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Pleistocene Rewilding: An Optimistic Agenda for Twenty-First Century Conservation

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ABSTRACT: Large vertebrates are strong interactors in food webs, yet they were lost from most ecosystems after the dispersal of modern humans from Africa and Eurasia. We call for restoration of missing ecological functions and evolutionary potential of lost North American megafauna using extant conspecifics and related taxa. We refer to this restoration as Pleistocene rewilding; it is conceived as carefully managed ecosystem manipulations whereby costs and benefits are objectively addressed on a case-by-case and locality-by-locality basis. Pleistocene rewilding would deliberately promote large, long-lived

species over pest and weed assemblages, facilitate the persistence and ecological effectiveness of megafauna on a global scale, and broaden the underlying premise of conservation from managing extinction to encompass restoring ecological and evolutionary processes. Pleistocene rewilding can begin immediately with species such as Bolson tortoises and feral horses and continue through the coming decades with elephants and Holarctic lions. Our exemplar taxa would contribute biological, economic, and cultural benefits to North America. Owners of large tracts of private land in the central and western United States could be the first to implement this restoration. Risks of Pleistocene rewilding include the possibility of altered disease ecology and associated human health implications, as well as unexpected ecological and sociopolitical consequences of reintroductions. Establishment of programs to monitor suites of species interactions and their consequences for biodiversity and ecosystem health will be a significant challenge. Secure fencing would be a major economic cost, and social challenges will include acceptance of predation as an overriding natural process and the incorporation of pre-Columbian ecological frameworks into conservation strategies.

Keywords: carnivores, ecological history, megafauna, predation, re-introduction, taxon substitutions.

Far more than any other species in the history of life on Earth, humans alter their environments by eliminating species and changing ecosystem function, thereby affecting the very future of evolution (Sala et al. 2000; Myers and Knoll 2001; Smith 2003; Thomas et al. 2004a, 2004b; Meyer 2004; Flannery 2006). We will surely continue to do so for the foreseeable future, either by default or by design (Wilson and Willis 1975; Western 2001). Earth is now nowhere pristine, in the sense of being substantially free from human influence, and indeed, most major land

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masses have sustained many thousands of years of human occupancy and impacts (Flannery 1995, 2001; Vitousek et al. 1997; Heckenberger et al. 2003; Mason 2004; Burney and Flannery 2005). Human economics, politics, demographics, and chemicals pervade every ecosystem; even the largest parks require management to prevent extinction (Newmark 1995; Berger 2003). Human-induced environmental impacts are now unprecedented in their magnitude and cosmopolitan in their distribution, and they show alarming signs of worsening.

Human influences on the environment take on a variety of well-known and often interrelated general forms, including habitat alteration and fragmentation, pollution, and resource reductions as a result of exploitation. Large vertebrates (the megafauna) are often the first species to disappear in the wake of these influences because of their inherently low population densities and the fact that they are often the focus of human exploitation (Flannery 1995; Burney and Flannery 2005; Cardillo et al. 2005). Substantial loss of megafaunal biodiversity has already occurred in Europe, Australia, the Americas, and large continental islands. In Africa and Asia, which are the only places where a diverse megafauna remains relatively intact, many large mammals are threatened with extinction (Musters et al. 2000; Vogel 2000; Balmford et al. 2001; Marchant 2001; Blake and Hedges 2004; Goossens et al. 2006), especially in regions where increasingly scarce resources provoke war, corruption, and political turmoil (André and Platteu 1998; Smith et al. 2003c; Diamond 2004).

In the Americas, most large mammals and their commensals were lost by ~13,000 years ago (Martin 1958, 2005*b*; Burney and Flannery 2005). Because large body size and endothermy correlate with interaction strength (Borer et al. 2005), this extraordinary impoverishment must have precipitated a cascading series of small- to large-scale ecological and evolutionary changes (Janzen and Martin 1982; Terborgh 2005; Donlan et al., forthcoming). The prehistoric, historic, and contemporary extinction of large vertebrates and loss of their associated ecological roles thus hold paramount but still underappreciated implications for biodiversity conservation (Estes 1996; Martin 1999, 2005; Martin and Burney 1999; Terborgh et al. 1999; Flannery 2001; Jackson et al. 2001; Springer et al. 2003; Ray et al. 2005; Donlan et al., forthcoming).

Pleistocene history has been largely ignored as both conservation biologists and the public, seemingly hampered by an implicit post-Columbian bias, struggle with our biodiversity crisis. Basing our judgments on a deeper history offers a new vista, one with widespread implications for how humans might perceive and manage nature. The islands of Oceania provide a stark example (Steadman, forthcoming). Before the onset of human impacts 3,000 years ago, these islands were home to more than 2,000

bird species that are now extinct—more than 20% of the extant avifauna worldwide (Monroe and Sibley 1993; Steadman 1995; Steadman and Martin 2003). Over the past three decades, conservation practitioners have developed techniques to halt insular extinctions and restore island ecosystems (Veitch and Clout 2002; Donlan et al. 2003), yet they have largely failed to develop a conceptual basis for restoration that encompasses ecological history (however, see Atkinson 2001). This is at least in part because the ecological consequences of the historical losses are unknown and even unimagined.

Pleistocene history and taxon substitutions can provide us with new benchmarks for restoration. Such benchmarks would be defined not only by the presence or absence of species but also by the presence or absence of species interactions—the true functional fabric of nature (Estes 2002). To this end, we advocate Pleistocene rewilding—reinstating ecological and evolutionary processes that were transformed or eliminated by megafaunal extinctions—as a conservation priority in North America (Donlan et al. 2005; see also Martin 1999, 2005*b*; Martin and Burney 1999). The events and processes underlying our proposal apply not only to North America (Martin and Burney 1999; Flannery 2001; Donlan et al. 2005) but to most island archipelagos and continental ecosystems. This proposed program for twenty-first century conservation is both optimistic and defensible on multiple grounds, and it echoes and expands on similar proposals for eastern Siberia (Stone 1998; Zimov 2005), South America (Galetti 2004), and certain island archipelagos (Atkinson 2001; Burney et al. 2002; Lazell 2002; Burney 2003; Steadman and Martin 2003).

This article follows a preliminary and much shorter version (Donlan et al. 2005), and here we lay out a more substantive argument for Pleistocene rewilding. We first present ecological arguments for the rewilding proposal and then discuss its evolutionary, conservation, and cultural benefits. We next describe eight exemplar taxa, chosen to illustrate a range of benefits as well as provide a focus for the subsequent section discussing costs, challenges, and objections. Finally, we describe several possible implementation scenarios. Our broad purpose here is to inform further widespread discussion of this topic.

Ecological Arguments for Pleistocene Rewilding

For the past 200 million years, large carnivores and megaherbivores have been dominant features of most ecosystems. With a few exceptions, primarily in Africa, these animals became functionally extinct worldwide by the late Pleistocene. Any thoughtful natural historian should wonder about how the loss of these large vertebrates subsequently influenced biodiversity and ecosystem func-

tion (Terborgh 2005). If these influences were important, would an attempt to partially restore large carnivores and megaherbivores have positive or negative consequences for biodiversity and human welfare? Heretofore, these important questions have received little serious consideration.

The general lack of attention to the functional importance of the extinct megafauna occurs at a time when the focus of conservation biology is expanding to include not only species but species interactions (Soulé et al. 2003, 2005). A variety of evidence indicates that the functional roles of large carnivores and megaherbivores are often significant (Owen-Smith 1988; Soulé et al. 1988; Estes et al. 1998; Terborgh et al. 1999, 2001; Berger et al. 2001; Jackson et al. 2001; Sinclair et al. 2003; Ray et al. 2005) and that degraded systems may both cause and result from the loss of these species (Springer et al. 2003; Terborgh et al. 2006; Terborgh and Feeley, forthcoming). It follows that many extinct large mammals must have shaped the life histories of extant species and ecosystem characteristics through the selective forces of strong species interactions (Greenwood and Atkinson 1977; Janzen and Martin 1982; Zimov et al. 1995; Byers 1997; Barlow 2000). The likely consequence of so much large vertebrate-induced change in functionality is ecosystem dysfunction (Jackson 1997; Pandolfi et al. 2003; Terborgh and Feeley, forthcoming), driven in part by anachronistic attributes of the surviving species (Janzen and Martin 1982) and ecological chain reactions that lead to further extinctions (Springer et al. 2003; Koh et al. 2004; Terborgh et al. 2006; Donlan et al., forthcoming).

Species interactions are difficult to observe and understand, even for the most easily studied extant species in modern ecosystems (e.g., lizards on islands [Spiller and Schoener 1994], fish in lakes [Carpenter and Kitchell 1996], and sea stars in rocky intertidal communities [Paine 1966]). Species interactions are impossible to observe and vastly more difficult to understand when looking back in time. Nonetheless, the strong interactors in paleoecosystems should have left evidence of their influence through their evolutionary effects on other species (Janzen and Martin 1982; Janzen 1986). Various North American species have characteristics that in modern landscapes appear to be anachronistic, probably having coevolved with large native vertebrates that became extinct in the late Pleistocene (for South American examples, see Guix et al. 2005). We briefly describe two of the many suspected anachronisms for which detailed experimental studies are sorely needed (Barlow 2000).

Large-fruited Maclura. The interglacial Pleistocene fossil plant record reveals several species of *Maclura* throughout North America, while the pre-European historical record documents only Osage orange (*M. pomifera*) in the Red River floodplains of Arkansas (Barlow 2000; Schambach

2000). The loss of proboscideans and other megaherbivores capable and suspected of dispersing the large fruits of these trees may have caused or contributed to the extinction of the other *Maclura* species, whereas Osage orange fortuitously survived as a small remnant and spread because of dispersal by modern humans (Barlow 2000). Many other large-seeded temperate and tropical American plants are arguably in some disequilibrium due to the loss of large vertebrate seed dispersers and herbivores (Janzen and Martin 1982; Janzen 1986; but see Howe 1985 for an alternative viewpoint). When dozens of large herbivores in the Americas became extinct in the late Pleistocene, important ecological and evolutionary interactions such as frugivory and herbivory were disrupted, and subsequently, seed dispersal and thus distributions of many plant species were altered. While such ideas were brought to the forefront of evolutionary ecology more than two decades ago (Janzen and Martin 1982; Janzen 1986), they have yet to penetrate conservation biology and applied ecology.

"Overbuilt" speed in Antilocapra. Various traits in the North American pronghorn (*Antilocapra americana*) appear to have resulted from 4 million years of selection in North American grasslands (e.g., maternal behavior, patterns of sex allocation, and mate selection; Byers 1997). Among the specific factors that led to these traits was predation by the extinct American cheetah (*Micracimonyx trumani*), which purportedly played a pivotal role in shaping the pronghorn's astounding speed (Byers 1997). The pronghorn appears overbuilt today in precisely those traits that make it so distinctive among North American mammals, raising the question of whether a reconstitution of Pleistocene selective pressures warrants consideration.

Many other anachronistic traits and dysfunctional interactions resulting from the loss of large vertebrates have been proposed (Greenwood and Atkinson 1977; Janzen and Martin 1982; Barlow 2000; Springer et al. 2003; ESKILDSEN et al. 2004). Gray wolves (*Canis lupus*) are a documented contemporary example. The recent loss of these apex predators from much of North America has facilitated population increases of their large ungulate prey, thereby intensifying herbivory and reducing the distribution and abundance of aspen and other tree species (Ripple and Larsen 2000; Berger et al. 2001; Ripple et al. 2001; Soulé et al. 2003; Hebblewhite et al. 2005). The indirect effects of this trophic cascade range from the abundance and distribution of passerine birds (Berger et al. 2001; Hebblewhite et al. 2005) to flood plain sediment and nutrient dynamics (Ripple and Beschta 2004). Similar patterns and processes have been discovered through the reintroduction of wolves to the Yellowstone ecosystem. The restoration of functionality from the reintroduction of wolves may even include a buffering of Yellowstone's bio-

diversity to climate change (Smith et al. 2003a; Willmers and Getz 2005). Similarly complex but now extinct ecological roles for the dozens of lost Pleistocene predators and megaherbivores of North America would seem possible if not likely. The inferred ecological roles of Pleistocene megafauna imply numerous hypotheses that could be tested with their modern conspecifics or proxies during the stages of rewilding that we describe below (fig. 1; Bond et al. 2004; Eskildsen et al. 2004).

Such hypotheses are similar to those currently being tested by the scientific community, the main difference being a strong emphasis on ecological history. Our current ignorance over the roles of large vertebrates in food web dynamics results from a variety of factors, including the inherent difficulties in (1) viewing the world from a temporal baseline lacking recently extinct keystone species, (2) elucidating and documenting the power of top-down forcing processes operating at large spatial scales, and (3) understanding food web dynamics without experimental evidence, particularly the diversity, complexity, and power of indirect interactions (Estes 2005). Such indirect interactions are highly significant in some contemporary ecosystems and thus are likely to have played pivotal roles before the loss of North American megafauna. The reintroduction of North American megafaunal proxies in an experimental framework would provide an unprecedented opportunity

to study these potentially important interactions so as to better understand the ecology of North America.

Such new understanding may have far-reaching benefits for humanity. For example, the recent Lyme disease epidemic in the northeastern United States (Ostfeld 1997) might be an indirect effect of the extinction of large predatory mammals. Lyme disease is caused by *Borellia*, a spirochete bacterium, which is transmitted to humans by black-legged ticks (*Ixodes dammini*). Disease prevalence is strongly influenced by tick abundance and in turn by obligate relationships with white-footed mice (*Peromyscus leucopus*; for nymphal blood meals) and white-tailed deer (*Odocoileus virginianus*; for adult blood meals). Deer and mouse populations are driven by various biotic and environmental processes (Jones et al. 1998). However, deer populations in eastern North America are at historically high levels due to the extinction of large social canids (McShea et al. 1997; Terborgh et al. 1999), cessation of subsistence hunting by Native Americans and market hunting by European colonists, and habitat restoration and other game management practices (Miller et al. 2003). Gray wolves probably caused deer to avoid heavily wooded areas where they are more easily ambushed and killed. The risk of Lyme disease is now greatest in wooded areas, and the ecological extinction of gray wolves from eastern North America therefore was plausibly an essential ingredient in

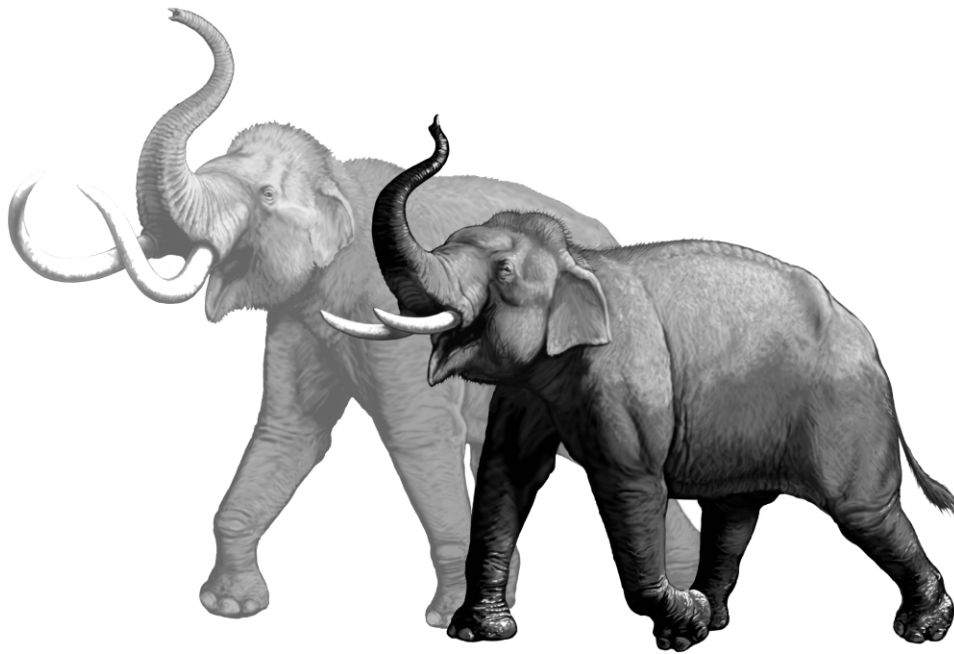


Figure 1: Could the Asian elephant (*right*) serve as an ecological proxy for North American mammoths (*left*) in an effort to restore megaherbivore function to North America? Illustration by Carl Buell.

the recent Lyme disease epidemic (Estes 2002). It follows that the risk of Lyme disease might be reduced through reestablishment of gray wolves in that region.

Wild animals carry a variety of other diseases that are pathogenic in humans, and in some cases, their incidence in humans might be influenced by the extent to which their particular vector or host populations are controlled by large vertebrate predators (Ostfeld and Holt 2004). Many diseases are carried by rodents (Ostfeld and Holt 2004), and since many rodent populations are controlled by their predators (Hanski et al. 2001), incidence of human diseases such as hantavirus, monkeypox, typhus, bubonic plague, and hemorrhagic fever might be strongly influenced by the presence or absence of large predators.

The evidence that large vertebrates play disproportionately important and heretofore unrecognized roles in ecosystems—from controlling species diversity to buffering climate change to affecting human health—and the realization that these roles have been largely absent in the majority of ecosystems since the late Pleistocene should elicit concern over the general failure of ecologists and conservation biologists to include large vertebrates and ecological history in their visions for restoration ecology. Pleistocene rewilding offers an experimental framework to better understand the biology of a continent that vanished 13,000 years ago, while simultaneously providing evolutionary, conservation, economic, and cultural incentives and benefits.

Evolutionary and Conservation Benefits of Pleistocene Rewilding

Cultural conventions dictate which taxa are regarded as native and which are not, usually irrespective of ecological and historical insights (Donlan and Martin 2004; Martin 2005a). In North America, we routinely turn to the Columbian landfall of AD 1492 as a de facto restoration baseline (Leopold et al. 1963), thereby discounting significant earlier ecological impacts by humans (Martin and Szuter 1999; Kay and Simmons 2002). The late Pleistocene arrival of the very first Americans (Haynes 2002) and the contemporaneous extinctions constitute a less arbitrary benchmark that is justifiable from multiple perspectives. Ever more evidence points to early humans having precipitated the late Pleistocene extinction events across multiple landmasses (MacPhee 1999; Barnosky et al. 2004; Lyons et al. 2004; Burney and Flannery 2005; Martin 2005b; Miller et al. 2005; Robinson et al. 2005). Such attestation also raises important ethical questions regarding our conservation benchmarks and strategies.

Before the late Pleistocene extinctions, mammal body-size distributions were remarkably similar across all continents despite little overlap in species composition (Smith

et al. 2004). The subsequent extinction of most large mammals in Australia and the Americas drastically altered those distributions to favor smaller taxa (fig. 2; Lyons et al. 2004). Given that body size is highly conserved across taxa (Smith et al. 2004), these losses are significant with respect to ecological and evolutionary processes, particularly in the Americas, where the losses were greatest (Janzen and Martin 1982; Purvis et al. 2000; Guix et al. 2005; Terborgh 2005; Donlan et al., forthcoming).

While evolutionary perspectives have become a part of some conservation planning (Frankel and Soulé 1981; Erwin 1991), they have usually emphasized conserving existing processes (Woodruff 2001; Ashley et al. 2003) rather than restoring recently extinct interactions (Martin 1999; Martin and Burney 1999; Atkinson 2001; Burney et al. 2002). The bold actions needed to preserve evolutionary potential in the wake of global change and the drastic decline in biodiversity generally have not been addressed. Africa and parts of Asia are now the only continents where megafauna remain relatively intact, and the loss of some of these species within this century seems likely (Balmford et al. 2001; Marchant 2001; Gros 2002; Blake and Hedges 2004; Thomas et al. 2004a). The widespread disruptions of population dynamics and of the potential for adaptive responses to climate change suggest that without significant conservation interventions, the speciation of large vertebrates on a global basis is largely over (Soulé 1980). Must we accept this prospect, or shall we take responsibility for partially restoring that potential? Given the demonstrable extinction risks for the Earth's remaining megafauna and the possibility that North American sites could serve as additional refugia to help preserve that evolutionary potential, regional rewilding (Soulé and Noss 1998; Foreman 2004) carries global conservation implications.

The most straightforward conservation advantage of Pleistocene rewilding would be to enhance the persistence of endangered large vertebrates with a multicontinent system of reserves inspired by evolutionary and ecological history. This has been a positive approach to the conservation of rare species, as illustrated by the reintroduction of Przewalski horses (*Equus caballus przewalski*) from North American and European zoos to a semiwild state in their native habitats in central Asia. Additional viable populations could also enlarge the possibilities for adaptation by target species to global change as well as provide the selective regimes that have fostered existing genotypes. Range fragmentation arguably might provide opportunities for speciation, but that potential "positive" effect on biodiversity is surely countered by the threat of small population size, failure to adapt, and stochastic extinction.

In a general sense, Pleistocene rewilding could be part of a movement to transform conservation biology, which

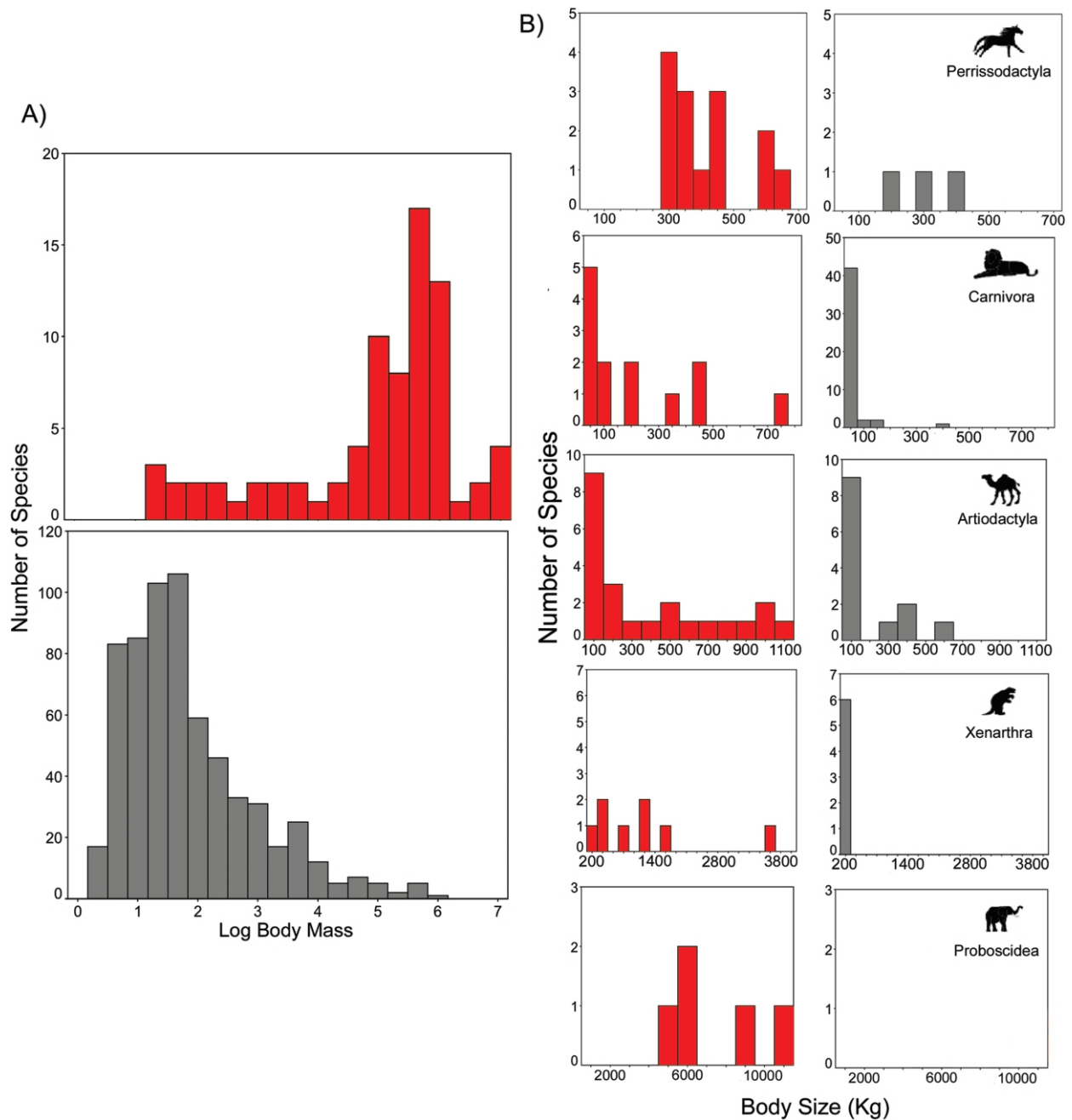


Figure 2: A, Body size distributions (log body mass) of terrestrial North American mammals (including bats) that did (red) and did not (gray) become extinct during the late Pleistocene (LP) extinctions (north of the Isthmus of Tehuantepec). B, Body size distributions (kg) of five large-bodied (>44 kg) taxonomic groups before and after LP extinctions. Extant distribution of Perissodactyla includes Old World horses and burros. Modified from Lyons et al. 2004.

is currently too easily characterized as a “doom and gloom” discipline (*The Economist* 1997; Myers 2003) because we have acquiesced to a default goal of exposing and merely slowing the rate of biodiversity loss. Together these attributes minimize excitement for conservation and even

actively discourage it (Redford and Sanjayan 2003). Moving away from managing extinction and toward actively restoring ecological and evolutionary processes using Pleistocene history as a guide provides an exciting new platform for conservation biology.

Cultural and Economic Benefits of Pleistocene Rewilding

Humans probably were responsible to some significant degree for late Pleistocene extinctions in North America and elsewhere (Martin 1966, 2005*b*; Martin and Steadman 1999; Lyons et al. 2004; Burney and Flannery 2005; Miller et al. 2005; Robinson et al. 2005; Steadman et al. 2005; Surovell et al. 2005). Our subsequent activities have curtailed survival prospects and evolutionary potential for most large vertebrates on regional and global scales, through persecution and habitat fragmentation and the subsequent effects of both on population genetic attributes (Soulé 1980). For these reasons, as well as for the sake of future human generations and the earth's biota, citizens and scientists bear an ethical responsibility to vigorously redress these problems insofar as possible (Ehrlich 2001).

Humans have strong emotional and cultural relationships with large predators and herbivores that began in the Pleistocene and have reached forward to contemporary times (Shepard 1998; Quammen 2003; Peacock and Peacock 2006). Ancient rock art, cars and sports teams named after large mammals, and conservation programs centered on large animals are evidence of our fascination with charismatic megafauna. Between 1999 and 2004, more than 1.5 million people per year visited San Diego Zoo's Wild Animal Park to catch glimpses of large mammals (C. Simmons, personal communication). Only 12 United States national parks received more than 1.5 million visitors in 2000 (National Park Service 2000). Alarming, per capita visitation to United States national parks has been declining since 1987—the first time since the 1930s (Pergams et al. 2004).

Pleistocene rewilding would probably increase the appeal, social benefits, and economic value of both private and public parks and reserves. The reintroduction of wolves to Yellowstone National Park has resulted in significant benefits; total economic and social benefits are estimated to be on the order of \$6–\$9 million per year, in contrast to an estimated annual cost of \$0.5–\$0.9 million to society (Duffield and Neher 1996; Reed 2004). Even the possibility of catching a glimpse of a wolf in Yellowstone National Park improves and contributes to the anticipation, authenticity, and enjoyment of a tourist's wild experience (Montag et al. 2005). A public understanding of ecological and evolutionary history, inspired by tangible aesthetic experiences with megafauna, would strengthen overall support for the conservation of biodiversity and wilderness (Dayton 2003; Greene 2005).

Exemplar Taxa

We envision a continuum of stages of Pleistocene rewilding starting today and moving toward the coming century with

a suite of potential conspecifics and proxy taxa (table 1). All differ in their potential costs and benefits, and all are already present in the United States either as free-roaming populations or in a captive setting. All potential restoration programs would be experimental, science driven, and evaluated from a cost-benefit perspective. We start our discussion with two taxa that have been successfully reintroduced to North America, move on to species that are present in North America but are viewed as nonnative species, and end with potential proxy species that could replace some of our lost Pleistocene megafauna. While this is not an exhaustive list, these selected taxa exemplify the central issues for discussions of Pleistocene rewilding.

The North American Peregrine Falcon

Celebrated as one of the most successful conservation efforts, the North American peregrine falcon (*Falco peregrinus*) has been saved from near extinction caused by DDT contaminants (Cade and Burnham 2003). The widespread recovery program relied on large numbers of captive-bred birds. Because of a lack of genetically more appropriate founders, falcons that were released into the eastern and midwestern United States and parts of Canada came from captive stock of seven subspecies from North America, Europe, South America, and Australia, totaling more than 2,500 birds (Tordoff and Redig 2001). Despite substantial morphological and ecological variation among the founders, there were no differences among subspecies in subsequent breeding success of the reintroduced birds (Tordoff and Redig 2001). Falcons from four continents now serve as a collective proxy for the midwestern peregrine population that became extinct in the 1960s. The peregrine falcon not only serves as a testament that species recovery can succeed on continental scales, but it also demonstrates that, at least in some cases, taxon substitutions are culturally acceptable as a powerful conservation tool.

Giant Vultures

The California condor (*Gymnogyps californianus*) was present throughout North America until the late Pleistocene and then disappeared across most of its range, along with the megafauna on which it fed. Condors survived solely along the West Coast, relying heavily on carcasses of marine mammals (Chamberlain et al. 2005), and they last roamed over the Grand Canyon 10,000 years ago, where they scavenged on North American mammoths (*Mammuthus* sp.), horses, camels, and other extinct taxa (Emslie 1987). Condors may have returned briefly to the southwest United States in the 1700s, in response to the introduction of domesticated cattle, horses, and sheep, but

Table 1: Magnitude of biodiversity loss of North American megafauna (north of the Isthmus of Tehuantepec) and potential benefits and costs of Pleistocene rewilding

Order or family	LP	Current (T/E)	Proxy ^a	Ecological benefits	Ecological costs	Economic benefits	Economic costs	Ease of establishment	Popularity
Predators:									
Felidae	13	8 (3)	Cheetah	Predation ^b	?	Tourism	Fencing; livestock mortality? ^c	++	+++
			Lion	Predation	?	Tourism; hunting	Human conflict	++	+++
Ursidae	6	3 (2)							
Canidae	9	8 (3)							
Herbivores:									
Xenarthra	14	6 (2)							
Bovidae	13	5 (2)							
Equidae	11	0	Equids	Seed dispersal; prey ^d	Potential overgrazing	Tourism	Fencing; compete with cattle	+++	++
Cervidae	10	6							
Antilocapridae	6	1							
Proboscidea	5	0	Elephants	Heterogeneity; seed dispersal ^e	Density- and scale-dependent effects	Tourism; hunting	Fencing	+	+++
Camelidae	4	0	Camels	Heterogeneity; seed dispersal ^f	Potential overbrowsing	Meat, fiber production	Fencing	+++	++
Tapiridae	4	1							
Tayassuidae	3	1							
Hydrochoeridae	2	0							
Castoridae	2	1							
Testudinidae	4	0	Bolson tortoise	Heterogeneity ^g	None/slight	Tourism	None	+++	+
Total	106	40 (10)							

Note: The table displays Late Pleistocene (LP) and current diversity of continental, large-bodied North American mammalian orders and families and some potential species proxies. The “Current” column excludes insular taxa. Extant species in each taxon are significantly biased toward smaller body size (Lyons et al. 2004). T/E = threatened or endangered, listed by United States Endangered Species Act or in the International Union for Conservation of Nature and Natural Resources 2001 Red List category “Near Threatened” (or equivalent 1994 categories “LR-cd” or “LR-nt”). A plus sign represents an increase in respective qualitative category.

^a Potential proxies. Camel: *Camelus dromedarius*, *Camelus ferus*, *Lama guanicoe*, *Vicugna vicugna*; equid: *Equus caballus*, *Equus przewalski*, *Equus hemionus*; cheetah: *Acinonyx jubatus*; lion: *Panthera leo*; elephant: *Elephas maximus*, *Loxodonta africana*; Bolson tortoise: *Gopherus flavomarginatus*.

^b Predation on mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) would be limited latitudinally by climate.

^c Work in Namibia has demonstrated coexistence with ranchers and cheetah through education and alternative pastoral practices (Marker et al. 2003b).

^d Janzen and Martin 1982; Berger 1986; Barlow 2000.

^e Janzen and Martin 1982; Barlow 2000; Whyte et al. 2003; Western and Maitumo 2004.

^f Barlow 2000; Hare 2001.

^g Kaczor and Hartnett 1990.

the validity of those records is unclear (S. Emslie, personal communication; L. Kiff, personal communication; *Federal Register* 1996); nonetheless, by the time European settlers arrived, *Gymnogyps* was found only in a narrow Pacific coastal strip. The National Park Service set a precedent for pre-1492 benchmarks with the repatriation of condors to the southwestern United States. Because of captive breeding programs and active interventions, condors now soar over Colorado River canyons. While this program is unsustainable without active management (slaughtered cattle carcasses are provided as a food source), few would argue against efforts to save and establish new condor populations, costs notwithstanding (Snyder and Snyder 2000; Beissinger 2001). By returning the large herbivores and their carnivores that collectively once fed these giant scavengers, California condors could perhaps become viable without the management costs currently endured.

An Extant Endangered Turtle

The Bolson tortoise (*Gopherus flavomarginatus*) was probably widely distributed across the Chihuahuan Desert until the late Pleistocene (Van Devender et al. 1976; Bury et al. 1988). Weighing up to 50 kg and susceptible to human overkill, the Bolson tortoise disappeared from more than 90% of its range by the end of the Pleistocene; today it is critically endangered and found only in a small area in central Mexico (Morafka 1982; Morafka and McCoy 1988). Chelonians were part of the exploited Pleistocene megafauna in the American Southwest and elsewhere (Moodie and Van Devender 1979; Taylor 1982; Stiner et al. 1999). Harsh winters could have played a contributing role in their decline (Van Devender et al. 1976; Moodie and Van Devender 1979), but *G. flavomarginatus* is relatively cold tolerant, as evidenced by a reproducing captive population in southeast Arizona (Appleton 1978).

An earlier proposal to reintroduce the tortoise into Big Bend National Park (Aquirre and Adest 1991) was rejected by the National Park Service on the basis that, notwithstanding its endangered status, *G. flavomarginatus* is a non-native species (Houston and Schreiner 1995). This conclusion is counter to ecological and historical insights and inconsistent with subsequent restoration of California condors to the Grand Canyon (Donlan and Martin 2004). Along with providing conservation benefits for the species, tortoise reintroductions to the southwestern United States might increase local biodiversity by promoting landscape heterogeneity via burrow construction (Kaczor and Hartnett 1990). Repatriating the continent's largest surviving temperate terrestrial reptile could precipitate a variety of ecological, evolutionary, economic, and cultural benefits, with no apparent costs (table 1).

Equids

Feral equids (*Equus caballus*, *Equus asinus*) have been abundant in North America since they were introduced by Europeans five centuries ago (Berger 1986). From an evolutionary and ecological perspective, equids are native to North America, where they were present for most of the last 50 million years, interacting strongly with a variety of grass species. Some lineages later spread to Eurasia, and they were diverse globally until the late Pleistocene (Stebbins 1981; MacFadden 1992; Oakenfull and Clegg 1998). Today, feral horses and burros in North America are widely viewed as ecological pests (Houston and Schreiner 1995), but the former are conspecific with late Pleistocene North American horses and the latter are representative of the "stenoid" lineage of *Equus* (asses and zebras) that originated in the New World and persisted there until the end of the Pleistocene (Vilà et al. 2001; Weinstock et al. 2005). On the basis of molecular systematic studies (Weinstock et al. 2005), *E. caballus* is arguably as similar to late Pleistocene North American horses as the aforementioned peregrine falcons from five continents and the contemporary populations of California condors are to their respective Pleistocene ancestors. Both horses and burros, and perhaps other extant Old World equids, are plausible taxonomic and ecological proxies for extinct New World taxa (Martin 1970; Donlan and Martin 2004).

Although the ecological impacts of feral horses are variable (Berger 1986; Levin et al. 2002; Menard et al. 2002), they disperse large-seeded plants and thus may compensate for certain large Pleistocene mammals now absent in North America (Janzen 1981, 1982; Janzen and Martin 1982). Moreover, wild asses (e.g., *Equus hemionus*) and Przewalski's horses are critically endangered or extinct in the wild (Moehlman 2002), so free-roaming North American populations would help curtail extinction and further repatriate equids to their evolutionary homeland. Przewalski's horse coexisted with humans and domesticated livestock in the Dzungarian Basin for millennia before its decline, which has been attributed to elevated livestock densities and military activity (Ryder 1993). The overall landscape impacts of free-living equids in North America could be positive or negative in local ecological and economic contexts, depending on temporal and spatial dynamics (Zervanos 1998; Levin et al. 2002; Kuiters 2003; Beaver and Brussard 2004; Zalba and Cozzani 2004). A potentially important factor in the overall context for free-ranging horses is the presence of predators (Turner et al. 1992), including the experimental introduction of lions.

Camelids

The center of camelid evolution was North America, where four species of camels and llamas were present in the late

Pleistocene (Kurtén and Anderson 1980; Honey et al. 1998; Smith et al. 2003b). Today, two species of Old World camelinines and four species of South American lamalinines are extant globally. Wild Bactrian camels (*Camelus bactrianus*) are on the verge of extinction, with fewer than 1,000 free-living animals remaining in Asia (Hare 2001). Domestic or captive-bred camelids could be introduced to parts of North America, further assuring their semiwild persistence and serving as ecological proxies for extinct late Pleistocene lamalinines (e.g., *Camelops*; Webb 1965; Honey et al. 1998).

Camelids potentially offer biodiversity benefits to arid and semiarid North American ecosystems by browsing on woody species that now often dominate areas that formerly were mixed desert scrub and grassland (table 1; Martin 1969; Van Auken 2000; Mengli et al., forthcoming). In the 1850s, when Lieutenant Beale successfully led the Camel Military Corps from Texas to California, his animals browsed on creosote (*Larrea tridentata*) and other brush species that today dominate many southwestern landscapes (Connelly 1966; Martin 1969). In Australia, largely anecdotal evidence indicates that large numbers of feral camels appear to be having an unfavorable ecological impact in the Northern Territory, where they are not supported by ecological history (Edwards et al. 2004); however, in eastern Australia, camels are being used as browsers to counter the invasion of unwanted leguminous shrubs (F. Keenan, personal communication). Experimental introductions of camels to the southwestern United States offer unique research opportunities to gain insights into the ecology of interactions between large herbivores and grasslands—interactions that were present in North America since the Miocene and ended just 13,000 years ago (Stebbins 1981).

Camelids might bring economic benefits to North America as well; in Australia, well-managed cograzing programs of cattle and camels have brought meat, milk, and fiber to market without negatively affecting cattle production (Phillips et al. 2001). Organized trekking with camelinines and lamalinines, long popular in Australia, is already present in the United States (e.g., <http://www.texascamelcorps.com>). Camelids thus exemplify how managed reintroductions could demonstrate benefits and costs of Pleistocene rewilding under carefully controlled, experimental conditions.

Cheetahs

The extinct Plio-Pleistocene North American cheetahs (two species of *Micracinonyx*), extant Old World cheetah (*Acinonyx jubatus*), and puma (*Puma concolor*) are closely related, but the most recent molecular phylogenetic data are controversial in terms of whether Old and New World

cheetahs are each other's closest relatives (Barnett et al. 2005; Johnson et al. 2006). The extent to which resemblances between those two cursorial lineages represent homology or convergence remains uncertain, although anatomically the Old World cheetah is somewhat more specialized than was its extinct New World relatives (Van Valkenburgh et al. 1990). In any case, North America cheetahs arguably were the principal agent influencing selection for speed and visual acuity in the pronghorn antelope (Byers 1997), and perhaps the Old World cheetah could replace those extinct cats as an ecological proxy.

The Old World cheetah was once widespread in Africa and Asia; today, the species' distribution has been greatly reduced, and it has only a modest chance of persisting in the wild into the next century (Caro 1994; Gros 2002). Breeding programs are not self-sustaining and wild populations continue to sustain captive ones (Marker-Kraus 1997). Some of the more than 1,000 animals in captivity (Caro 1994; Marker-Kraus 1997) could be used to establish an experimental free-living North American population. Conservation scenarios for cheetahs are unique in that the majority of the remaining individuals are located outside of protected areas, commonly on farmland for commercial livestock and game (Caro 1994; Marker et al. 2003b). Most (~90%) of Namibia's cheetahs live on commercial livestock farmland, where lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) have been eliminated (Marker et al. 2003a). While farmers often perceive cheetahs as threats and persecute them, environmental education and alternative pastoral practices have recently promoted coexistence with humans (Marker et al. 2003b).

Cheetah populations in the southwestern United States could potentially facilitate economic alternatives to ranchers through ecotourism, with little cost to other ranching revenue streams (table 1). Restoring cheetahs to North America could also reinstitute what must have been strong interactions with pronghorn antelopes and perhaps help save the world's fastest land mammal from extinction. One intriguing anecdote hints that the pronghorn's speed and tactics for escaping a cheetah have not been entirely lost: "In the 1930s, I saw a man traveling with a pet cheetah turn it loose to pursue a pronghorn, a young female, until she sailed over a deep ravine that the big cat refused to negotiate" (Frison 2004, p. 124).

Proboscideans

Five species of proboscideans roamed North America in the Pleistocene (Kurtén and Anderson 1980; Smith et al. 2003b). Asian elephants (*Elephas maximus*) are more closely related to North American mammoths (i.e., *Mammuthus primigenius*) than they are to African elephants (*Loxodonta africana*; Krause et al. 2006; Poinar et al. 2006;

Rogaev et al. 2006). African and Asian elephants play key-stone roles as megaherbivores (Owen-Smith 1988; Dublin 1995), just as mastodons, mammoths, and gomphotheres surely once did in the Americas (Janzen and Martin 1982; Barlow 2000). Collectively, proboscideans may have even influenced the global carbon cycle by altering vegetation dynamics around 20 million years ago as they expanded out of Africa (Flannery 2006). Could extant elephant species play similar ecological roles to those that North American proboscideans occupied for millennia (fig. 1)? African elephants inhibit woodland regeneration and promote grasslands; elevated population densities appear to be the primary driver of woodland loss (Whyte et al. 2003; Western and Maitumo 2004). Encroachment of woody and shrub plant species over the past century now threatens the arid grasslands of western North America (Van Auken 2000). While the causes are complex and controversial (Brown et al. 1997; Van Auken 2000), browsing elephants might counter shrub and tree (e.g., *Prosopis*, *Juniperus*) invasion and increase landscape heterogeneity.

In the absence of cloned mammoths for restoration (Agenbroad 2005) and recognizing that extinct proboscideans were surely ecologically different in some ways from their extant relatives (Guthrie 2006), managed African and/or Asian elephants in North America could potentially enhance biodiversity and economically benefit ranchers through grassland maintenance and ecotourism (table 1). Further, many elephant populations, particularly in Asia and West Africa, are in grave danger of extinction (Blake and Hedges 2004), and captive breeding programs are not self-sustaining for either species (Olson and Wiese 2000; Wiese 2000; Rees 2003). Proboscideans played a variety of ecologically and evolutionarily significant roles across North American landscapes for millennia (Janzen and Martin 1982; Janzen 1986; Barlow 2000). With the appropriate resources and vision, using captive stock and some of the 16,000 domesticated elephants in Asia (Lair 1997) might reveal some of those roles and contribute to the wild future of these flagship species by initiating a North American repatriation.

Holarctic Lions

Lions, which prey on wild equids and other large herbivores, offer a bold and exciting vision for Pleistocene rewilding. Current molecular, morphological, and paleontological evidence suggests that the Holarctic lion should be treated as a single species (Burger et al. 2004; Yamaguchi et al. 2004) and that *Panthera leo* (sensu lato) perhaps was once the widest-ranging wild land mammal of all time (Kurtén and Anderson 1980).

Today, lions play a pivotal role in regulating prey populations in African savanna ecosystems (Sinclair et al.

2003), as they surely once did in the Americas and Eurasia. With their estimated population dropping from 76,000 to less than 40,000 over the past 20 years (IUCN 2006), African lions are increasingly threatened by habitat degradation, human conflict, reduction in prey base, and disease (Nowell and Jackson 1996; Roelke-Parker et al. 1996; Marchant 2001; IUCN 2006). The Asiatic lion (*Panthera leo persica*) is critically endangered, with a single population in the Gir Forest of India; establishing additional populations is vital for their long-term persistence, but recent attempts in India have failed (Nowell and Jackson 1996). However, lions have been reestablished or managed in African and Indian reserves that are of a size similar to some contiguous private and public lands in the western United States (e.g., Umfolozi Game Reserve, South Africa [96,000 ha], and Gir Forest, India [138,000 ha]; Anderson 1980; Saberwal et al. 1994). The idea of repatriating lions to North America merits a serious scientific debate.

Given the public's attraction to large predators, the potential aesthetic and economic benefits of restoring lions to North America are obvious—as are the challenges (table 1). An appropriate prey base would be a prerequisite. Another central dilemma lies in public acceptance of an animal that could cause human harm. While tourism-related deaths attributed to lions, elephants, and other large mammals in South Africa are rare (Durrheim and Leggat 1999), local human-lion conflicts (including deaths) are serious problems in some other parts of Africa and India (Saberwal et al. 1994; Packer et al. 2005). Mitigating for human-carnivore conflict is by no means a new conservation challenge (Saberwal et al. 1994; Treves and Karanth 2003), and it is clear that the momentous obstacles would have to be overcome with a detailed, science-based management and education program (Packer et al. 2005) before lions could be restored to North America.

Nevertheless, models of carnivore repatriation exist, with goals ranging from the simple placement of carnivores back into communities for public viewing to the instigation of ecologically functional relationships. For instance, at least 173 discrete introductions of predatory carnivores have occurred globally (Reading and Clark 1996; Gittleman and Gompfer 2001), with at least those of cheetahs and lions in African reserves being demographically successful and reinstilling normative behavior in their ungulate prey (Hunter and Skinner 1998), as has happened with grizzly bears and wolves in the Yellowstone region (Pyare and Berger 2003).

Success in reintroducing large, dangerous carnivores depends on the critical question of reserve size. If reintroduced carnivore populations are at a density that minimizes their chances of extinction, at least a threshold of recovery will be reached. However, problems may persist if reserves are small, whether unfenced or fenced to protect

humans or economic interests beyond reserve boundaries. If carnivores are not provided with supplemental food, prey might be harvested at unsustainable rates, perhaps leading critics to dismiss the plan to restore a functional ecological relationship and claim that the reserve is nothing more than a large zoo. However, differences among types of reserve—zoo, small protected area, big protected area, or large functioning system—are a matter of spatial gradation and choice of a management goal. Our view of rewilding is to begin modestly. Some private South African game parks with reintroduced lions have now attained sizes between 15,000 and 75,000 ha, smaller than some large ranches in southwestern North America.

Risks, Costs, Challenges, and Objections to Pleistocene Rewilding

Legitimate and potentially serious objections to Pleistocene rewilding must be faced objectively, with all available information and within a cost-benefit context that includes the aforementioned ecological, evolutionary, economic, aesthetic, and ethical considerations. We must first ask whether a pre-1492 benchmark for conservation is realistic in our current world and for the foreseeable future. There are many emerging ecological and anthropological arguments against using a Columbian benchmark (Jackson 1997; Kay and Simmons 2002; Donlan and Martin 2004; Martin 2005*b*), yet temporal scales of restoration and baselines have received little debate (but see Gobster and Hull 2000; Callicott 2002). Nonetheless, the recent restoration of condors to Arizona suggests that a late Pleistocene benchmark warrants consideration, and it counters objections that attempts to bring back megafauna are a futile waste of precious conservation dollars. Obviously, a Pleistocene benchmark is not appropriate for much of North America, but we argue that it should be debated, particularly in areas where establishment of reserves may be a real possibility.

There are a number of key issues to be considered when discussing Pleistocene rewilding. The proposed megafaunal components often differ from their extant conspecifics or related proxies, underscoring the importance of carefully framing the choice of restoration taxa in terms of specified goals. For example, Old World conspecifics or ecological proxies may be considerably smaller than their extinct North American counterparts (e.g., 162 kg vs. 400 kg for the lion, 50 kg vs. 88 kg for the cheetah; Smith et al. 2003*a*). What role does nutrition play with respect to differences in observed body size? Do mass differences result in different ecological function, and would such differences be more pronounced and/or important for herbivores, where body size is known to influence forage selection and utilization (Gwynne and Bell 1968; Calder

1984; Owen-Smith 1988; Murray and Brown 1993)? Along with concerns about body size will come questions and objections regarding genetics. How genetically different were Pleistocene cheetahs, lions, elephants, and horses from extant populations? With the rapidly advancing field of paleogenomics, these questions are being increasingly answered (Weinstock et al. 2005; Johnson et al. 2006; Poinar et al. 2006), comprising one of multiple factors to inform decisions regarding the use of taxon substitutions. The case of the peregrine falcon illustrates how such questions can be addressed in the context of specific conservation objectives.

Careful studies of potential proxies and their ecological roles need to be undertaken (Simberloff 1990; Atkinson 2001). Thus far, extinct taxa cannot be restored, so the costs, benefits, and even legalities (Rees 2001) of reintroductions and taxon substitutions deserve much more detailed scrutiny in conservation philosophy and planning if the goals of conservation are the restoration of ecological and evolutionary processes (Atkinson 1998, 2001). While the idea of using taxon substitutions as a conservation tool is gathering attention (Nicholls 2006), many aspects of the use of ecological proxies remain unexplored. Aspects such as phylogenetic relatedness, ecological function, and the conservation value of proposed proxies are in need of widespread discussion. That said, we foresee that taxonomic substitutions will become increasingly important on both continents and island archipelagos as habitats are protected and restored (Atkinson 2001; Steadman and Martin 2003). Objections to the costs and goals of using ecological proxies may be mitigated by successful projects such as the peregrine falcon, the North African red-necked ostrich (*Struthio camelus camelus*) as proxy for the Arabian ostrich (*Struthio camelus syriacus*; see Sedon and Soorae 1999), night herons, and giant land tortoises.

In Bermuda, the yellow-crowned night heron (*Nycticorax violacea*) was introduced in the mid-1970s as a proxy for a closely related endemic night heron (*Nycticorax* sp.) that was extirpated in the seventeenth century (Wingate 1982; Olson et al. 2005). The established breeding population subsequently exhibited top-down control on land crabs (*Gecarcinus lateralis*), which are a major prey species of night herons; before the heron introduction, the crabs were exceptionally abundant and the cause of economic damage (Wingate 1982). Restoration on Bermuda, particularly on Nonsuch Island, exemplifies a holistic conservation approach that embraces ecological history (Wingate 1985); it also highlights the need to factor and integrate both historical and present ecological states into conservation planning and action (Davenport et al. 2001).

Under an experimental framework, scientists from the Mauritian Wildlife Foundation are using giant tortoises from Aldabra Island (*Aldabrachelys gigantea*) as ecological

proxies for the two extinct species of the Mascarene Islands (*Cylindraspis inepta* and *Cylindraspis triserrata*). Tortoises were first introduced into enclosures on Ile aux Aigrettes, and now, tortoises roam free on the island, resulting in both increased seed dispersal and tourism (Jones 2002; V. Tatayah, personal communication). Tortoise proxies are effective at dispersing seeds for the endangered tree *Syzygium mamillatum*, whose native seed dispersers are extinct (D. Hansen, personal communication). These giant tortoise proxies appear to be restoring the broader functional role of their extinct relatives in the Mascarene archipelago, along with providing economic benefits.

While using ecological history as a conservation guide is not a new concept, our recent brief exposition (Donlan et al. 2005) elicited substantial positive and negative reactions from diverse sectors (Kristof 2005; Nicholls 2006; Stolzenburg 2006). The criticisms of Pleistocene rewilding generally focused on opportunity, costs, and uncertainty (Chapron 2005; Dinnerstein and Irvin 2005; Schlaepfer 2005) rather than on benchmark selection, taxon substitutions, and other core conceptual issues. We believe that all conservation initiatives must be evaluated relative to potential costs and benefits. Furthermore, conservation dollars are often nontransferable, and novel initiatives often generate new funding sources. We do not advocate Pleistocene rewilding as a substitute for or priority over ongoing and successful conservation projects in Africa or North America. Our proposal instead centers on restoring ecological function to North America, although it does carry implications for the global conservation of Earth's remaining megafauna.

Other objections to Pleistocene rewilding (Schlaepfer 2005; Smith 2005) include the possibility of catastrophic disease transmission (e.g., Dazak et al. 2000), the fact that habitats have not remained static since the end of the Pleistocene (e.g., Davis and Shaw 2001), and unexpected ecological consequences of species introductions, as viewed from an invasive species perspective (e.g., Roemer et al. 2002). Preventing disease transmission and the disease ecology associated with reintroductions in general will be a premier concern. Precautions and protocols will be needed and implemented, just as they are advocated for other reintroduction and translocation programs (Viggers et al. 1993; Cunningham 1996). The temporal dynamics of habitats are well established; the ecological implications for conservation depend on temporal and spatial scales. While vegetation communities have shifted and changed before and after the late Pleistocene, the major missing component in contemporary ecosystems is large vertebrates. Very few plants and small mammals suffered extinction during the late Pleistocene (Jackson and Weng 1999; Lyons et al. 2004).

The taxa we discuss differ critically when compared to

nonnative species that have wreaked ecological havoc in many ecosystems (e.g., rabbits in Australia and rats on islands). The proposed taxa are supported by ecological history and the fossil record, and in some cases, they recently were present in North America; they also have low reproductive rates and thus are more easily managed. Nonetheless, unexpected ecological consequences are a legitimate concern. For example, large carnivores typically depress mesopredator abundance, thus potentially favoring their rodent prey and thereby, under some conditions, potentially increasing the incidence of various human diseases (Ostfeld and Holt 2004; Karesh and Cook 2005). These are problems that must be addressed in advance by sound research, prescient management plans, and informed public discourse for each species on a case-by-case and locality-by-locality basis. Well-designed, hypothesis-driven field experiments will be needed to assess the impacts of potential introductions before large-scale releases take place. Monitoring programs that include a suite of objectives will be required, including designs that capture multiple levels of biodiversity dynamics, spatial and temporal heterogeneity, and other holistic measures of ecosystem health. All of these concerns hinge on insights into ecological history, from the late Pleistocene and beyond (Martin 1969, 1970; Estes 2002; Donlan and Martin 2004; Donlan et al. 2005; Terborgh 2005).

Some will argue that Pleistocene rewilding is simply not feasible, either ecologically or socially. For example, Smith (2005) suggested that camels used in the Camel Military Corps of the mid-1800s failed to survive in the deserts of the southwestern United States and thus that reintroduction attempts now would probably fail. While the Camel Military Corps failed as a military project (largely for political reasons; Connelly 1966), the camel demonstrated remarkable adaptability to the American southwest. Lieutenant Beale wrote in 1857, while moving through Texas and Arizona, "It is certainly gratifying to find these animals eating, by their own preference, the coarse and bitter, hitherto of no value, which abound always in the most sterile and desolate parts ... with all this work they are perfectly content to eat anything, from the driest greasewood bush to a thorny prickly pear" (Martin 1969, p. 37). Not only are experimental camel introductions feasible, they could shed light on the possibility of camels refilling the niche that they once occupied in the late Pleistocene.

While we encourage a detailed analysis of the claim that Pleistocene rewilding would negatively affect Africa's ecotourism sector and thus cripple conservation there if North Americans choose instead to see large animals on their own continent (Bosire 2005), no evidence supports that concern. In Africa, international tourism receipts in 1999 and 2000 were approximately US\$10–\$11 billion annually,

and in 1999, only 4.1% of African tourist arrivals were from the Americas, while 58% of the arrivals were inter-regional, and 38.3% were European (World Tourism Organization 2001). Perhaps more importantly, foreign ecotourism is beyond the economic means of most United States citizens, and those who do travel to Africa are apparently seeking something more than just lions eating equids: “There are unique places and natural attractions that few other regions can match. This is true not only for its natural resources but also for its culture, traditions, and customs. Therein lies the greatest fascination of what African destinations have to offer” (World Tourism Organization 2001).

Much knowledge and experience can be gained from Africa that will aid efforts to establish Pleistocene rewilding. First, there is an optimistic perspective, in terms of the long-term feasibility of restoring megafauna. When it was established, Kruger National Park was hardly the celebrated mainstay of southern African biodiversity that it is today. In 1903, there were no elephants, 9 lions, 8 buffalo, and very few cheetahs within the boundaries of the park. One hundred years later, due to the vision and dedication of African conservationists, 7,300 elephants, 2,300 lions, 28,000 buffalo, and 250 cheetahs roamed Kruger, as do 700,000 tourists bringing with them US\$26 million annually (Chapman 1993). Practitioners and ecologists of Africa’s national parks could play pivotal roles in restoring large vertebrates to North America. Second, it provides models and case studies where ecotourism programs on private lands, many based on megafauna, have been successful in bringing economic and social benefits to poor rural communities (Ashley and Roe 2002; Mahony and Zyl 2002; Spenceley and Seif 2003).

With respect to local economic, political, and cultural interests (Schlaepfer 2005; Shay 2005), we argue that local incentives for stakeholders (economic, aesthetic, or otherwise) would be prerequisite for restoration success and that parts of the central and southwestern United States show special promise for Pleistocene rewilding (Donlan et al. 2005). Nearly 20 years after Deborah and Frank Popper proposed the Buffalo Commons (Popper and Popper 1987), a long-term native grass and wildlife restoration project, as a way to counter the boom-and-bust economic cycles that have visited the Midwest since the 1860s, residents are embracing the idea (contra Shay’s [2005, p. 476] claim that “local people overwhelmingly rejected the project”). Even former Kansas governor Mike Hayden, once a staunch opponent of the idea, now says, “The Poppers were right” (Charton 2004); a variety of private landowners, conservation organizations, and Native American groups have embraced the Buffalo Commons as a positive factor for improving the Midwestern economy and biodiversity (Popper and Popper 2004).

Implementing Pleistocene Rewilding

Pleistocene rewilding scales globally and is already under way on the fringes of the conservation community. All of these efforts are using ecological history as a guide to actively restore ecological and evolutionary processes rather than merely managing extinction. Using the fossil record as a guide, scientists are reintroducing endangered birds from Marquesas and Tongan islands to nearby islands that lack anthropogenic threats such as nonnative predators, thus making long-term persistence more likely (Burney et al. 2002; Steadman and Martin 2003). At the 6,000-ha nature reserve Oostvaardersplassen, The Netherlands, practitioners are restoring habitats with an emphasis on ecological history and process, including the use of contemporary proxy species such as Przewalski’s horses, roe deer (*Capreolus capreolus*), and Heck cattle (Vera 2000; Sutherland 2002). Beavers (*Castor fiber*) are being reintroduced throughout Europe to restore ecological processes and heterogeneity to landscapes; in some cases, the beavers and their associated community interactions have been absent for thousands of years (Gamborg and Sandøe 2004). By combining science and restoration driven by history, an international team of ecologists is moving forward on a bold plan to reintroduce large herbivores back to the Siberian steppe, including Yakutian horses, wood bison, and musk ox (Zimov et al. 1995; Stone 1998; Zimov 2005). Galetti (2004) has cogently argued for a similar vision in South America, as has Burney (2003) for Madagascar. All of these efforts are unprecedented opportunities to learn about the ecology and restoration of ecosystems and could provide important insights into when the reintroduction of large vertebrates can restore ecosystem function; alternatively, in some cases, plant restoration may prove as or more important to reach the desired conservation goal.

We envision several scenarios for Pleistocene rewilding in North America, and some of them are already under way. Equids, camelids, and other ungulates are increasingly prevalent on western landscapes, and there is widespread discussion of a Buffalo Commons in the Great Plains, with much restoration already being implemented (Popper and Popper 1999, 2004). Restoration of Bolson tortoises to ranches in southern New Mexico by the Turner Endangered Species Fund is currently under way (M. Phillips, personal communication). Experiments are urgently needed to assess the economic, ecological, and cultural implications of more widespread reintroductions of these and other herbivores. Large tracts of private and public lands in the southwestern United States (Mittermeier et al. 2003) are potentially appropriate for Pleistocene rewilding, using the fossil record and carefully designed research as guideposts and safeguards. Private lands probably

hold the most immediate potential; for example, more than 77,000 Asian and African large mammals (71 species) are present on Texas ranches (Schmidly 2002) although their significance in terms of conservation remains largely unevaluated and their landscape impacts unexplored.

Other projects could also begin immediately, with the experimental maintenance on private property of small numbers of cheetahs, lions, and elephants guided by experts from a variety of disciplines so the ecological impact and biology of these species can be studied. The requisite animals are present in the United States or can be readily produced by captive breeding; the primary logistical innovation at this point would be to provide them with securely enclosed landscapes and naturalistic selective regimes, including predator-prey relationships among herbivores and carnivores. This last point merits special emphasis since almost all captive animals in this country, even those in large outdoor confines, are largely shielded from naturalistic selective regimes. Whereas earlier considerations recommended an absence of planned directional selection (Frankham et al. 1986), recent experimental studies demonstrate that this is not the same as no selection (McPhee 2003). If captive animals are to have any realistic significance for conservation, other than for education and limited research (Robinson 2001), "humane" considerations need to be balanced with providing more natural lifestyles. That balance could stem from collaborative efforts and opportunities among zoo practitioners, animal welfare proponents, and ecologists. We envision that Pleistocene rewilding would be tackled on a species-by-species basis, with expert research groups for each taxon (e.g., cheetah) advising, implementing, and evaluating potential reintroduction programs.

A third and more ambitious scenario would be exemplified by an enormous ecological history park encompassing thousands of square miles in economically depressed parts of the Great Plains (Popper and Popper 1999). Secure game fencing, which can effectively mitigate conflict with humans (Hoare 1995), would limit the movements of free-living ungulates, elephants, and large carnivores, including lions. As in Africa and regions surrounding some North American national parks, nearby towns would benefit economically from land management and tourism-related jobs. The initiation and precise nature of each of these stages would depend on information derived from previous efforts, such that risks would be identified and negative effects minimized. Two prerequisites of critical importance are rigid adherence to established restoration protocols, including specification of goal criteria and monitoring regimes, and adequate incentives for local landowners and other stakeholders.

In the coming century, we will decide, by default or design, on the extent to which humanity tolerates other

species and thus the future of biodiversity. The default scenario will surely include ever more landscapes dominated by pests and weeds, the global extinction of more large vertebrates, and a continuing struggle to slow the loss of biodiversity. Pleistocene rewilding informs an optimistic, alternative conceptual framework that fundamentally challenges our views of nature and seeks to transform conservation biology from a reactive into a proactive discipline. The potential benefits of several proposed proxies have been outlined here. While sound science can help mitigate the risks of Pleistocene rewilding, the potential for unexpected consequences will worry many conservationists. Yet, given the apparent dysfunction of New World ecosystems and Earth's overall state, there are likely significant risks of inaction as well (see Springer et al. 2003 for a potential example). In the face of tremendous uncertainty, science and society must weigh the costs and benefits of Pleistocene rewilding against the equally uncertain, costly, and often obscure benefits provided by the prevailing conservation model—maintaining the status quo or, at best, retrieving something of the very recent past.

We ask those who find objections to Pleistocene rewilding compelling, are you content with the negative slope of our current conservation philosophy? Are you willing to risk the extinction of the remaining megafauna should economic, political, and climate change prove catastrophic for Bolson tortoises, cheetahs, camelids, lions, elephants, and other species within their current ranges? Are you content that your descendants might well live in a world devoid of these and other large species? Are you willing to settle for an American wilderness that is severely depauperate relative to just 100 centuries ago? We reiterate our earlier plea (Donlan et al. 2005) that, although the obstacles to Pleistocene rewilding are substantial and the risks are not trivial, we can no longer accept a hands-off approach to wilderness preservation as realistic, defensible, or costfree. It is time to not only save wild places but rewild and reinvigorate them.

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