the 200 kg lion (*Panthera leo*) to the 5 kg wild cat (*Felis sylvestris*). The larger the carnivore, the greater is its range of prey sizes (Fig. 4). Thus, the diet of lions ranges from buffalo (450 kg) to dik dik (*Madoqua kirkii*) (10 kg), a small antelope, whereas that of caracal (*Felis caracal*) ranges from duiker (15 kg) to 100 g rodents (Avenant and Nel 1997). The consequence of this is that in the Serengeti system, for example, smaller ungulates have as many as 7 predator species, intermediate sized antelope such as topi (*Damaliscus korrigum*) (120 kg) have 4 predators, and very large ones like eland (*Taurotragus oryx*) have only one. Thus, smaller ungulates must experience more predation and be predator regulated if they are not migrants, and so have less effect on vegetation. Direct measures of mortality by predators are consistent with this prediction. We have found that in small antelope such as oribi (*Ourebia ourebi*) (10 kg), nearly all mortality of adults is accounted for by predators; in zebra (*Equus burchelli*) (250 kg) this is about 73 %, while in buffalo it is 23 % (Sinclair 1977).

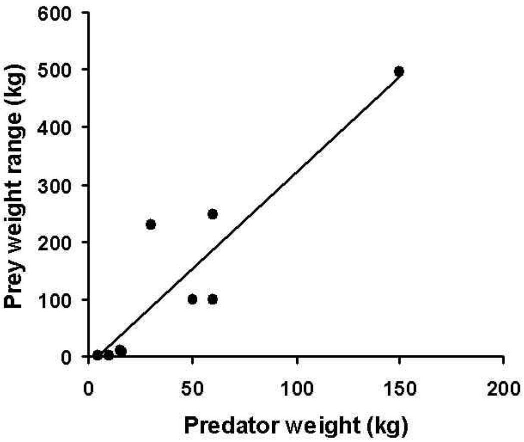

Fig. 4. The range of mammal prey sizes for Serengeti carnivores. The larger the carnivore the greater the prey range. Thus, small ungulates can have as many as 9 different predator species whereas larger prey have only one or none (Avenant and Nel 1997, personal observations).

Therefore, in a multi-species mammal community, large herbivores will structure the landscape whereas smaller ones cannot. The effect of large herbivores on vegetation structure is enhanced because they also feed in a broader range of habitats than do smaller species. Thus, elephants can range from tropical forests to deserts whereas the smallest ungulates are confined to single habitats.

The Direction of Regulation

In many biomes of the temperate and arctic regions there is only one major predator and one or a few species of mammalian prey. Landscape structure and composition in these areas are determined by whether there is top-down or bottom-up regulation. In some cases the direction of regulation is obligatory, in others, both top-down and bottom-up regulation can occur with the system switching from one state to another depending on disturbances from outside the system. Obviously, bottom-up regulation occurs when predators are absent. In this case browsing mammals must have an impact on the rate of regeneration of juvenile woody plants simply from feeding. However, such effects would not necessarily prevent the formation of the eventual mature climax. The issue is whether mammals can hold the vegetation in a different state. In some cases they do. In Europe, where predators have been removed, browsing by red deer (*C. elaphus*), wild boar (*Sus scrofa*), and chamois (*Rupicapra* spp.) changed forested areas into grasslands and held them there (Miller et al. 1982); these browsers maintain a different state.

Examples of obligatory top-down regulation are less prevalent. Wolves apparently regulate moose in parts of Canada (Messier 1994). When wolves were absent on Isle Royale, moose had major effects on vegetation structure. Even when wolves arrived on the island their numbers appeared to track moose numbers and did not regulate that population (Peterson and Vucetich 2001).

In other systems, either top-down or bottom-up regulation can occur with consequent differences in the landscape structure. For example, I have mentioned above the effect of elk in transforming aspen stands to open parklands in Banff National Park, Canada. This occurred when wolves were removed in the 1930s. In 1985 wolves reappeared and since then they have both reduced elk numbers and confined them to a subset of the habitats. In elk-free areas, young trees are regenerating and more dense aspen stands should appear in the next decades (White 2001). The recent increase of wolf numbers in Yellowstone should also change the aspen structure there. Thus, which of the two landscapes occur (woodland or parkland) is determined by the presence or absence of both mammalian herbivores and carnivores. (Note, either state is a normal or ‘natural’ configuration of indigenous species, neither should be regarded as aberrant in terms of conservation and management).

MEGAHERBIVORES AND PALEOHISTORY

Present-day elephants, rhinos, and other megaherbivores clearly play a major role in shaping the landscapes in which they live. We must remember that megaherbivores were far more abundant in the Pliocene and Pleistocene, even 20,000 years ago they were common, and they died out a mere 10,000 years ago on all continents except Africa (Owen-Smith 1988). Before this, even larger ancient mammals such as Brontotheres (30 M b.p.), Indricotheres and Chalicotheres (20 M b.p.), and Litopterns (10 M b.p.) must have imposed important evolutionary pressures on the vegetation.

Mammoths, mastodons, and woolly rhinos roamed the tundra of the Holarctic. On tundra only 13 % of annual production is currently consumed (C. J. Krebs, personal communication), the remainder in the Pleistocene most likely eaten by the mammoths. Mastodons fed on trees and shrubs in both the boreal and tropical rain forests of the New World while giant ground sloths and glyptodonts fed in Mexican deserts (Janzen 1986). Thus, the impacts of mammals in these biomes would have been more similar to those we currently see in African landscapes. As in Africa, the biomes of Eurasia and the Americas would have evolved adaptations to tolerate or mitigate the impacts of megaherbivores, adaptations that are probably still present. Janzen and Martin (1982) have suggested that many of the seedpods in Costa Rican forests are designed for ingestion and dispersal by mastodons, and Janzen (1986) proposes the fleshy fruits of *Opuntia* cactus are designed for extinct large mammals. The lack of such dispersal agents today suggests New World forests now have a different structure and species dispersion pattern from the one when large mammals were common. Similarly, the present-day boreal forests of North America and Asia, characterized by homogeneous stands with few tree species, were once a mosaic of mature conifers and regenerating deciduous patches, and with a more diverse fauna associated with the mosaic. Thus, the lack of large mammal impacts today could be an artifact of human induced extinctions in the recent past.

CONCLUSION

The main theme of this paper is that the role of mammals in ecosystems is to modify vegetation structure, alter pathways of nutrients, and thereby change species composition. The large-scale structuring effects make large mammals ‘ecological landscapers’ that influence both ecosystem function and biodiversity. Moose in boreal forests provide a classic example of such effects.

Landscaping effects occur when mammals are regulated by food, a bottom-up trophic process, rather than by predators. This condition occurs, or is constrained, by 4 factors: when (1) body size is large enough to avoid predators; (2) populations adopt large scale migration behaviour because predators are unable to follow them; (3) in multi-species communities with a range of predator and prey sizes (savanna, grassland), only the largest species can avoid predation because they simultaneously subsidize predators that regulate smaller prey species; and (4) in single predator-prey systems (tundra, desert, boreal, and temperate forests) ecological conditions determine whether or not predators regulate prey.

The landscaping role of mammals in maintaining species diversity is evident not just in vegetation, but also in birds, other mammals, and invertebrates. This role makes them prime candidates as ‘umbrella species’ for conservation. Protection of large mammal species and their habitats also conserves a large part of the remaining community. Such mammals become the ’indicator species’ for the health of the ecosystem. Thus, if the wildebeest population were to go into a prolonged decline, for example, the Serengeti ecosystem would disappear.

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REFERENCES

ALVERSON, W. S., and D. M. WALLER. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. Pages 280-297 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The Science of Overabundance. Smithsonian Institution Press, Washington, D.C., USA.

AUGUSTINE, D. J., and S. J. MCNAUGHTON. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62: 1165-1183.

AVENANT, N. L., and J. A. J. NEL. 1997. Prey use by syntopic carnivores in a strandveld ecosystem. South African Journal of Wildlife Research 27:86-93.

BELL, R. H. V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. Pages 359-404 *in* B. J. Huntley and B. H. Walker, editors. Ecology of Tropical Savannas. Ecological Studies 42. Springer-Verlag, Berlin, Germany.

BOTKIN, D. B., J. M. MELLILO, and L. S-Y. WU. 1981. How ecosystem processes are linked to large mammal population dynamics. Pages 373-387 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of Large Mammal Populations. John Wiley & Sons, New York, New York, USA.

CID, M. S., J. K DETLING, A. D.WHICKER, and M. A. BRIZUELA. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. Journal of Range Management 44:100-105.

COPPOCK, D. L., J. K. DETLING, J. E. ELLIS, and M. I. DYER. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of Black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

CORFIELD, T. F. 1973. Elephant mortality in Tsavo National Park, Kenya. East African Wildlife Journal 11:339-368.

DANELL, K., and R. BERGSTROM. 1989. Winter browsing by moose on two birch species: impact on food resources. Oikos 54:11-18.

_______, _______, and L. EDENIUS. 1994. Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. Journal of Mammalogy 75:833-844.

_______, K. HUSS-DANELL, and R. BERGSTROM. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology 66:1867-1878.

DEN HERDER, M., M-M. KYTOIITA, and P. NIEMALA. 2003. Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. Ecography 26: 3-12.

DUBLIN, H. T. 1986. Decline of the Mara woodlands: the role of fire and elephants. Ph.D. Thesis, University of British Columbia, Vancouver, British Columbia, Canada.

_______. 1995. Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire and other factors. Pages71-90 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. University of Chicago Press, Chicago, Illinois, USA.

_______, A. R. E. SINCLAIR, and J. MCGLADE. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. Journal of Animal Ecology 59:1147-1164.

ELLENBROOK, G. A., and M. J. A. WERGER. 1988. Grazing, canopy structure and production of floodplain grasslands at Kafue Flats, Zambia. Pages 331-337 *in* M. J. A.Werger, H. J. During, and J. T. A. Verhoeven, editors. Plant Form and Vegetation Structure. SPB Academic

Publishing, The Hague, Netherlands.

FRANK, D. A., and R. D. EVANS. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78:2238-2248.

FROST, P. G. H. 1985a. The responses of savanna organisms to fire. Pages 232-237 *in* J. C. Tothill and J. J. Mott, editors. Ecology and Management of the World's Savannas. Australian Academy of Science, Canberra, Australia.

_______. 1985b. Organic matter and nutrient dynamics in a broadleaved savanna. Pages 200-206 *in* J. C. Tothill and J. J. Mott, editors. Ecology and Management of the World's Savannas. Australian Academy of Science, Canberra, Australia.

FRYXELL, J. M., and A. R. E. SINCLAIR. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3:237-241.

HOBBS, T. N. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695-713.

HOUSTON, D. B. 1982. The Northern Yellowstone Elk. Macmillan, New York, New York, USA.

HUNTLY, N., and R. INOUYE. 1988. Pocket gophers in ecosystems: patterns and mechanisms. Bioscience 38:786-793.

HURLBERT, S. H. 1997. Functional importance vs keystoneness: reformulating some questions in theoretical biocenology. Journal of Ecology 22:369-382.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501-528.

_______. 1971. Escape of *Cassia grandis* L. beans from predators in time and space. Ecology 52:964-979.

_______. 1986. Chihuahuan desert Nopaleras: defaunated big mammal vegetation. Annual Reviews of Ecology and Systematics 17:595-636.

_______, and P. S. MARTIN. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. Science 215:19-27.

JEFFERIES, R. L., D. R. KLEIN, and G. R. SHAVER. 1994. Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71:193-206.

JONES, C. G., J. H. LAWTON, and M. SHACHAK. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

_______, _______, and _______. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946-1957.

KREBS, C. J., S. BOUTIN, and R. BOONSTRA, editors. 2001. Ecosystem Dynamics of the Boreal Forest. Oxford University Press, Oxford, England.

LANDRES, P. B., J. VERNER, and J. W. THOMAS. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2:316-328.

LARTER, N. C., A. R. E. SINCLAIR, T. ELLSWORTH, J. NISHI, and C. C. GATES. 2000. Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. Animal Conservation 3:299-309.

MCINNES, P., R. J. NAIMAN, J. PASTOR, and Y. COHEN. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059-2075.

MCNAUGHTON, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevoloution. American Naturalist 124:863-886.

_______, F. F. BANYKWA, and M. M. MCNAUGHTON. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798-1800.

_______, and G. A. SABUNI. 1988. Large African mammals as regulators of vegetation structure. Pages 339-354 *in* M.

J. A.Werger, P. J. M. van der Aart, H. J. During, and J. T. A. Verhoeven, editors. Plant Form and Vegetation Structure. SPB Academic Publishing, The Hague, Netherlands.

McShea, W. J., and J. H. Rappole. 1997. Herbivores and the ecology of forest understory birds. Pages 298-309 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The Science of Overabundance. Smithsonian Institution Press, Washington, D.C., USA.

______, H. B. Underwood, and J. H. Rappole, editors. 1997. The Science of Overabundance. Smithsonian Institution Press, Washington, D.C., USA.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75: 478-488.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8:677-681.

Miller, G. R., J. W. Kinnaird, and P. Cummins. 1982. Liability of saplings to browsing on a red deer range in the Scottish highlands. Journal of Applied Ecology 19:941-951.

Naiman, R. J., and K. H. Rogers. 1997. Large animals and system-level characteristics in river corridors: implications for river management. Bioscience 47:521-529.

Noble, J. C. 1999. Fossil features of mulga *Acacia aneura* landscapes: possible imprinting by extinct Pleistocene fauna. Australian Zoology 31:396-402.

______, J. Gillen, G. Jacobson, W. A. Low, C. Miller, and the Mutitjulu Community. 2001. The potential for degradation of landscape function and cultural values following the extinction of mitika (*Bettongia lesueur*) in Central Australia. Pages 71-89 *in* A. J. Conacher, editor. Land Degredation. Kluwer Academic Publishing, Netherlands.

Norton-Griifiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Pages 310-352 *in* A. R. E. Sinclair and M. Norton-Griffiths, editors. Serengeti. Dynamics of an Ecosystem. University of Chicago Press, Chicago, Illinois, USA.

Owen-Smith, N. 1988. Megaherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge, UK.

Paine, R. T. 2000. Phycology for the mammalogist: marine rocky shores and mammal-dominated communities - how different are the structuring processes? Journal of Mammalogy 81:637-648.

Parker, I. S. C. 1983. The Tsavo story: an ecological case history. Pages 37-49 *in* R. N. Owen-Smith, editor. Management of Large Mammals in African Conservation Areas. Haum, Pretoria, South Africa.

Pastor, J., and K. Danell. 2003. Moose-vegetation-soil interactions: a dynamic system. Alces 39:177-192.

______, B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74:467-480.

______, and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:690-705.

______, ______, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. Bioscience 38:70-77.

Patterson, J. H. 1907. The Maneaters of Tsavo. Macmillan, London, UK.

Pellew, R. A. P. 1981. The giraffe (*Giraffa cemlopardalis tippelskirchi* Matschie) and its *Acacia* food resource in the Serengeti National Park. Ph.D. Thesis, University of London, UK.

______. 1983. The impacts of elephant, giraffe, and fire upon the *Acacia tortilis* woodlands of the Serengeti. African Journal of Ecology 21:41-74.

Peterson, R. O., and J. A. Vucetich. 2001. Ecological studies of wolves on Isle Royale. Annual Report 2000-2001. Michigan Technological University, Houghton, Michigan, USA.

Risenhoover, K. L., and S. A. Maass. 1987. The influence of moose on the composition and structure of Isle Royale forests. Canadian Journal of Forest Research 17:357-364.

Ross, J. 1982. Myxomatosis: the natural evolution of the disease. Pages 77-95 *in* M. A. Edwards and U. McDonnell, editors. Animal Disease in Relation to Animal Conservation. Academic Press, London, UK.

Sala, O. E. 1988. The effect of herbivory on vegetation structure. Pages 317-330 *in* M. J. A.Werger, P. J. M. van der Aart, H. J. During, and J. T. A. Verhoeven, editors. Plant Form and Vegetation Structure. SPB Academic Publishing, The Hague, Netherlands.

______, W. K. Lauenroth, S. J. McNaughton, G. Rusch, and X. Zhang. 1996. Biodiversity and ecosystem functioning in grasslands. Pages 130-149 *in* H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulz, editors. Functional Roles of Biodiversity: A Global Perspective. John Wiley and Sons, New York, New York, USA.

Schmitz O. J., and A. R. E. Sinclair. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201-223 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The Science of Overabundance. Smithsonian Institution Press, Washington, D.C., USA.

Schreiner, E. G., K. A. Krueger, P. J. Happe, and D. B. Houston. 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Canadian Journal of Forest Research 26:255-265.

Short, J., J. E. Kinnear, and A. Robley. 2000. Surplus killing by introduced predators in Australia – evidence for ineffective anti-predator adaptations in native prey species? Biological Conservation 103:283-301.

Sinclair, A. R. E. 1977. The African buffalo. A Study of Resource Limitation of Populations. University of Chicago Press, Chicago, Illinois, USA.

______. 1979. The eruption of the ruminants. Pages 82-103 *in* A. R. E. Sinclair and M. Norton-Griffiths, editors. Serengeti. Dynamics of an Ecosystem. University of Chicago Press, Chicago, Illinois, USA.

______. 1983. The function of distance movements in vertebrates. Pages 240-258 *in* I. R. Swingland and P. J. Greenwood, editors. The Ecology of Animal Movement. Oxford University Press, Oxford, UK.

______. 1995. Equilibria in plant-herbivore interactions. Pages 91-113 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. University of Chicago Press, Chicago, Illinois, USA.

______, and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society of London, Series B 357:1221-1231.

Tracy, B. E., and S. J. McNaughton. 1995. Elemental analysis of mineral lick soils from the Serengeti National Park, the Konza Prairie and Yellowstone National Park. Ecography 18:91-94.

Vesey-Fitzgerald, D. F. 1960. Grazing succession among East African game animals. Journal of Mammalogy 41:161-172.

WALKER, B. 1985. Structure and function of savannas: an overview. Pages 83-91 *in* J. C. Tothill and J. J. Mott, editors. Ecology and Management of the World's Savannas. Australian Academy of Science, Canberra, Australia.

WHICKER, A. D., and J. K. DETLING. 1988a. Modification of vegetation structure and ecosystem processes by North American grassland mammals. Pages 301-316 *in* M. J. A. Werger, H. J. During, and J. T. A. Verhoeven, editors. Plant Form and Vegetation Structure. SPB Academic Publishing, The Hague, Netherlands.

______, and ______. 1988b. Ecological consequences of prairie dog disturbances. Bioscience 38:778-793.

WHITE, C. A. 2001. Aspen, elk, and fire in the Canadian Rocky Mountains. Ph.D. Thesis. University of British Columbia, Vancouver, British Columbia, Canada.