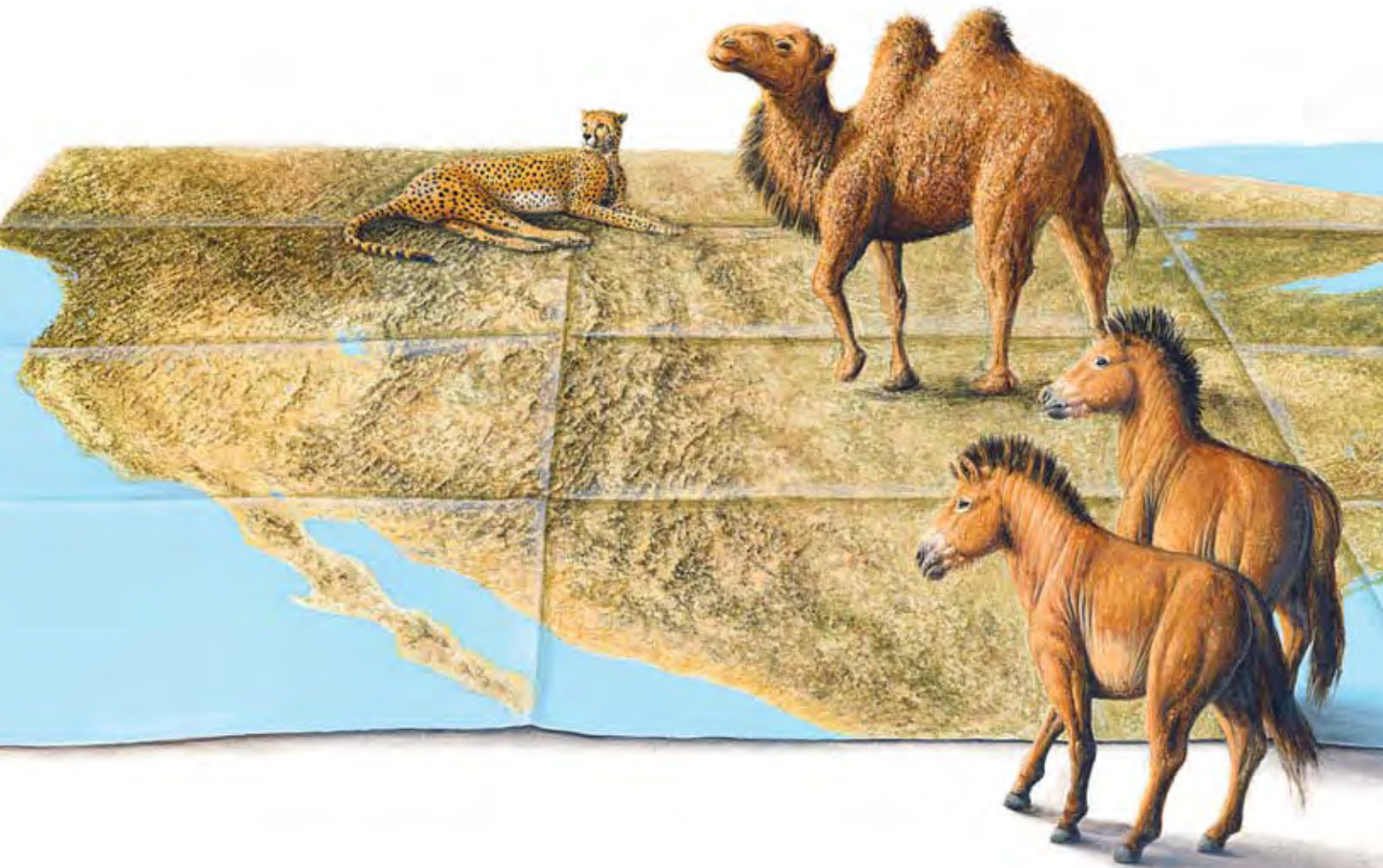


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Keywords: 1NA/cheetah/cougar/jaguar/lion/megafauna/Miracinonyx trumani/Panthera leo/Panthera onca/Pleistocene/Puma concolor/saber-toothed cat

Abstract: Pleistocene rewilding—a proposal to bring back animals that disappeared from North America 13,000 years ago—offers an optimistic agenda for 21st-century conservation. In the fall of 2004 a dozen conservation biologists gathered on a ranch in New Mexico to ponder a bold plan. The scientists, trained in a variety of disciplines, ranged from the grand old men of the field to those of us earlier in our careers. The idea we were mulling over was the reintroduction of large vertebrates—megafauna—to North America. Most of these animals, such as mammoths and cheetahs, died out roughly 13,000 years ago, when humans from Eurasia began migrating to the continent. The theory—propounded 40 years ago by Paul Martin of the University of Arizona—is that overhunting by the new arrivals reduced the numbers of large vertebrates so severely that the populations could not recover. Called Pleistocene overkill, the concept was highly controversial at the time, but the general thesis that humans played a significant role is now widely accepted. Martin was present at the meeting in New Mexico, and his ideas on the loss of these animals, the ecological consequences, and what we should do about it formed the foundation of the proposal that emerged, which we dubbed Pleistocene rewilding.

# RESTORING AMERICA'S



**I**n the fall of 2004 a dozen conservation biologists gathered on a ranch in New Mexico to ponder a bold plan. The scientists, trained in a variety of disciplines, ranged from the grand old men of the field to those of us earlier in our careers. The idea we were mulling over was the reintroduction of large vertebrates—megafauna—to North America.

Most of these animals, such as mammoths and cheetahs, died out roughly 13,000 years ago, when humans from Eurasia began migrating to the continent. The theory—propounded 40 years ago by Paul Martin of the University of Arizona—is that overhunting by the new arrivals reduced the numbers of large vertebrates so severely that the populations could not recover. Called Pleistocene overkill, the concept was highly controversial at the time, but the general thesis that humans played a significant role is now widely accepted. Martin was present at the meeting in New Mexico, and his ideas on the loss of these animals, the ecological consequences, and what we should do about it formed the foundation of the proposal that emerged, which we dubbed Pleistocene rewilding.

Although the cheetahs, lions and mammoths that once roamed North America are extinct, the same species or close relatives have survived elsewhere, and our discussions focused on introducing these substitutes to North American ecosystems. We believe that these efforts hold the potential to partially restore important ecological processes, such as predation and browsing, to ecosystems where they have been absent for millennia. The substitutes would also bring economic and cultural benefits. Not surprisingly, the published proposal evoked strong reactions. Those reactions are welcome, because debate about the conservation issues that underlie Pleistocene rewilding merit thorough discussion.

## Why Big Animals Are Important

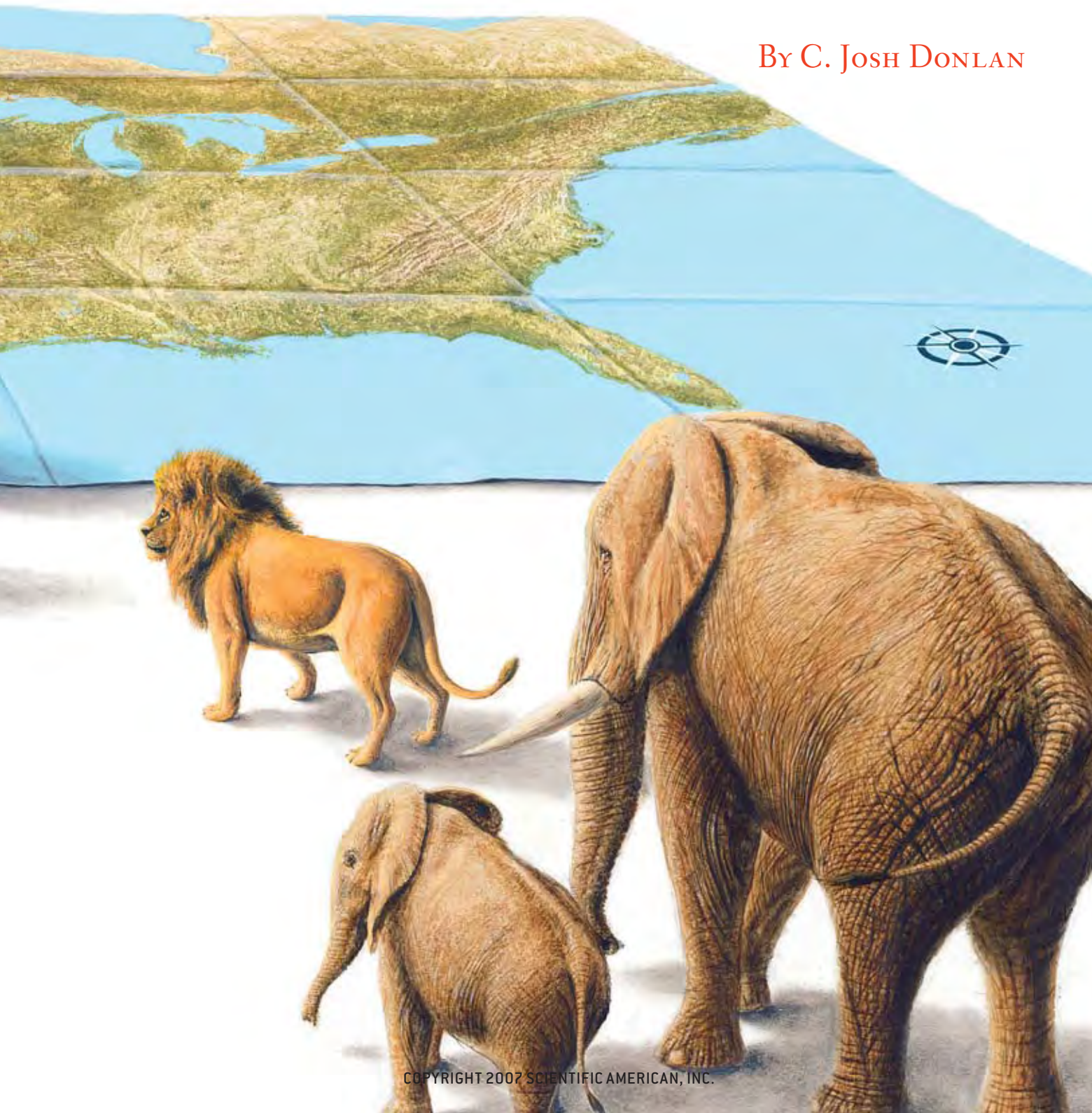
**OUR APPROACH** concentrates on large animals because they exercise a disproportionate effect on the environment. For tens of millions of years, megafauna dominated the globe, strongly interacting and co-evolving with other species and influencing entire ecosystems. Horses, camels, lions, ele-



# BIG, WILD ANIMALS

Pleistocene rewilding—a proposal to bring back animals that disappeared from North America 13,000 years ago—offers an optimistic agenda for 21st-century conservation

BY C. JOSH DONLAN



## Questions from Readers

*A summary of this article on our Web site invited readers to ask questions about rewilding. Many of the questions helped to shape the article, and answers appear throughout the text. The author replies to a few others here.*

phants and other large creatures were everywhere: megafauna were the norm. But starting roughly 50,000 years ago, the overwhelming majority went extinct. Today megafauna inhabit less than 10 percent of the globe.

Over the past decade, ecologist John Terborgh of Duke University has observed directly how critical large animals are to the health of ecosystems and how their loss adversely affects the natural world. When a hydroelectric dam flooded thousands of acres in Venezuela, Terborgh saw the water create dozens of islands—a fragmentation akin to the virtual islands created around the world as humans cut down trees, build shopping malls, and sprawl from urban centers. The islands in Venezuela were too small to support the creatures at the top of the food chain—predators such as jaguars, pumas and eagles. Their disappearance sparked a chain of reactions. Animals such as monkeys, leaf-cutter ants and other herbivores, whose populations were no longer kept in check by predation, thrived and subsequently destroyed vegetation—the ecosystems collapsed, with biodiversity being the ultimate loser.

Similar ecological disasters have occurred on other continents. Degraded ecosystems are not only bad for biodiversity; they are bad for human economies. In Central America, for instance, researchers have shown that intact tropical ecosystems are worth at least \$60,000 a year to a single coffee farm because of the services they provide, such as the pollination of coffee crops.

Where large predators and herbivores still remain, they play pivotal roles. In Alaska, sea otters maintain kelp forest

### **Won't African elephants and lions freeze to death in the Montana winter? Will these animals be kept indoors in the winter, as they are in zoos?** —Jason Raschka

The reader brings up an important point—that many questions, including climate suitability, would have to be answered by sound scientific studies during the process of Pleistocene rewilding. One could imagine scenarios in which animals would be free-living (albeit intensively managed) year-round in expansive reserves in the southwestern U.S. and perhaps other scenarios in locales farther north, where animals would be housed indoors during the coldest months. Even the latter alternative is arguably better than a zoo. Many zoos are struggling to find appropriate space for elephants and are choosing to abandon their elephant programs.



ELEPHANT at the Copenhagen zoo.

### **Aren't there big-game hunting ranches in Texas? Could we learn anything from them?** —Foster

There are many big-game hunting ranches throughout Texas, and some of them hold animals such as cheetahs that we know, from the fossil record, once lived in North America. To my knowledge, no conservation biologists have studied the ranch-held animals, but these ranches might present excellent research opportunities if they are willing to collaborate. Other ranches, however, have animals that are not supported by the fossil record and as such offer no potential for study.

### **Hasn't this general idea been around for a while?** —Kevin N.

Both the concept of rewilding and the term itself have been around for some time. Rewilding is the practice of reintroducing species to places from which they have been extirpated in the past few hundred years. Pleistocene rewilding, in contrast, involves introducing species descended from creatures that went extinct some 13,000 years ago or using similar species as proxies.

ecosystems by keeping herbivores that eat kelp, such as sea urchins, in check. In Africa, elephants are keystone players; as they move through an area, their knocking down trees and trampling create a

habitat in which certain plants and animals can flourish. Lions and other predators control the populations of African herbivores, which in turn influence the distribution of plants and soil nutrients.

In Pleistocene America, large predators and herbivores played similar roles. Today most of that vital influence is absent. For example, the American cheetah (a relative of the African cheetah) dashed across the grasslands in pursuit of pronghorn antelopes for millions of years. These chases shaped the pronghorn's astounding speed and other biological aspects of one of the fastest animals alive. In the absence of the cheetah, the pronghorn appears “overbuilt” for its environment today.

## Overview/Rewilding Our Vision

- A group of conservationists has proposed reintroducing to North America large animals that went extinct 13,000 years ago.
- Close relatives of these animals—elephants, camels, lions, cheetahs—survived elsewhere; returning them to America would reestablish key ecological processes that once thrived there, as well as providing a refuge for endangered species from Africa and Asia and creating opportunities for ecotourism.
- The proposal has, understandably, evoked strong reactions, but the bold suggestion has spurred debate and put a positive spin on conservation biology, whose role has been mainly a struggle to slow the loss of biodiversity.



Pleistocene rewilding is not about re-creating exactly some past state. Rather it is about restoring the kinds of species interactions that sustain thriving ecosystems. Giant tortoises, horses, camels, cheetahs, elephants and lions: they were all here, and they helped to shape North American ecosystems. Either the same species or closely related species are available for introduction as proxies, and many are already in captivity in the U.S. In essence, Pleistocene rewilding would help change the underlying premise of conservation biology from limiting extinction to actively restoring natural processes.

At first, our proposal may seem outrageous—lions in Montana? But the plan deserves serious debate for several reasons. First, nowhere on Earth is pristine, at least in terms of being substantially free of human influence. Our demographics, chemicals, economics and politics pervade every part of the planet. Even in our largest national parks, species go extinct without active intervention. And human encroachment shows alarming signs of worsening. Bold actions, rather than business as usual, will be needed to reverse such negative influences. Second, since conservation biology emerged as a discipline more than three decades ago, it has been mainly a business of doom and gloom, a struggle merely to slow the loss of biodiversity. But conservation need not be only reactive. A proactive approach would include restoring natural processes, starting with ones we know are disproportionately important, such as those influenced by megafauna.

Third, land in North America is available for the reintroduction of megafauna. Although the patterns of human land use are always shifting, in some areas, such as parts of the Great Plains and the Southwest, large private and public lands with low or declining human population densities might be used for the project. Fourth, bringing megafauna back to America would also bring tourist and other dollars into nearby communities and enhance the public's appreciation of the natural world. More than 1.5 million people visit San Diego's Wild Animal Park every year to catch a

# When the West Was Really Wild

Soon after humans crossed the Bering land bridge into North America some 13,000 years ago, almost 75 percent of the continent's large mammals (those weighing more than 45 kilograms) disappeared (color). One of the goals of Pleistocene rewilding is to restore some of these species or close proxies to the American West. For example, the same species of lion and cheetah that once lived in North America survive today in Africa; the African or Asian elephant could substitute for the extinct mammoth; and Bactrian camels might stand in for the extinct *Camelops*.

## Large Mammals of Pleistocene North America

### Xenarthra

- Glyptodont (*Glyptotherium floridanum*)
- Harlan's ground sloth (*Paramylodon harlani*)
- Jefferson's ground sloth (*Megalonyx jeffersonii*)
- Shasta ground sloth (*Nothrotheriops shastensis*)



### Carnivores (Carnivora)

- Dire wolf (*Canis dirus*)
- Gray wolf (*Canis lupus*)
- Black bear (*Ursus americanus*)
- Brown bear (*Ursus arctos*)
- Giant short-faced bear (*Arctodus simus*)
- Saber-toothed cat (*Smilodon fatalis*)
- American lion (*Panthera leo*)
- Jaguar (*Panthera onca*)
- American cheetah (*Miracinonyx trumani*)
- Mountain lion (*Puma concolor*)



### Elephants (Proboscidea)

- American mastodon (*Mammuthus americanum*)
- Columbian mammoth (*Mammuthus columbi*)
- Dwarf mammoth (*Mammuthus exilis*)
- Woolly mammoth (*Mammuthus primigenius*)



### Horses (Perissodactyla)

- Mexican horse (*Equus conversidens*)
- Western horse (*Equus occidentalis*)
- Other extinct horses and asses (*Equus spp.*)



### Even-Toed Ungulates (Artiodactyla)

- Western camel (*Camelops hesternus*)
- Long-legged llama (*Hemiauchenia macrocephala*)
- Long-nosed peccary (*Mylohyus nasutus*)
- Flat-headed peccary (*Platygonus compressus*)
- Mule deer (*Odocoileus hemionus*)
- White-tailed deer (*Odocoileus virginianus*)
- Mountain deer (*Navahoceros fricki*)
- Woodland caribou (*Rangifer tarandus*)
- Moose (*Alces alces*)
- Wapiti (*Cervus elaphus*)
- Pronghorn (*Antilocapra americana*)
- Harrington's mountain goat (*Oreamnos harringtoni*)
- Mountain goat (*Oreamnos americanus*)
- Bighorn sheep (*Ovis canadensis*)
- Shrub ox (*Euceratherium collinum*)
- Bonnet-headed musk ox (*Bootherium bombifrons*)
- Bison (*Bison bison*)
- Extinct bison (*Bison spp.*)









## Past, Present and Future

These artist's conceptions illustrate some of the ways that large animals influence the ecosystem and how Pleistocene rewilding could be beneficial. David Burney of the National Tropical Botanical Garden, who is a member of the Pleistocene rewilding group, worked with artist Larry Felder in conceiving the illustrations.

### ◀ LATE APRIL DURING THE PLEISTOCENE, 14,000 YEARS AGO

Humans have not yet appeared on the landscape, but glaciers have receded and the climate of what is now the western U.S. is similar to modern conditions, though a little cooler. Dense snow covers the Rocky Mountains. The river, flushed by snowmelt, is fairly high and a milky blue because of the fine particles carried from the young, postglacial soils. The banks are grazed down short but are generally green. A Columbian mammoth, a *Camelops*, a Shasta ground sloth, long-horned bison, horses and pronghorn antelope browse, while an American lion and two wolves watch from the opposite bank and a bald eagle glides over the river.

### ◀ APRIL 2007

The Rocky Mountains have snow on their upper summits only. The river, muddied by spring rains and by too many cattle on the banks, has widened, and the banks are eroded and broken down by hoofprints and cattle wallows. Grass is short, patches of soil are bare, thorny shrubs predominate. Bison graze in the background, and a wary coyote stands on the opposite shore.

### ◀ APRIL 2027

Vegetation is more summerlike—global warming conditions are in full swing. The mountains have no snow on the peaks. Drought, low humidity and absence of mountain snow have lowered the level of the river dramatically; the water is clear and dark. Erosion is less apparent; grass looks manicured from diversified grazing and browsing. An Asian elephant, Bactrian camel, bison, antelope and Przewalski's horses graze under the watchful eye of an African lion; a cheetah approaches from the distance. In the background a monorail carries tourists. A high-tech electrified fence with solar panels is out of view.

glimpse of large mammals. Only a handful of U.S. national parks receive that many visitors. Last, the loss of some of the remaining species of megafauna in Africa and Asia within this century seems likely—Pleistocene rewilding could help reverse that.

### How It Might Be Done

WE ARE NOT TALKING about backing up a van and kicking some cheetahs out into your backyard. Nor are we talking about doing it tomorrow. We conceive of Pleistocene rewilding as a series of staged, carefully managed ecosystem manipulations. What we are offering here is a vision—not a blueprint—of how this might be accomplished. And by no means are we suggesting that rewilding should be a priority over current conservation programs in North America or Africa. Pleistocene rewilding could proceed alongside such conservation efforts, and it would likely generate conservation dollars from new funding sources, rather than competing for funds with existing conservation efforts.

The long-term vision includes a vast, securely fenced ecological history park, encompassing thousands of square miles, where horses, camels, elephants and large carnivores would roam. As happens now in Africa and regions surrounding some U.S. national parks, the ecological history park would not only attract ecotourists but would also provide jobs related both to park management and to tourism.

To get to that distant point, we would need to start modestly, with relatively small-scale experiments that assess the impacts of megafauna on North American landscapes. These controlled experiments, guided by sound science and by the fossil record, which indicates what animals actually lived here, could occur first on donated or purchased pri-

vate lands and could begin immediately. They will be critical in answering the many questions about the reintroductions and would help lay out the costs and benefits of rewilding.

One of these experiments is already under way. Spurred by our 2004 meeting, biologists recently reintroduced Bolson tortoises to a private ranch in New Mexico. Bolson tortoises, some weighing more than 100 pounds, once grazed parts of the southwestern U.S. before disappearing around 10,000 years ago, victims of human hunting. This endangered tortoise now clings to survival, restricted to a single small area in central Mexico. Thus, the reintroduction not only repatriates the tortoise to the U.S., it increases the species' chance for survival. Similar experiments are also occurring outside North America [see box on page 77].

The reintroduction of wild horses and camels would be a logical part of these early experiments. Horses and camels originated on this continent, and many species were present in the late Pleistocene. Today's feral horses and asses that live in some areas throughout the West are plausible substitutes for extinct American species. Because most of the surviving Eurasian and African species are now critically endangered [see "Endangered Wild Equids," by Patricia D. Moehlan; *SCIENTIFIC AMERICAN*, March 2005], establishing Asian asses and Przewalski's horse in North America might help prevent the extinction of these animals. Bactrian camels, which are critically endangered in the Gobi Desert, could provide a modern proxy for *Camelops*, a late Pleistocene camel. Camels, introduced from captive or domesticated populations, might benefit U.S. ecosystems by browsing on woody plants that today are overtaking arid grasslands in the Southwest, an ecosystem that is increasingly endangered.

LARRY FELDER  
THE AUTHOR

C. JOSH DONLAN holds a Ph.D. in ecology and evolutionary biology from Cornell University, where he is a research biologist. Founder and director of Advanced Conservation Strategies, he serves as an adviser to the Galápagos National Park and to Island Conservation and is a senior fellow at the Robert and Patricia Switzer Foundation and Environmental Leadership Program. He was highlighted in the *New York Times Magazine*'s "Big Ideas of 2005" issue and named one of 25 "all-star" innovators for 2005 by *Outside* magazine. He spends much of his time in Tasmania, Australia and Santa Cruz, Calif., trying to halt extinctions on islands.

Another prong of the project would likely be more controversial but could also begin immediately. It would establish small numbers of elephants, cheetahs and lions on private property.

Introducing elephants could prove valuable to nearby human populations by attracting tourists and maintaining grasslands useful to ranchers (elephants could suppress the woody plants that threaten southwestern grasslands). In the late Pleistocene, at least four elephant species lived in North America. Under a scientific framework, captive elephants in the U.S. could be introduced as proxies for these extinct animals. The biggest cost involved would be fencing, which has helped reduce conflict between elephants and humans in Africa.

Many cheetahs are already in captivity in the U.S. The greatest challenge would be to provide them with large, securely fenced areas that have appropriate habitat and prey animals. Offsetting these costs are benefits—restoring what must have been strong interactions with

pronghorn, facilitating ecotourism as an economic alternative for ranchers, many of whom are struggling financially, and helping to save the world's fastest carnivore from extinction.

Lions are increasingly threatened, with populations in Asia and some parts of Africa critically endangered. Bringing back lions, which are the same species that once lived in North America, presents daunting challenges as well as many potential benefits. But private reserves in southern Africa where lions and other large animals have been successfully reintroduced offer a model—and these reserves are smaller than some private ranches in the Southwest.

If these early experiments with large herbivores and predators show promising results, more could be undertaken, moving toward the long-term goal of a huge ecological history park. What we need now are panels of experts who, for each species, could assess, advise and cautiously lead efforts in restoring megafauna to North America.

A real-world example of how the re-introduction of a top predator might work comes from the wolves of Yellowstone National Park [see “Lessons from the Wolf,” by Jim Robbins; *SCIENTIFIC AMERICAN*, June 2004]. The gray wolf became extinct in and around Yellowstone during the 1920s. The loss led to increases in their prey—moose and elk—which in turn reduced the distribution of aspens and other trees they eat. Lack of vegetation destroyed habitat for migratory birds and for beavers. Thus, the disappearance of the wolves propagated a trophic cascade from predators to herbivores to plants to birds and beavers. Scientists have started to document the ecosystem changes as reintroduced wolves regain the ecological role they played in Yellowstone for millennia. An additional insight researchers are learning from putting wolves back into Yellowstone is that they may be helping the park cope with climate change. As winters grow milder, fewer elk die, which means less carrion for scavengers such

## What the Critics Say

Since we proposed the rewilding idea in print, in *Nature* in 2005, commentators have pointed out a number of concerns, some legitimate, some not. “We all remember *Jurassic Park*,” wrote Dustin Rubenstein and his colleagues in the journal *Biological Conservation*. “Pleistocene re-wilding of North America is only a slightly less sensational proposal.” We disagree with this assessment because the majority of dinosaurs went extinct 65 million years ago, whereas many of North America’s original megafauna or very close relatives are alive today elsewhere in the world and can be both studied and saved.

Rubenstein and colleagues go on to say, “*Modern day proxies species are wrong ... different genetically from the species that occurred in North America during the Pleistocene.*” True, but not that different. Available evidence indicates that the lions in Africa and Asia today are the same species, albeit of smaller stature, as the lions that prowled North America 13 millennia ago. Recent studies of ancient DNA have elucidated close relationships between extinct elephant and horse species and those alive today. Further, introduction of proxies for now extinct species has proved successful in other experiments. Hundreds of peregrine falcons from Australia, Europe and South America were used, for example, in captive-breeding programs to reintroduce the peregrine falcon to parts of

the U.S. and Canada where DDT had wiped it out. Those birds were certainly different genetically from the ones that once soared over the Midwest, yet they have done well in their new homes.

“One can only imagine ... farmers coping with crop destruction by herds of elephants, or lions and cheetah attacking cattle, or even children,” Rubenstein and his colleagues warn. One

need not merely imagine the challenges of coexisting with large predators and herbivores. Africa and Asia have been struggling with them for centuries, and substantial progress has been made; in our plan the animals will not be unrestrained.

“Global climate change since the Pleistocene extinctions makes the restoration of vanished ecosystems through large-mammal introduction quite unlikely,” wrote Christopher Smith in a letter to *Nature* in the weeks following the initial proposal. Many have expressed concern about the fact that North America’s ecosystems are not the same today as they were 13,000 years ago and that reintroduced animals might therefore be unable to survive in them. Whereas habitats are and will continue to be dynamic on a timescale of thousands of years, very few plants or small mammals went extinct during the late Pleistocene. The major missing component of North American ecosystems today compared with the Pleistocene is the megafauna, which we can infer are critical cogs in the wheels. —C.J.D.





## Elsewhere in the World

as coyotes, ravens and bald eagles. Wolves provide carcasses throughout the winter for the scavengers to feed on, bestowing a certain degree of stability.

### The Challenges Ahead

AS OUR GROUP on the ranch in New Mexico discussed how Pleistocene rewilding might work, we foresaw many challenges that would have to be addressed and overcome. These include the possibility that introduced animals could bring novel diseases with them or that they might be unusually susceptible to diseases already present in the ecosystem; the fact that habitats have changed over the millennia and that reintroduced animals might not fare well in these altered environments; and the likelihood of unanticipated ecological consequences and unexpected reactions from neighboring human communities. Establishing programs that monitor the interactions among species and their consequences for the well-being of the ecosystem will require patience and expertise. And, of course, it will not be easy to convince the public to accept predation as an important natural process that actually nourishes the land and enables ecosystems to thrive. Other colleagues have raised additional concerns, albeit none that seems fatal [see box on opposite page].

Many people will claim that the concept of Pleistocene rewilding is simply not feasible in the world we live in today. I urge these people to look to Africa for inspiration. The year after the creation of Kruger National Park was announced, the site was hardly the celebrated mainstay of southern African biodiversity it is today. In 1903 zero elephants, nine lions, eight buffalo and very few cheetahs lived within its boundaries. Thanks to the vision and dedication of African conservationists, 7,300 elephants, 2,300 lions, 28,000 buffalo and 250 cheetahs roamed Kruger 100 years later—as did 700,000 tourists, bringing with them tens of millions of dollars.

In the coming century, humanity will decide, by default or design, the extent to which it will tolerate other species and thus how much biodiversity will endure. Pleistocene rewilding is not about trying

In other parts of the world, preliminary efforts have begun to reintroduce species to places from which they have long been absent.

- In April 2006 a team of Canadian and Russian biologists flew 30 wood bison from Canada's Elk Island National Park to Pleistocene Park reserve in the Republic of Sakha, Russia, where the closely related steppe bison vanished 5,000 years ago.
- At the 15,000-acre nature reserve Oostvaardersplassen in the Netherlands, conservationists are restoring horses, roe deer and Heck cattle.
- Beavers are being reintroduced throughout Europe, in some cases in areas where they have been absent for thousands of years.
- In the tropical Pacific, endangered birds from the Marquesas and Tongan islands have been reintroduced to nearby islands where fossils indicate they once lived.
- In the Indian Ocean, scientists from the Mauritian Wildlife Foundation are using giant tortoises from Aldabra Island to replace two extinct species of tortoise on the Mascarene Islands. Scientists have already documented increased seed dispersal for many of the island plants. The tortoises have also brought increased tourism.

—C.J.D.



KONIK HORSES stand in for the extinct tarpan horse at the Oostvaardersplassen reserve in the Netherlands.

to go back to the past; it is about using the past to inform society about how to maintain the functional fabric of nature. The potential scientific, conservation and cultural benefits of restoring megafauna are clear, as are the costs. Although sound science can help mitigate the potential costs, these ideas will make many uneasy. Yet given the apparent dysfunction of North American ecosystems and Earth's overall state, inac-

tion carries risks as well. In the face of tremendous uncertainty, science and society must weigh the costs and benefits of bold, aggressive actions like Pleistocene rewilding against those of business as usual, which has risks, uncertainties and costs that are often unacknowledged. We have a tendency to think that if we maintain the status quo, things will be fine. All the available information suggests the opposite. SA

### MORE TO EXPLORE

**The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms.** Connie Barlow. Basic Books, 2000.

**Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America.** Paul S. Martin. University of California Press, 2005.

**Pleistocene Rewilding: An Optimistic Agenda for Twenty-First Century Conservation.** C. J. Donlan, J. Berger, C. E. Bock, J. H. Bock, D. A. Burney, J. A. Estes, D. Foreman, P. S. Martin, G. W. Roemer, F. A. Smith, M. E. Soulé and H. W. Greene in *American Naturalist*, Vol. 168, No. 5, pages 660–681; November 2006.