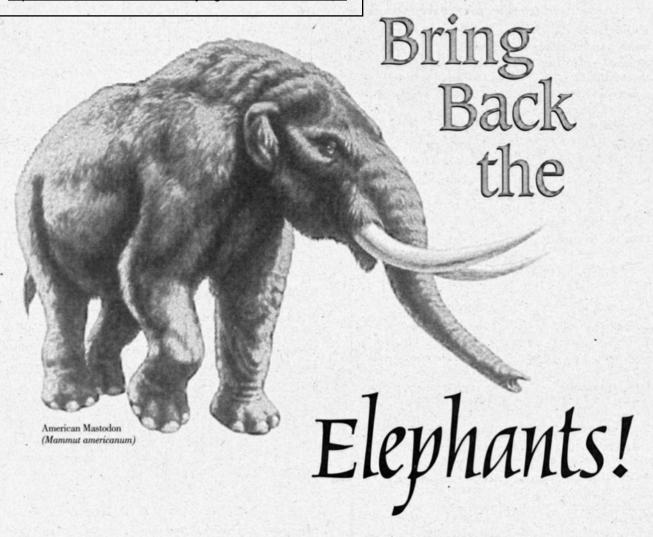
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EXTINCTION of large continental vertebrates at the end of the Pleistocene (late Quaternary) has long been apparent to paleontologists (Martin and Wright 1967). Recently the consequences of this phenomenon have attracted the attention of conservationists and visionaries. "This land is the mastodon's land; while *Home on the Range* commemorates buffalo, deer, and pronghorn it misses the mammoths, glyptodonts, and camels. There was a wild America considerably wilder than any brought to us on TV. Our late Pleistocene legacy means we can imagine more, not fewer, kinds of large animals on public lands" (Martin 1992).

A decade ago, Michael Soulé predicted that "the reintroduction of these large animals will be controversial, but I would not be surprised to read someday that cheetahs are helping to control deer and that mesquite is being 'overbrowsed' by rhinoceroses." Soulé's presidential address at the third annual meeting of the Society for Conservation Biology was intended to prod conservationists to peer into the future of their discipline, and to acknowledge that such taxa as lions, camels, elephants, horses, and spectacled bears once native to North America disappeared relatively recently (Soulé 1990, Owen-Smith 1989).

by Paul S. Martin and David A. Burney

Table 1. Extinct and living species of large (>45 kg) land mammals of the late Quaternary inhabiting the western United States and northern Mexico, arranged by order and family (after Martin and Szuter 1999). An asterisk (*) indicates extinct species, including five species of the Order Proboscidea (elephants and their allies). The more common species have terminal radiocarbon dates of around 13,000 calendar years ago (Stuart 1991).

EDENTATA

Glyptotherium floridanum* glyptodont

Glossotherium harlani* big-tongued ground sloth

Megalonyx jeffersonii* Jefferson's ground sloth

Nothrotheriops shastensis* Shasta ground sloth

CARNIVORA

Canis dirus*

Canis lupus gray wolf

Ursus americanus black bear

Ursus arctos brown (grizzly) bear

Arctodus simus* giant short-faced bear

Smilodon fatalis*

Panthera leo atrox* American lion

Panthera onca jaguar

Miracinonyx trumani* American cheetah

Felis concolor mountain lion

PROBOSCIDEA

Mammut americanum* American mastodon

Mammuthus columbi* Columbian mammoth

Mammuthus exilis* dwarf mammoth

Mammuthus jeffersonii* Jefferson's mammoth

Mammuthus primigenius* woolly mammoth

PERISSODACTYLA

Equus conversidens' Mexican horse

Equus occidentalis* western horse

Equus sp.* other extinct horses or asses

Tapirus californicus* extinct tapir

ARTIODACTYLA

Camelops hesternus* western camel

Hemiauchenia macrocephala* long-legged llama

Mylohyus nasutus* long-nosed peccary

Platygonus compressus* flat-headed peccary

Odocoileus hemionus mule deer

Odocoileus virginianus white-tailed deer

Navahoceros fricki* mountain deer

Rangifer tarandus woodland caribou

Alces alces moose, moose deer

Cervus elaphus wapiti, elk

Antilocapra americana pronghorn

Oreamnos harringtoni* extinct mountain goat

Oreamnos americanus mountain goat

Ovis canadensis

Euceratherium collinum* shrub ox

Bootherium bombifrons* bonnet-headed musk ox

Bison spp.*
extinct taxa of bison

Bison bison bison

The Ultimate in Rewilding

In the fall 1998 issue of Wild Earth, Michael Soulé and Reed Noss proposed rewilding as the foundation of a continental conservation strategy. Central to this proposition is the recovery of existing top predators such as grizzlies, cougars, and wolves to large parts of their native ranges. Here we consider the ultimate in rewilding. While the diversity of America's charismatic megafauna was severely impoverished in the late Pleistocene (for western North America extinctions see Table 1), we can turn to Africa and India for surrogates for restoration. We suggest that the project begin by restarting the evolution of the most influential of the missing species, the extinct animals most likely to have exerted the greatest influence on their natural environment. Based on what is known of living megaherbivores in Africa and Asia, and based on the fossil record of the New World, there is one clear choice, animals as potent as fire in their dynamic influence on ecosystems. If we want the "superkeystone species" (Shoshani and Tassy 1996), second only to our own in their capability for altering habitats and faunas (Buss 1990, Sukumar 1994), we should start with the restoration of living proboscideans-with African and Asian elephants.

We fully expect that the initial reaction to the proposal of free-ranging elephants in the Americas will shock and confound many conservationists and naturalists. What could be more foreign in the New World than free-ranging elephants? Isn't this a heretical idea for those of us inclined toward deep reverence for the wild?

It all turns on what one regards as wild. For example, the gomphotheres, a family of Neotropical elephants that prospered in the Americas for well over ten million years (Shoshani and Tassy 1996), vanished at the end of the Pleistocene around 13,000 years ago, along with mammoths and mastodons. All deserve consideration as a natural part of Wild America. With such a rich fossil record and such a late American extinction, it is natural to consider restarting New World evolution of the Proboscidea with whatever taxa of elephants are left.

We are keenly aware that living African (Loxodonta africana) and Asian (Elephas maximus) elephants are not conspecific with fossil Mammuthus (mammoths) or other native Proboscidea of the New World. But all are in the same family and some taxonomists have considered Elephas and Mammuthus to be quite close, even congeneric; thus, an Asian elephant living today in Thailand is more closely related to the extinct mammoths of North America than to its African cousin. African and Asian elephants are the only members of the Order Proboscidea that were not lost in the megafaunal crisis of the late Pleistocene. Thanks to a surging human population and to

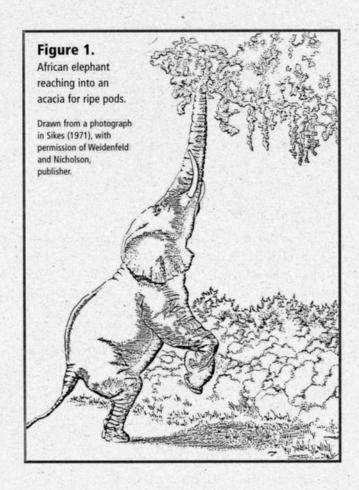
poaching for ivory, elephant numbers have crashed in this century and they are now at risk in many parts of their historic range. Recent estimates of numbers of African elephants are 550,000 to 650,000 (Douglas-Hamilton and Michelmore 1996). Numbers of surviving wild Asian Elephas are less by an order of magnitude, estimated between 37,500 and 54,600 animals (Sukumar and Santiapillai 1996).

Unlike explosively reproducing aliens of the New World such as kudzu, Africanized bees, or zebra mussels, animals reproducing as slowly as elephants, with an intrinsic rate of increase of about five percent per year, should be controllable. To avoid unacceptable methods of regulation (for 20 years park rangers shot 300 to 800 elephants annually in the Kruger National Park, Republic of South Africa) Jay Kirkpatrick of ZooMontana and his collaborators (ms.) have perfected a technique for limiting elephant populations by darting females with a long-lasting birth-control compound. Elephant forays beyond the perimeter of a reserve can be deterred, as in Amboseli National Park in Kenya, by an electrified wire. For a New World elephant park suitable for wide-ranging family units, we suggest a part of the lower Colorado River or the Rio Grande. Like most of North America, both regions were once ranged by mammoths. Both river systems are heavily invaded by alien Tamarix, riparian trees widely regarded as undesirable and a potential target for removal by elephants. The river banks support alien Bermuda grass (Cynodon dactylon), an African species eaten by elephants (Moss 1988). Other potential sites for elephant introductions would be anthropogenic savannas in Central or South Americaonce home to gomphotheres—now pasturing livestock.

Raising the Columbian Curtain

In planning New World restorations, conservationists have endowed the large mammals of historic time with the exclusive status of hallmarks, or flagships, overlooking the missing large mammals of the late Pleistocene. The animals that the first explorers and settlers saw and wrote about became incorporated in ideas of what constituted American wildness. The viewpoint imposed by a "Columbian Curtain" is unrealistic in evolutionary time. The historic fauna lacks the largest and most representative animals of the continent. Among the more common fossils of the late Pleistocene, which was dominated by equids, camelids, bovids, and especially bones, teeth, or tooth plates of proboscideans, only bison is represented (Graham and Lundelius 1994).

The opportunity is at hand to explore the evolutionary view. During the Cold War the US Fish and Wildlife Service took the first step in intercontinental restoration by shipping American musk oxen to Siberia to reestablish breeding herds in the north-



ern part of a continent where musk oxen lived until around three thousand years ago. Recently Sergi Zimov has started a Pleistocene Park in Siberia and plans to add woodland bison from Athabaska, Canada, to his mix of Siberian ponies and musk oxen. Zimov expects that under heavy use, unpalatable plants such as mosses and ericads will be torn up, trampled, and manured, to be replaced by more productive steppe tundra of subarctic grasses, a community that vanished with the extinction of mammoths (Stone 1998). His experiment merits watching. However, Asia and Africa have much more to offer the New World than vice versa.

As a result of the late Pleistocene extinctions we live in a continent of ghosts, their prehistoric presence hinted at by sweettasting bean pods of mesquite (Prosopis), honey locusts (Gleditsia), and monkey ear (Enterolobium). Such fruits are the bait evolved to attract native large animals that served as seed dispersers (Janzen and Martin 1982; Fig. 1). Foraging behavior of introduced livestock can help us understand how thorns, repellent oils, terpenes, tannins, and other secondary compounds might have protected plants from being overeaten by extinct megaherbivores.

When megafaunal extinction struck North America in the late Pleistocene, at least seven species of proboscideans-and the entire Order Proboscidea-vanished. Unlike erratic background extinctions that sputter along randomly through the eons, often in step with evolutionary replacements, the late Pleistocene extinctions were catastrophic and there were no replacements. Given their evident success over the last 15 million years and the late hour of their New World extinction, a mere 13,000 years ago or so, we suggest that bringing back the Proboscidea is by no means as witless as it might seem at first. It is not the same as introducing goats or pigs onto an oceanic island whose native plants lost long ago whatever defenses they once had to protect themselves against onslaught by the tongues and teeth of large herbivores.

In evolutionary time the flood plains, grasslands, and savannas of North America harbored a stunning variety of large animals—some 41 species in western North America alone, over three times as many as were present historically when Lewis and Clark detected bison, elk, pronghorn, brown (grizzly) bears, and ten others listed in Table 1. The losses included native mammals in size classes to match the largest found in Africa and Asia (Stuart 1991). Since totally unrelated groups of organisms, including marine invertebrates, did not vanish, as at the end of the Cretaceous 65 million years ago, the end of the Pleistocene was not a time of mass extinction. Instead, what happened in America was an extinction of the massive (plus their parasites and commensals, see Schmidt et al. 1992).

With time the distinction may vanish. Recently the blighting of coral reefs and the destruction of tropical forest biota, for example, suggests that the late Pleistocene extinctions are no more than the overture to a full-blown mass extinction underway right now, potentially capable of overtaking the Cretaceous in magnitude of loss, and, unlike the mass extinction at the end of the Cretaceous, undeniably of our own making.

Jefferson and Living Behemoths

Two and a half centuries ago the fossils of the late Pleistocene fascinated Ben Franklin, the Quaker naturalist John Bartram, and Thomas Jefferson. Jefferson philosophized against the idea of extinction and thought the fossil bones of mastodons and ground sloths meant that behemoths were still alive. According to Jefferson, the Indians knew of them. Big bones of proboscideans had been found in Big Bone Lick in Kentucky. In the early 1800s the public flocked to see the first skeleton of a mastodon exhibited in the new nation's first museum of natural science and art, located in Philadelphia. Charles Wilson Peale, owner of the museum, purchased the rights and excavated a mastodon in Orange County, New York. Adding the mastodon to his other natural history displays, Peale charged 25 cents at the front door and an additional 50 cents to enter the special room

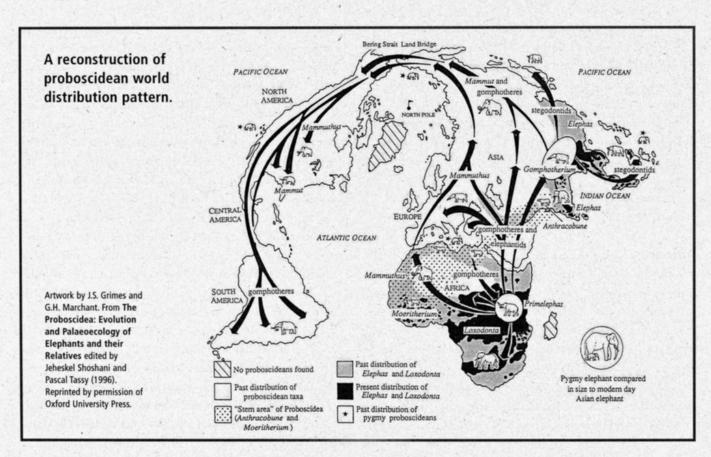
with the mastodon skeleton (Sellers 1980). Some of the public excitement reflected a lingering debate about whether the animals were actually extinct.

While the Indians as well as European explorers encountered the fossil bones or teeth of large extinct animals, no solid evidence emerged of living American proboscidea. What we know of the American mastodons, the Columbian mammoths, the imperial mammoths, the woolly mammoths of the boreal and subarctic regions, the dwarf mammoths of Santa Rosa and other islands off the California coast, and the gomphotheres of the tropics comes strictly from fossils and the fossil record.

Bones of the ice age megafauna turn up in lake sediments, spring deposits, flood plain alluvium, frozen ground, ancient dune deposits, and caves. Over one hundred fossil mammoth localities are known from Arizona alone, and there are almost two hundred localities for mammoths and mastodons in Michigan. On the Atlantic Coast the great molars of mammoths and mastodons appear in the haul of trawlers fishing the shallow bottom of the continental shelf and mastodon remains have been dredged from the Harlem River Canal in Manhattan. The permafrost of the unglaciated subarctic in Alaska and Siberia is richer in mammoth remains than most temperate regions, probably due to better preservation of fossils rather than a result of larger populations of mammoths living in the subarctic. Occasionally both the frozen ground and the driest of desert caves yield not only bones but dung, hair, hide, horns, hooves, and the desiccated tissues of extinct animals, including mammoths. Thanks to many radiocarbon dates, it appears that both North America's proboscideans and many other genera of large mammals made their exit 11,000 radiocarbon years ago (Martin 1990, Stuart 1991) which geochemists calibrate to about 13,000 calendar years.

What caused such a loss, so late in the Pleistocene? Could it have been an asteroid hit, a circumstance that many believe accounts for heavy extinction including the loss of dinosaurs at the end of the Cretaceous? Evidently not. There is no trace of an asteroid impact large enough to generate global repercussions that late in the fossil record.

Moreover, throughout the islands and continents of the planet, late Pleistocene extinctions were not synchronous, as would be expected in the case of a cosmic or climatic accident. Radiocarbon dates show that they were globally sequential, or what geologists call "time transgressive." The time transgressive pattern creates problems for models based on sudden global change including changes in climate. While large animal extinctions impoverished North and probably South America around 13,000 years ago, they seem to have struck Australia much earlier, perhaps 50,000 years ago (Miller et al. 1999). The



last population of woolly mammoths—including some dwarfs just two meters tall—vanished from Wrangel Island in the Arctic Ocean off Siberia only 4000 years ago, surviving their North American kin by roughly 9000 years. In imagining that mammoths might still be alive it turns out that Thomas Jefferson was off by only four millennia!

A Deadly Syncopation

In the South Pacific over 3000 years ago the extinctions of thousands of species or populations of flightless birds began with the spread of the Lapita Culture from the southern Solomon Islands to Fiji and Tonga (Steadman 1995). Insular extinctions involving megapodes, pigeons, parrots, flightless rails, and populations of pelagic sea birds-extinctions much more severe than those recognized in historic time-swept through the South Pacific, reaching New Zealand to obliterate its giant flightless birds, the moas, beginning 1000 years ago. By then the shadow of extinction had already reached Madagascar. The island continent lost some 16 species of giant lemurs up to the size of a gorilla (living lemurs do not exceed 10 kg), at least two species each of hippos and giant tortoises, and several giant flightless birds, perhaps including the roc mentioned by Marco Polo. In dramatic contrast, over the last 40,000 years Africa and tropical Asia lost only a few large ungulate species.

These prehistoric extinctions follow the ancient footsteps of our species, out of Afro-Asia and onto other continents and eventually even to remote oceanic islands, in what Ross MacPhee of the American Museum calls a "deadly syncopation" of human arrival and faunal loss, the size of animals lost scaled to size of land mass. It's impossible to fit this pattern to any known climatic or cosmic event.

To be sure the traditional view, that climatic or environmental change must also be involved, persists. However, it is worth emphasizing that the idea of humans triggering late Pleistocene extinctions—perhaps by overkill—debated in Martin and Wright (1967) and Martin and Klein (1984), is gaining traction (Brown and Lomolino 1998, MacPhee 1999, Soulé and Noss 1998, Ward 1997). And the question of exactly what caused the extinctions need not deflect us from the prospect of repairing some of the damage.

In the long pull all species are doomed to extinction, just as death is the inevitable fate of all individuals. Most species that ever lived on Earth are no more. But this is a poor excuse for turning our back on the extraordinary loss of flagship species on our watch. By "loss on our watch" we mean not just the extinctions of this or the last five centuries of European conquest in the New World; we mean the time scale of our species on this continent, the last 13,000 years at least. While human remains

are rarely associated with extinct megafauna, dates on the Clovis culture and the extinct fauna overlap around 13,000 years ago (Stuart 1991). We have the opportunity to restart the evolution of proboscideans, along with horses, camels, and other extinct groups native in the Americas for millions or tens of millions of years. The global pattern of extinction outlined above involved many kinds of animals of tremendous interest to us, in particular warm-blooded, bright-eyed terrestrial vertebrates, mammals, and birds, including many of large size. Our strongest emotions are generated by those animals most like ourselves in intelligence and behavior. What can be done?

American Requiem; African Visions

For starters, it is time to mourn our dead, especially the total loss of the mammalian Order Proboscidea. In North America we need a "Mammoth Extinction Day" and in South America a "Gomphothere Extinction Day." This might take place sometime around the summer solstice. Any of the numerous fossil localities known to yield bones of Proboscidea would be suitable, such as Rancho la Brea with its magnificent Page Museum in Hancock Park, Los Angeles, California. An especially appropriate place for a wake would be at the Mammoth Site in Hot Springs, South Dakota, a paleoecological cathedral where 100,000 visitors a year pay a modest admission to marvel at a unique in situ exhibit of splendidly preserved mammoth bones in the process of being excavated from the most concentrated natural deposit of mammoths known on the continent. With the help of Earth Watch teams, Professors Larry Agenbroad and Jim Mead of Northern Arizona University have uncovered some fifty individual mammoths of two species plus bones of the giant bear, Arctodus.

The dimensions of the unexcavated sinkhole deposit suggest that along with other Pleistocene fossils another fifty mammoths remain to be discovered. Most of the animals sexed to date have proved to be subadult males, suggesting that females, like African elephants, ranged in matriarchal herds led by an experienced elderly matriarch, smart enough to escape the treacherous if enticing sinkhole. The Mammoth Site publishes books on research, symposium volumes, and popular interpretations of the site and its mammoths as part of their outreach to the general and scholarly public.

From the Hot Springs Mammoth Site tourists drive to Wind Cave National Park to see a free-ranging bison herd. There ecologists study the interrelationships between short grasses, grazing, and fire. Bison are increasingly popular as a meat animal. Near Truth or Consequences, New Mexico, over 1000 bison, as well as prairie dogs and mountain sheep, were recently established in place of cattle on the 600 square mile Armendaris Ranch. But

bison are a small part of the pre-extinction Wild West. Furthermore, according to the fossil record bison entered North America only a quarter of a million years ago, well after the arrival and evolution of New World Proboscidea. Even more interesting than determining the adaptability of bison on the Armendaris (where they were unknown historically) would be to determine the adaptability of elephant family units mixed in with the bison.

Thanks to the fossil record we are not totally ignorant of the paleoecology of extinct American Proboscidea. A remarkable chance to learn about mammoth diet has been gleaned from the dry dung deposits found in a large cave in southern Utah (Agenbroad and Mead 1996). Dung balls nine inches in diameter discovered in the 1980s by a National Park Service team of resource managers proved too big and the texture of the plant remains in the boluses too coarse to match those of the only other species they resembled, the Shasta ground sloths, whose dung is known from other caves in the region. The mean of 16 radiocarbon dates on mammoth dung balls was 14,500 calendar years, and the plant material in the dung indicated a cooler climate than occurs in southern Utah today. The extinct mammoths ate mainly grasses, sedges, and other riparian plants, salt bush, prickly pear, and even some needles of blue spruce. The cathedral-like cave they entered was more than large enough for mammoths. The animals deposited an estimated 255 cubic meters of manure. But much more about elephant ecology can only be learned from live animals.

When elephants dig for water in the dry season the water holes they leave behind attract other species. They thin out dense stands of low trees and shrubs. Undoubtedly the extinct mammoths, mastodons, and gomphotheres did the same. In the process elephants improve forage production for other grazers (Owen-Smith 1988, Buss 1990). The most interesting prospect for restarting the Proboscidea in America comes from what managers have discovered in Kenya's Amboseli Park just north of Kilimanjaro. According to David Western (1997):

If elephants and cattle had their way, they would trade places. In Amboseli...you see herds of cattle filing into the park to graze, passing elephants headed out to browse. With elephants and cattle transforming the habitat in ways inimical to their own survival but beneficial to each other, they create an unstable interplay, advancing and retreating around each other like phantom dancers in a languid ecological minuet playing continuously over decades and centuries. Habitats oscillate in space like a humming top, driving and being driven by climate, animals, and people.

In the New World we can substitute bison for cattle to see if bison, too, will dance the languid ecological minuet with African elephants, surrogates for the extinct American Proboscidea, to the benefit of the American range!

the New World is not to conduct an agricultural but an ecolog-

Our proposal to establish free-ranging elephant herds in

ical experiment. We have an extraordinary opportunity to learn more about how Nature works. How are fruits dispersed? What is the relationship between elephants, vegetation, and wildfire? Long smitten with the beguiling concept of a "forest primeval" (the climatic climax of Clementsian ecologists), North American conservation biologists have had to shift gears, adopting a more flexible concept of multiple stable states or discordant harmonies (Botkin 1990, Drury 1998). Over twenty years ago conservation ecologist Graeme Caughley (1976) found no attainable natural equilibrium between elephants and forests in eastern and southern Africa. More recently Sinclair (1995) reported that African elephants and fire reach multiple stable states. It appears that introduced elephants might have a great deal to teach us about the dynamic nature of wildness in America in evolutionary time. In the absence of elephants, inferences made on the dynamics of American vegetation types could be as one-sided as those made in the

Conclusions

absence of fire.

The demise of Proboscidea in North America represents not only the loss of ecological relationships and evolutionary possibilities, but a foreclosure on entire realms of scientific inquiry. Clearly American ecologists suffer blind spots if the largest and most potent megaherbivores native to the continent are missing. What might we learn from their reintroduction? David Western's vision of a timeless minuet between grazers and browsing elephants in Amboseli fuels thoughts of how to attempt an American experiment. Here elephants need not dance with grazing cattle. We have bison. People, bison, and elephants once coexisted in America. We see this in the Clovis sites excavated by the Arizona State Museum along the San Pedro River in southeastern Arizona. Clovis points, a shaft straightener of mammoth bone, stone blades, knives, and lithic debris are associated with the bones of mammoths, bison, and other extinct megafauna. Judging by many radiocarbon dates on

A Mammoth Memorial Service

will be held June 26, 1999, at the Mammoth Site of Hot Springs, South Dakota. Join Paul Martin, Connie Barlow, museum staff, excavation volunteers, and visitors for what may well be the first memorial service conducted for an extinct Pleistocene animal. The service will be one component of a weekend commemoration of the 25th anniversary of the discovery of this mammoth graveyard, the largest accumulation of intact mammoth bones in the Western Hemisphere. More than fifty skeletons have been unearthed, and excavation is still underway. Hot Springs is

in the southwestern corner of South Dakota, very near the national bison range of Wind Cave

National Park. For more information contact museum staff at 605-745-6017, or www.mammothsite.com. If you have ideas for participating in the service itself, contact:

Connie Barlow (cbtanager@aol.com) or Paul Martin (pmartin@geo.arizona.edu).

Columbian Mammoth (Mammuthus columbi)

charcoal from hearths, people, mammoths, and bison co-occurred briefly around 13,000 years ago (Taylor et al. 1996). The early Americans speared and processed Proboscidea. We suspect they spent many days watching them very closely, as closely as Cynthia Moss or David Western or the Masai watch African elephants today in

Amboseli National Park at the foot of Kilimanjaro. While we doubt she was thinking of the New World, Cynthia Moss's words (1988) are compelling:

I have realized that more than anything else, more than scientific discoveries or acceptance, what I care about and what I will fight for is the conservation, for as long as possible, not of just a certain number of elephants, but of the whole way of life of elephants. My priority, my love, my life are the Amboseli elephants, but I also want to ensure that there are elephants in other places that are able to exist in all the complexity and joy that elephants are capable of.

From mammoths and mastodons the Clovis foragers would have learned much about edible wild plants, where they grew, their season of fruiting, and their palatability. In the New World we suspect it was the extinct megafauna that introduced the first Americans to the sweet bean pods (or péchita, an Indian name becoming part of borderland Spanish) of the mesquites, a valuable food plant for people living off the land. From the large mammals of the New World the newcomers learned the right season to rip apart dagger-leafed agaves for their sugary hearts, a rich source of calories. Surely the early Americans followed the game trails of the last New World elephants through the tropics, in the process learning about palm fruits and other fruits as attractive to people as to Proboscidea.

Now African Loxodonta, or Asian Elephas, or both, can show us some of the coevolutionary secrets of America when it was truly wild. Beyond Pleistocene parks we need Pleistocene proving grounds, places to fathom as well as to celebrate our lost wildness. Above all the time has come to consider restarting elephant evolution by enabling elephants to reinvent their ecology on the continent that once constituted an important part of their global range. What is at stake is complexity, joy, and the whole way of life of elephants. C

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Acknowledgements For editorial or technical help we thank Larry Agenbroad, Connie Barlow, Julio Betancourt, Gary Haynes, Mary Ellen Morbeck, Mary Kay O'Rourke, George Rabb, Joe Truett, Raymond M. Turner, David Western, and Bill Willers.

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