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Pleistocene Park: Does re-wilding North America represent sound conservation for the 21st century?

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ABSTRACT

A group of conservation biologists recently proposed to populate western North America with African and Asian megafauna, including lions, elephants, cheetahs, and camels, to create a facsimile of a species assemblage that disappeared from the continent some 13,000 years ago. The goals of this program, known as "Pleistocene re-wilding", are to restore some of the evolutionary and ecological potential that was lost from North America during the Pleistocene extinctions, and help prevent the extinction of selected African and Asian mammals. Pleistocene re-wilders justify this conservation strategy on ethical and aesthetic grounds, arguing that humans have a moral responsibility to make amends for overexploitation by our ancestors. They believe that the flora of many North American terrestrial ecosystems has gone basically unchanged since the end of the Pleistocene, so re-wilding would help restore evolutionary and ecological potential and improve ecosystem functioning. This paper discusses some of the pros and cons of this proposal, including the ethical, aesthetic, ecological, and evolutionary issues, assesses its potential economic and political impacts on other conservation practices, both in North America and elsewhere, and reviews the realities of large mammal reintroductions. It is concluded that Pleistocene re-wilding with exotic species will not restore the evolutionary or ecological potential of native North American species nor extinct Pleistocene megafauna and their ancient ecosystems, but may instead jeopardize indigenous species and North American ecosystems. Resources would be better spent on preserving threatened organisms in their native habitats and reintroducing them to places in their historical ranges from which they were only recently extirpated.

1. Introduction

Ancestors of elephants and lions once roamed much of North America (Martin, 1984). Recently, a diverse group of conservation biologists has proposed to create a facsimile of this bygone era by reintroducing charismatic African and Asian megafauna to western North America to replace species that disappeared during the Pleistocene extinctions, some 13,000 years ago (Donlan et al., 2005). Arguing that their vision is justified on "ecological, evolutionary, economic, aesthetic and ethical grounds", Donlan et al. (2005) believe that modern "Pleistocene Parks" would provide refuges for species that are themselves threatened or endangered, and that repopulating the American west with these large mammals would

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improve local landscapes, restore ecological and evolutionary potential, and make amends for the ecological excesses of our ancestors.

To understand the uniqueness of this proposal, a terminological clarification is necessary. The "re-wilding" of ecosystems is the practice of reintroducing extant species (captive-bred or wild caught) back to places from which they were extirpated in historical times (i.e., in the past several hundred years). Because re-wilding deals with recently extirpated species and short evolutionary time scales, it is reasonable to assume that there have been minimal evolutionary changes in the target species and their native habitats. Re-wilding of ecosystems is not a new conservation practice and, indeed, it has become a standard management tool (Foreman, 2004).

By contrast, "Pleistocene re-wilding" of ecosystems is a revolutionary idea that would involve introducing to present-day habitats either (1) extant species that are descended from species that occurred in those habitats during the Pleistocene, but that went extinct about 13,000 years ago, or (2) modern-day ecological proxies for extinct Pleistocene species. Pleistocene re-wilding is thus a novel plan for ecological restoration on a more grandiose temporal and spatial scale than is re-wilding (Callicott, 2002).

Pleistocene re-wilding has been discussed for many years (Soulé, 1990; Martin and Burney, 1999), and in 1989, it was attempted in Siberia, Russia, when mega-herbivores including wood bison (*Bison bison athabascae*), Yakutian horses (*Equus* sp.), and muskoxen (*Ovibos moschatus*) were introduced in an effort to recreate the grassland ecosystem of the Pleistocene (Zimov, 2005). However, the North American Pleistocene re-wilding proposal of Donlan et al. (2005) is far more ambitious than this because it aims to reconstruct an ancient ecosystem by translocating a more diverse array of African and Asian megafauna to geographical regions and plant communities that have evolved without such creatures since the Pleistocene. Species targeted for introduction span several trophic levels and include predators such as African cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*), and large herbivores like African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants, various equids (*Equus* spp.), and Bactrian camels (*Camelus bactranus*) (Donlan et al., 2005). This plan includes animals that are both descendant species of extinct taxa and ecological proxies for extinct species.

Pleistocene re-wilding of North America has two principle goals: (1) to restore some of the evolutionary and ecological potential that was lost from North America 13,000 years ago; and (2) to help prevent the extinction of some of the world's existing megafauna by creating new, and presumably better protected, populations in North America (Donlan et al., 2005). Discussion of the proposal is just beginning (Soulé, 1990; Martin and Burney, 1999; Callicott, 2002; Foreman, 2004; Donlan et al., 2005) and, although some initial concerns have been raised (Chapron, 2005; Dinerstein and Irvin, 2005; Schlaepfer, 2005; Shay, 2005; Smith, 2005), supporters and detractors agree that Pleistocene re-wilding is a bold and innovative idea, deserving of careful consideration. This paper was developed with the intent of extending healthy and fruitful scientific debate about Pleistocene re-wilding of North America.

2. The ecology and evolution of Pleistocene re-wilding: restoring ecological potential to North American ecosystems

Although an ethical desire to redress the excesses of our ancestors might serve as an initial justification for Pleistocene re-wilding, the ecological and evolutionary merits of such a plan must be considered carefully. Pleistocene re-wilding of North America would involve a monumental introduction of large mammals into areas where they have been extinct for millenia, and into habitats that have existed without such creatures for similarly long periods of evolutionary time. The potential negative ecological effects of transplanting exotic species to non-native habitats are well-known (Mack et al., 2000). The results of Pleistocene re-wilding in North America are unknown and might well be catastrophic; ecosystem functioning could be disrupted, native flora and fauna, including species of conservation value (Smith, 2005), could be negatively impacted, and a host of other unanticipated ecological problems could arise.

Pleistocene re-wilders believe that it is possible to enhance ecological potential, that is, to recreate evolutionarily-relevant mammalian species assemblages and restore ecosystem functioning to Pleistocene levels, because they believe that the flora of North American ecosystems is essentially unchanged since the Pleistocene (Soulé, 1990; Donlan et al., 2005). However, plant communities are dynamic and constantly in flux, genotypically and phenotypically, and there has been over 13,000 years for grassland and shrub-steppe communities to evolve and plant assemblages to change in the absence of the full suite of Pleistocene mega-herbivores (Zazula et al., 2003). When managers discuss restoring ecological potential, or simply ecosystem restoration, it is important for them to be clear about what they are trying to restore and to what level of restoration they are trying to reach (Jordan et al., 1987). Whereas Pleistocene re-wilding could potentially increase the ecological potential of some of North America's ecosystems by reintroducing predators on species like pronghorn or bighorn sheep (and thus, indirectly restoring the *evolutionary* potential of these prey species), or by restoring herbivorous keystone species like elephants to the temperate grasslands, it is questionable whether it would restore ecological potential to Pleistocene levels.

Indeed, rather than restoring our "contemporary" wild ecosystems to the "historic" wild ecosystems of the Pleistocene and their original levels of ecosystem functioning, which are unknown, Pleistocene re-wilding could instead result in "re-wilded" novel, or emerging, ecosystems with unique species compositions and new or altered levels of ecosystem functioning (Hobbs et al., 2006) (Fig. 1). Biogeographic assemblages and evolutionary lineages would be co-mingled in novel ways; new parasites and diseases could be introduced (Viggers et al., 1993; Cunningham, 1996); and food chains would be disrupted. Moreover, without really knowing how Pleistocene ecosystems functioned, there will be no way to determine whether Pleistocene re-wilding restored ancient ecosystems or disrupted contemporary ones.

While the reintroduction of large grazers can, in some cases, shape and restore grassland ecosystems (Zimov et al., 1995), this will depend on whether the grazers are indigenous

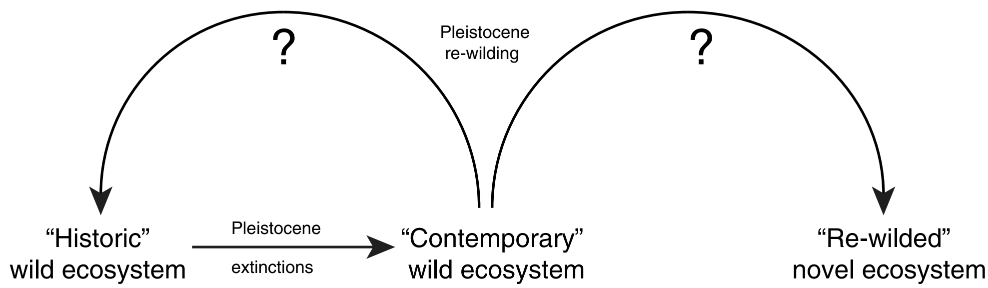

Fig. 1 – Re-wilders believe that Pleistocene re-wilding will lead to a restoration of the historic wild ecosystem and original ecosystem functioning. However, re-wilding could result in a re-wilded novel ecosystem with unique species compositions and new ecosystem functioning.

or exotic. Modern introductions of exotic feral horses have dramatically altered vegetation in marsh (Levin et al., 2002) and grassland (Zalba and Cozzani, 2004) ecosystems throughout the New World, and these changes have had direct impacts on a variety of native animal species, some positive, but some negative. Moreover, exotic grazers, such as the one-humped camel (*Camelus dromedarius*), have wreaked havoc upon desert ecosystems in Australia by selectively eating rare plant species (Edwards et al., 2001). Similarly, the reintroduction of large predators can also have unexpected results on populations of prey species. For instance, wolves reintroduced to Yellowstone National Park, USA preyed upon elk more, and other species of ungulates less, than what was predicted prior to reintroduction (White and Garrott, 2005).

Of course, it might be argued that these problems would quickly become apparent if Pleistocene re-wilding were first attempted on a small-scale, experimental basis. However, experiments of this nature cannot be done quickly and may take decades and generations to play out. For instance, the Siberian Pleistocene Park experiment began in 1989, and as of yet, few of the results have been published (Zimov, 2005). Moreover, it may not be possible to conduct adequate, meaningful experiments on small spatial scales because many of these species have large home ranges or migrate great distances. For instance, African cheetahs can have home ranges of nearly 200 km^2 (Broomhall et al., 2003), and African elephants can migrate distances of up to nearly 150 km or more (Thouless, 1995).

Despite the potential dangers to ecosystem functioning, the reintroductions proposed by Donlan et al. (2005) would place many of the animals in temperate grasslands and shrub-steppe habitats, which are among the most threatened, but least protected, ecosystems in the world (Hoekstra et al., 2005). If the reintroduction of exotic megafauna could help preserve these ecosystems, conservationists must weigh the possibility of preserving disrupted or novel North American ecosystems against the possibility of losing those ecosystems altogether.

3. The ethics and aesthetics of Pleistocene re-wilding: protecting and restoring the evolutionary potential of threatened megafauna

Humans were at least partly responsible for exterminating some species of Pleistocene megafauna (Martin, 1984; Burney and Flannery, 2005) and, today, anthropogenic impacts continue to contribute to the extinction of the world's remaining megafauna (IUCN, 2004). Donlan et al. (2005) argue that humans bear an ethical responsibility to prevent future megafaunal extinctions and redress past losses. They suggest that introducing large Asian and African vertebrates to North America will not only ensure their long-term survival, but also restore their evolutionary potential (i.e., increase the number of individuals worldwide to allow them greater chances to radiate and generate new phenotypic and genotypic variants). Although this plan is certainly well-intentioned, the underlying reasoning is flawed. In essence, it is an attempt to preserve charismatic African and Asian species that are being driven to extinction by humans in their native habitats by refocusing efforts in places where those species have never occurred and where humans drove their distant ancestors extinct. Although Donlan et al. (2005) do not advocate giving up on conserving megafauna in developing nations, diverting attention from some of the world's most economically poor, but most biologically rich, countries to make amends for the ecological excesses of our North American ancestors could cripple, rather than assist, the conservation movement worldwide (Chapron, 2005).

The human population is growing and natural habitats are declining in extent and diversity everywhere. Couple this with the political and economic strife that is occurring in many developing nations and it is not difficult to see why native megafauna, especially large mammals, are declining in numbers worldwide (Muwanika et al., 2005). Despite this dire situation, Pleistocene re-wilding of North America is not the only viable solution to preserve the world's megafauna. In the developing world, new conservation models are being implemented that go hand-in-hand with human development as wildlife must pay for itself by generating economic benefits for local citizenry to help alleviate poverty (Kiss, 2004; Naidoo and Adamowicz, 2005). Although there are many challenges in developing such programs, there is much to be gained by overcoming them because most of the native megafauna in developing regions inhabit private, often unprotected, lands outside of parks. For instance, across Africa, 84% of African elephant habitat is outside of protected areas (Blanc et al., 2003), and in Kenya, 70% of the wildlife lives outside of protected areas for at least part of the year (Norton-Griffiths, 1998).

Conserving African and Asian megafauna does not require relocating them to North America. However, it will require new conservation plans that ensure local citizenry receive economic benefits from wildlife. Available human and financial resources might be better expended on preserving land, promoting ecotourism, building fences in areas of high human–wildlife conflict, and establishing educational and research programs in areas of Africa and Asia where indigenous megafauna are most at risk, rather than on introducing those same large, exotic species to North America.

In addition, the question of how the Pleistocene re-wilding plan would affect existing conservation efforts in North America must be considered. Conservationists often struggle with local opposition to re-wilding with native predators, and even the reintroduction of relatively benign large mammals (e.g., moose) meets resistance (Lauber and Knuth, 1999). The introduction of modern relatives of extinct predators will be opposed even more strongly by state governments and locally-affected citizens (Shay, 2005). And, with good reason: escapes are inevitable, resulting in human–wildlife conflict as often occurs near protected areas in Africa and Asia. Ironically, an article in the same journal issue as the one on Pleistocene re-wilding of North America (Donlan et al., 2005) documents the increasing numbers of humans killed by lions in Tanzania (Packer et al., 2005). And only a few weeks later, news reports surfaced from Ethiopia indicating that lions disturbed by deforestation killed 20 people and devoured 750 domestic animals during August, 2005 (Anon, 2005). It is difficult enough for North American conservationists to address the real concerns of local citizens about attacks by mountain lions (native predators) on joggers. One can only imagine the anti-conservation backlash that would be generated by news coverage of farmers coping with crop destruction by herds of elephants, or lions and cheetahs attacking cattle, or even children.

While Pleistocene re-wilding may help maintain the evolutionary potential of modern, extant species, it cannot restore the evolutionary potential of extinct species that no longer exist. And even attempting to restore evolutionary potential of endangered species using modern-day species from foreign continents as proxies for creatures that went extinct in North America is controversial. Donlan et al. (2005) highlighted the peregrine falcon (*Falco peregrinus*) to illustrate how using similar, but not genetically identical, (sub-)species can indeed serve as proxies for nearly-extinct taxa. Moreover, for nearly two decades, conservation biologists have proposed introducing closely related proxy species for extinct birds on New Zealand and other Pacific islands (Atkinson, 1988, 2001). However, species that went extinct some 13,000 years ago are probably more genetically different from their modern-day proxies, who have continued to evolve for millennia, than are two sub-species of modern falcons or modern Pacific island birds. For instance, although recent molecular data suggest that the common horse (*Equus caballus*) is genetically similar to its evolutionary ancestral species (Weinstock et al., 2005), modern elephants (Surovell et al., 2005), cheetahs (Barnett et al., 2005), and lions (Barnett et al., unpublished manuscript) are quite genetically distinct from their extinct Pleistocene relatives.

Rather than use modern-day species from foreign continents as proxies for creatures that went extinct in North America, conservation efforts should focus on re-wilding native species into their historical ranges throughout North America to restore ecosystems and increase the evolutionary potential of indigenous species (Dinerstein and Irvin, 2005; Schlaepfer, 2005). For instance, native herbivores like bison (*Bison bison*), pronghorn (*Antilcapra americana*), elk (*Cervus elaphus*), jack rabbits (*Lepus townsendii*), and various ground-dwelling squirrels (*Spermophilus* spp.) and prairie dogs (*Cynomys* spp.), as well as native predators like black-footed ferrets (*Mustela nigripes*), bobcats (*Lynx rufus*), badgers (*Taxidea taxus*), and swift foxes (*Vulpes velox*) are likely candidates for reintroduction to geographic regions from which they were extirpated in the past several hundred years (Hoogland, 2006).

Donlan et al. (2005) suggested that another appropriate candidate for reintroduction is the Bolson tortoise (*Gopherus flavomarginatus*). Because this animal once lived throughout the southwestern United States and still persists in small areas of similar habitat in Mexico, it may not differ greatly from its ancestral form and, therefore, it might be a reasonable candidate for reintroduction. However, before attempting such a reintroduction, one would also have to consider how much the plant and animal communities in the tortoise's native geographic habitats have changed (evolved) since this reptile went locally extinct.

If reintroducing charismatic megafauna is an important goal of Pleistocene re-wilding because of its possible galvanizing effect on public support for conservation, then one might consider expanding reintroductions of some of North America's own megafauna like wolves (*Canis lupus*) or grizzly bears (*Urus arctos*) to other portions of their known recent (i.e., historical) ranges. And if more predators are deemed necessary, an even better candidate for re-wilding would be the puma (*Puma concolor*), because it is more genetically similar to the long-extinct American cheetah (*Miracinonyx trumani*) than the African cheetah is to the American cheetah (Barnett et al., 2005). Moreover, the puma is a native mammalian predator that barely survived the Pleistocene extinctions 13,000 years ago, and still remains threatened throughout much of its North American range (Culver et al., 2000).

4. The economics and politics of Pleistocene re-wilding: uncertainty and tradeoffs

The political and economic ramifications of Pleistocene re-wilding of North America are unclear. Certainly, it will be expensive because land acquisition and preparation, translocation, monitoring, protection, and containment require considerable human and financial resources (Fischer and Lindenmayer, 2000). Moreover, all of these efforts would likely cost proportionally more in North America than they would in Africa or Asia, given the higher prices of salaries and supplies. Because conservation funding is limited, Pleistocene re-wilding may compete for resources that might otherwise have gone to local conservation efforts (Chapron, 2005). Although it is possible that introducing charismatic African and Asian megafauna to North America could ignite public and political support, ultimately leading to an overall increase in funding for conservation projects worldwide, other new ideas might increase the pool of resources with less risk to North American ecosystems and conservation efforts worldwide.

Donlan et al. (2005) are careful to point out that the initial steps of Pleistocene re-wilding can occur without large-scale translocations of proxy species because many of these animals are already in captivity in the United States. This would potentially reduce costs, as well as avoid potential political problems between the United States and developing nations, the ultimate "sources" for the animals. However, reintroductions from wild populations have been more successful than those from captive populations (Fischer and Lindenmayer, 2000; Griffith et al., 1989), and Pleistocene re-wilding inevitably would involve translocating animals from Asia and Africa to North America, either to increase population numbers or to improve population viability by augmenting genetic diversity. Such translocations of megafauna into areas where they were recently extirpated occur routinely throughout Africa and Asia (Fischer and Lindenmayer, 2000), and learning from these examples could shed some light on the practicality of Pleistocene re-wilding of North America.

5. The practicality of Pleistocene re-wilding: the reality of reintroductions

One of the goals of Pleistocene re-wilding of North America is to "...restore equid species to their evolutionary homeland" (Donlan et al., 2005) and, indeed, some of the best known and most successful reintroductions of endangered species to their historical ranges involve equids (Moehlman, 2002). For example, the Tahki, or Przewalski's horse (*Equus ferus przewalskii*), which is endemic to Mongolia and China, was considered extinct in the wild by the end of the 1960s and fewer than 400 Tahki remained in captivity in 1979. By the beginning of the 1990s, however, efforts began to reestablish populations in the wild and two reintroduction sites were chosen in Mongolia. By 2000, the population at one site had declined only slightly, while that at the other had increased by 50% (Wakefield et al., 2002). These encouraging trends led to a third introduction in 2005 and suggest that the re-wilding of the Tahki's historic range is likely to succeed.

In an attempt to repopulate Israel with recently extirpated biblical animals, onagers, a race of Asian asses (*Equus hemionus*), were translocated from Israel's Hai Bar breeding reserve to a nearby erosional crater in the Negev desert. Between 1968 and 1993 multiple reintroductions of 50 individuals took place. It was not until the end of the 1990s, however, before the population started to expand numerically and spatially. Low fertility of translocated adult females relative to that of their wild-born daughters and male-biased sex ratios among the progeny limited recruitment (Saltz and Rubenstein, 1995). These unanticipated biological constraints suggest that even reintroductions of native species to their historical habitats are not assured of succeeding.

Repopulating the historic range of the endangered Grevy's zebra (*Equus grevyi*) in east Africa is viewed as critically important to saving the species from extinction (Moehlman, 2002). Fewer then 2000 Grevy's zebras remain in small areas of Ethiopia and northern Kenya, whereas only 35 years ago, over 20,000 individuals inhabited areas all the way to the horn of Africa. Efforts to repopulate areas of the Grevy's historic range have involved capturing and moving small groups of appropriate sex ratios and age structures to holding areas before subsequent release. While two such reintroductions in Kenya, one to Tsavo National Park and one to Meru National Park, began successfully, neither has led to expanding populations. In fact, in Meru, differences in the composition and abundance of mammal species in the Grevy's zebras' new range have, at times, led to rapid declines in their numbers (D.I. Rubenstein pers. obs). Therefore, even reintroductions within the natural geographic regions of a species are often fraught with surprises due to diseases, unexpected differences in environmental conditions, and naïveté toward predators.

The Przewalski's horse and the Asian ass are presented by Donlan et al. (2005) as two candidate examples of endangered equid species that could be saved from extinction, while also being used to help restore equid species to their "evolutionary homelands" in North America. Small-scale reintroductions of these and other endangered equid species throughout Asia, their historically-known evolutionary homeland, appear to be working. These are appropriate reintroductions and the sort of re-wilding that makes evolutionary and ecological sense because the time between the species' extirpation and reintroduction has been short enough that neither the native ecosystem nor the animals themselves have changed (evolved) very much. However, as both the onager and the Grevy's zebra reintroduction programs illustrate, success is not assured until more is known, underscoring the need to treat reintroductions as continuing experiments in adaptive management. Moreover, increasing the scope of reintroductions of extant endangered equids into places from which they were extirpated recently, the only evolutionary homelands that we can be sure are suitable for them, is more justifiable evolutionarily and ecologically than introducing them to North American habitats where they have not existed for millenia.

6. Another Jurassic Park?

We all remember "Jurassic Park", Crichton's (1990) fictional account of re-wilding an isolated island with extinct dinosaurs recreated from ancient DNA. Pleistocene re-wilding of North America is only a slightly less sensational proposal. It is a little like proposing that two wrongs somehow will make a right: both the modern-day proxy species are "wrong" (i.e., different genetically from the species that occurred in North America during the Pleistocene), and the ecosystems into which they are to be reintroduced are "wrong" (i.e., different in composition from the Pleistocene ecosystems, as well as from those in which the modern-day proxy species evolved). Pleistocene re-wilding of North America will not restore evolutionary potential of North America's extinct megafauna because the species in question are evolutionarily distinct, nor will it restore ecological potential of North America's modern ecosystems because they have continued to evolve over the past 13,000 years. In addition, there is a third and potentially greater "wrong" proposed: adding these exotic species to current ecological communities could potentially devastate populations of indigenous, native animals and plants.

Although Donlan et al. (2005) argued that Pleistocene re-wilding of North America is justified for ecological, evolutionary, economic, aesthetic, and ethical reasons, there are clearly numerous ecological and evolutionary concerns. On the one hand, the plan might help conserve and maintain the evolutionary potential of some endangered African and Asian megafauna, as well as indirectly enhance the evolutionary potential of native North American prey species that have lacked appropriate predators since the Pleistocene. On the other hand, the plan cannot restore the evolutionary potential of extinct species and it is unlikely to restore the ecological potential of western North America's grassland and shrubsteppe communities. Instead, it may irreparably disrupt current ecosystems and species assemblages. Moreover, there are many potential practical limitations to Donlan et al.'s (2005) plan. Reintroduced camels did not survive for long in the deserts of the American West (Smith, 2005). Could African megafauna, especially large carnivores, really populate the same areas? Would the genetically depauperate cheetah (O'Brien et al., 1985) succumb to novel diseases? Would elephants survive the harsh prairie winters, lacking the thick coats of their mastodon ancestors?

Answering these questions and accomplishing Pleistocene re-wilding of North America would require a massive effort and infusion of funds and could take more time to experimentally test than some of these critically endangered species have left to survive in their existing native habitats. If financial and physical resources were available on this scale, they would be better spent on developing and field-testing new ways to manage and conserve indigenous populations of African, Asian, and North American wildlife in their historically-populated native habitats, on conducting ecological, behavioral, and demographic studies of these organisms in the environments in which they evolved, and on educating the public on each continent about the wonders of their own dwindling flora and fauna.

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