Fire and Mammals

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IN THE definition of ecological factors important to mammals fire usually has not been ranked with temperature, moisture, or light, or even with soil, shelter, or seasonality. However, fire and fire perpetuated environments, such as grasslands, have been of the utmost importance in the evolution of mammals, and directly or indirectly are a significant force in the lives of a large segment of today's mammals.

The first mammals very likely were insect eaters, but early in the history of mammals pastoral forms (specialized for feeding on vegetation) began to develop. First there were browsers; later grazers. The coniferous forests that dominated the scene at the dawn of the era of mammals gave way to evolving broad-leaved deciduous hardwood forests while the major mammalian groups radiated in the early Cenozoic. The early browsing mammals were contemporaneous with the broad-leaved hardwoods. It was not until the middle of the Cenozoic, in late Oligocene or early Miocene, that grazing mammals began to flourish. Apparently grasses became an important floral element at about the same time. It appears that the evolution of grasses and grasslands and the evolution of grazing mammals were intimately related.

Komarek (1965 : 195–196) has pointed out that: "Natural grasslands consist of a great variety of grasses and forbs so that the prairies, plains, or steppes are not uniform in their ability to carry fire under the same conditions. Then, too, many of the animals that live in the grasslands create conditions by their own activities that either change the vegetations or cause the effect of fire to be different. Grazing animals . . . played their part in making the grasslands and subsequent fires as variable as they are." No doubt, the natural fires that favored the evolution of grasslands also had a role in the evolution of grazing mammals and their predators.

Because they were more likely to be preserved than forest mammals, those species that lived in the grasslands are better known as fossils than their forest kin. Indeed, the fossil record is remarkably complete for some grazing mammals, showing not only their origin but also many of the steps in their differentiation and evolution. Fossil grazing mammals thus have an important place in the study of paleoecology and in our knowledge of ancient grasslands, for seldom is there much direct evidence of this habitat, in the form of fossil vegetation, seeds, or pollen. The peculiar adaptations of the grazing mammals, together with the details of their distribution and abundance provide data for mapping the distribution in time and space of the grasslands of the past.

Today, grassland mammals are most abundant and varied in the temperate portions of each continent and in tropical Africa and Asia. There is a vast array of contemporary rabbits, hares, ground squirrels, pocket mice, kangaroo rats, pocket gophers, and cricetid mice and rats in the more arid parts of North America and cricetid voles in the more mesic parts. Coyotes, foxes, badgers and weasels are the associated carnivores. The present dominance of small pastoral forms, a result, in part, of the destructive nature of man, is peculiar in the faunal history of North America. Until less than a million years ago the North American grassland fauna resembled or even exceeded the present fauna of tropical Africa in abundance and variety of large forms. Besides kinds that have no modern counterpart it included horses, camels, rhinoceroses, tapirs, elephants, peccaries, antilocaprids, ground sloths, wolves, and great cats. Before that there were more primitive, but equally impressive plains-dwelling faunas in North America.

Temperate Asia, before the onslaught of man, had a fauna of large grazing mammals including horses, asses, camels, yak, antelopes, gazelles, and sheep. Now, as in North America, smaller wild species and domesticated ungulates are dominant. Europe had its bison and aurochs, but otherwise, for lack of extensive natural grasslands, has not had much of a grassland fauna in Recent times. Australia, with its pastoral kangaroos, wallabies, wombats, and placental rodents had an abundant grassland fauna before the introduction of rabbits and sheep. The Recent (post-Pleistocene) grassland fauna of tropical Africa, on the other hand, is quite different. It resembles in variety and abundance the earlier faunas of North Temperate lands that flourished millions of years ago. Almost the same can be said of tropical Southeast Asia, with its wild cattle, rhinoceroses, elephant, deer, antelopes and gazelles.

Grass habitats are found in most parts of the world. They include deserts, tundras, punas, steppes, savannas, prairies, scrublands, and conifer forests. Even within broad-leaved forests there are grass habitats—in bogs, meadows, streambanks, tree falls, and rock outcrops—often extensive enough to support pastoral mammals. The canopy of the forest itself serves as a habitat for some pastoral species such as the sloths, porcupines, and some of the spiny rats.

Most pastoral species are terrestrial, but some are good climbers, and some have become semiarboreal or even truly arboreal (tree mice, *Phenacomys*, and bamboo rats, *Dactylomys*). The amphibious hippopotamus grazes both in the water and on land, and the moose, usually a browser, frequently becomes an aquatic grazer in summer. The sirenians (dugong and manatees) are entirely aquatic and crop submerged vegetation.

Pastoral mammals feed mainly on grasses, herbs, and the leaves of trees and shrubs, but some include bark, lichens, and various kinds of animal matter in their diets. Over half of the species of living mammals are herbivorous in one sense or another, and a great many of these feed on grass. If most natural grasslands, particularly those in the temperate zones, originally developed with fire and are at least in part perpetuated by it, then a large proportion of the mammals of the world must be at least indirectly adapted to fire.

How can an adaptation to fire be recognized? The behavioral adaptation is obvious enough among kites and eagles coursing over the fire front on an African prairie, capturing insects, birds, lizards, and rodents flushed by the advancing fire. The Kirtland's warbler, nesting only in early stages of succession in jack pine forest is certainly adapted to fire. However, in most instances it is difficult, if not impossible, to determine whether a mammal is adapted to fire or to some aspect of its environment which is adapted to or perpetuated by fire. Burrowing, for example, protects a grassland mammal from a periodic fire, but maybe no more than once or twice, if ever, in its lifetime (the average burrowing rodent has a life expectancy of less than a year). The same burrow, on the other hand, protects it every day of its life against predators, and protects it every day of its life from the vagaries of climate—maintaining a more uniform temperature, higher relative humidity, and lower evaporation rate than it would encounter at the surface of the ground. Is the burrowing habit an adaptation to fire or to other environmental factors?

Most ecological texts index fire in relation to animals only as a potentially lethal hazard. Thus, Allee, Emerson, Park, Park, and Schmidt in *Principles of Animal Ecology* (1949: 210), one of the bibles of ecology, state: "Fire is an environmental factor to which forest and grassland animals have been exposed spasmodically from time immemorial. The *fire hazard* depends on the combination of a number of variables . . . (italics mine). Fire can be and often is a disaster for mammals dwelling in forests or other places where fires are infrequent. On the other hand, mammals living where fire is a regular and frequently occurring feature of the environment, as in grasslands, survive fires because of their adaptations to them.

Certainly mammals adapted to fire "live dangerously," but the fire hazard is minimized by their adaptations. Some are mobile and run from fire. Others retreat into deep burrows or shallow "pop-holes" when fire approaches. In Africa the large burrows of the aardvark provide refuge for a remarkable variety of mammals, even including duikers, warthogs, porcupines, ratels, and small cats. Probably a rodent could survive a grass fire with no more than a singe simply by hugging the ground while the fire passed over. A larger mammal might lie in a depression. The more mobile terrestrial mammals of open country have precocial young that can move soon after birth and mature rapidly. Those with initially helpless and slow-maturing altricial young usually shelter them in nests in burrows, in depressions, or on the surface of the ground. Arboreal savanna inhabitants construct their nests in trees well above the normal danger zone of grass fires.

Natural fires in grasslands usually are remarkably cool near the ground and normally do not progress rapidly on a continuous front. Most often they burn irregularly, with fits and spurts, depending upon variations in wind, moisture, burnable litter, spacing of vegetation, etc., leaving unburned islands and various degrees of burn in a mosaic pattern. This has the effect of allowing mammals to move clear of the fire and of leaving shelter and "old" food areas near fire renewed areas.

Hot fires or fire storms are of course a different matter. Fires of this nature might overtake runners, suffocate or incinerate burrowers, burn up tree holes, and induce starvation. But this would likely be a local phenomenon and would not wipe out whole habitats or whole populations. Catastrophies of this nature are not limited to fire, but include wind storms, floods, drought, ice and snow storms, etc.

Actually, of course, the relationship of mammals to fire extends far beyond the mere hazard. Many species depend on frequent fires for their very existence. At least ecological, morphological, behavioral, and psychological adaptations can be cataloged. Here I have reference only to wild mammals, which have a passive relationship to fire. The manipulation of fire by man for the benefit of himself and his domestic animals already has received the attention of many authors, particularly in the pages of the Proceedings of the Tall Timbers Fire Ecology Conferences. For most wild grassland mammals the primary factors related to fire are those concerned with habitat, food and feeding, and shelter and protection.

The grassland provides food and minerals, periodically renewed by fire. Komarek (1965 : 186) has pointed out that, "When grasslands are burned, the animals eating the tender herbage that sprout shortly thereafter will, of necessity, not only eat a considerable amount of ash, but sand and other debris as well. But even more important is the fact that in the grazing of this tender herbage, the basal stems of the plants that have either been burned off or at least subjected to heat, are mixed with this herbage. These stems have an exceedingly heavy concentration of silica . . ."

Coarse, abrasive forage led inevitably to evolution of specialized teeth, specialized digestive systems, and specialized feeding habits in the grazing mammals. The cheek teeth (molars and premolars) typically became higher, plane surfaced, often ever-growing, and an often intricate system of hard enamel ridges or crests developed on their crowns (see Hershkovitz, 1962 : 86, for an enumeration and illustration of molar specializations).

Such responses to tough, abrasive food evolved independently in many groups of mammals—marsupials, edentates, lagomorphs, rodents, hyraxes, proboscideans, sirenians, perissodactyls, and artiodactyls. Whereas the larger bodied of these could effectively crop tough vegetation and thus did not need specialized incisors, the smaller lagomorphs and rodents cut rather than cropped. They evolved sharp, chisel-like evergrowing incisors.

To accomplish the difficult task of cellulose digestion, thorough grinding and mastication of the plant material was not enough. Various modifications of the digestive tract evolved: a multiple chambered stomach, permitting an unusual amount of enzyme action and regurgitation of the food for additional mastication (in the ruminants); elongation of the intestine (in rodents); and development of an unusually extensive bacterial flora in the intestines (horses). The lagomorphs reached the same end by way of reingestion—repetition of the entire digestive cycle by eating the feces after the first passage of food through the alimentary canal.

Seasonal fluctuations in the availability of food in the grasslands—fluctuations often closely related to burning—have evoked numerous behavioral adaptations. The pika and many rodents collect, dry, and store vegetation during the season of abundance. An extreme of hay-storage behavior is exhibited by *Microtus* (*Phaiomys*) *brandti*, a vole that inhabits the cold Mongolian steppes. "In August the vole families begin to widen and clean underground chambers of their burrows for storage space and begin to gather winter food reserves. This activity is intense and methodical. Foods stored include stems, leaves and whole plants pulled up by the roots. Before cold weather sets in, the chambers of the burrows contain up to 30 kg. of food collected usually by 10–12 voles. . . . These animals spend the winter in their burrows feeding only on stored food. Holes are plugged with earth, and the mice do not appear on the surface for over 4 months." (Formozov, 1966 : 214–215).

Many species avoid the season of food scarcity by hibernating (winter) or aestivating (summer). They greatly increase their fat reserves by heavy eating. When sufficiently obese they become torpid through drastic reduction of metabolism. The animal then survives up to 7–9 months of fasting by slowly oxidizing its fat reserves. Hibernation and aestivation are particularly frequent in grasslands mammals whose habitat provides less shelter and greater temperature extremes than are encountered in most other habitats.

Grassland ungulates are noted for traveling great distances in search of food. Before the intervention of man some species migrated en masse—by the millions in the case of the American bison and the South African springbok. Migrations of wildebeests and some other bovids on the plains of East Africa are much better documented. Their migrations follow a regular pattern related to rainfall and fire. Irregular wandering from burn to burn is characteristic of some species such as the steinbok and gemsbok of southern Africa.

Physiological adjustment of reproductive rhythms and fecundity in response to variation in the condition and abundance of food is particularly marked in grassland mammals. Often these responses are linked with patterns of movement—migration or wandering.

It is possible for grasslands to be shared by many species, often with vast numbers of individuals, by avoidance of competition for food. Some species are nocturnal feeders, others diurnal. Some specialize in eating only particular species or groups of plants. Some eat only certain growth stages of particular plants. The most adaptable are those that accept a wide variety of vegetation as food. They may adjust their diets according to availability of various plants—thus making it possible for them to survive an extensive burn for example. The fossorial species—the tunnelers—avoid competition by consuming the underground parts of plants.

Similarly, variation in hunting techniques and in the species hunted, reduces competition among the carnivore fauna that preys upon the herbivores. The pressure of predation is often great. This is particularly true after burns when much of the concealing vegetation has been temporarily destroyed. Adaptive responses may take the form of morphological or behavioral specializations. Limbs and bodies have been modified in several ways to achieve speed and the fleetest of mammals, the pronghorn, gazelles, and cheetah are grassland inhabitants. In some groups (as the horses and hares) the face has become elongated and the eyes have reached a position high up on the head. These modifications permit the animal to scan its surroundings even while cropping or cutting vegetation. Modification for erratic leaping (impala, kangaroo rat, kangaroo) provides another means of escape from predators.

Concealing coloration may make an animal more difficult to detect in the absence of cover. The pelage of many grassland species (as the cotton rat, *Sigmodon hispidus*) is coarse or shaggy and more or less streaked or spotted. In others coloration closely matches that of the substrate after it has been burned over. The young of many species, in addition to being precocial, are even better camouflaged than their parents. Countershading (underparts paler than the upper) is well developed in many species—in hares for example. Disruptive coloration helps conceal animals such as gemsbok and zebra.

Related to cryptic coloration are short legs and the habits of scurrying and sprawling, highly developed in some open country mammals. Formozov (1966 : 211) says: "The ability of *Lagurus lagurus*, *Citellus pygmaeus* and others to sprawl flat, completely blending into the substrate, is remarkable. Airplane observations have shown me that diurnal mammals which are cryptically colored are betrayed by their shadow if they stand erect or move without flattening out. The sprawling reaction changes the outlines of the bodies, helps to shrink the shadow to a minimum and produces a maximum effect of cryptic coloration."

Among the smaller plains mammals most are rather heavily built and short legged (*e.g.*, prairie dog) and thus are not fast runners. They must spot danger quickly. They stand on their hind legs to survey their surroundings better—they "stand tall. . . ." Often they gain added height by standing on the mound of earth surrounding the mouth of their burrows (this also serves as a dike to prevent flooding of burrows when it rains). Colonialism is widespread among open country mammals. One of its functions is defensive. Lookouts warn the whole community of approaching danger with visual or acoustic signals (white sides of jackrabbit, white rump of pronghorn, chirps and whistles of prairie dog, pika, and marmots).

The vegetative cover of many grasslands does not provide shelter for mammals from wind, cold, heat, fire, or enemies. Up to 75 percent of the terrestrial species in temperate zone grasslands use burrows as their main or sole place of refuge. Some species characteristically plug their burrows when they are inside, providing greater climatic stability and better protection from predators. Others leave their burrows permanently open.

Many of the rodents cut vegetation and carry it to the safety of their burrows for eating. Ruminants graze quickly, scarcely masticating the vegetation cropped, then retire to a safer spot to "chew the cud"—regurgitate and masticate.

Other relationships between mammals and fire and other adaptations of mammals to life in fire perpetuated environments could be cited. However, those cataloged here should be sufficient to show that fire should indeed be regarded as an important factor in mammalian ecology.

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