

ON THE ECOLOGY OF INVASIVE SPECIES, EXTINCTION, ECOLOGICAL
HISTORY, AND BIODIVERSITY CONSERVATION

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ON THE ECOLOGY OF INVASIVE SPECIES, EXTINCTION, ECOLOGICAL
HISTORY, AND BIODIVERSITY CONSERVATION

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For thousand of years, invasive species have changed ecosystems and caused extinctions. Nowhere is this more apparent than on islands. Those ecosystem changes and extinctions are result of strong species interactions between invasive species and native communities. However, extinctions are rarely random and are often influenced by a suite of biotic and abiotic factors. Understanding the intricacies of invasions and their consequences is central to ecology and conservation. Here, I explore three aspects of invasion biology: 1) the ability to remove invasive mammals from islands and the biodiversity benefits, 2) the ability to predict extinctions caused by invasive species, and 3) the role ecological history plays in dictating nativeness with respect to restoration.

Chapter one provides a brief overview of the three-decade progress of invasive mammal eradication on islands. I review the history of eradication techniques developed in New Zealand, and describe some recent successes in western Mexico and Galápagos that I have been part of over the past decade. Chapter two provides one example of the biodiversity benefits of eradication: the recovery of the Galápagos rail that was heavily impacted by invasive goat and pig populations prior to their removal from Santiago Island. Chapter three and four test advocated and explore new conservation tools for their ability to predict extinction-prone species. At the core of these two chapters is an attempt to evaluate whether biogeography tools are useful in

predicting species endangerment, or whether knowing the autecological details of a species and their community interactions is necessary to correctly gauge extinction risk.

Chapter five tackles the role ecological history in gauging “nativeness”. I provide a framework that justifies the restoration of missing ecological functions and evolutionary potential of extinct species using extant conspecifics and related taxa. Pleistocene Rewilding is conceived as managed ecosystem manipulations whereby costs and benefits are addressed on a case-by-case basis. It would broaden the underlying premise of conservation from managing extinction to encompass restoring ecological and evolutionary processes. Risks of Pleistocene Rewilding include the possibility of disease transmission, and unexpected ecological and sociopolitical consequences of reintroductions. Social challenges will include incorporation of pre-Columbian ecological frameworks into conservation strategies.

BIOGRAPHICAL SKETCH

Charles Joseph (“Josh”) Donlan was born in the Tidewater area of Virginia. He was lucky enough to be raised in the backwaters of the Chesapeake Bay, where he canoed, crabbed, and swam. At a young age, he was also lucky enough to become employed as the “kid” at several ski and outdoor shops; these experiences formed the foundation of Josh’s relationship with the nature. At least initially, he largely skied, climbed, hiked, and paddled his way to the field of conservation biology. After two years of college in the mountains of Virginia at James Madison University, Josh packed up and moved to the Wasatch Mountains of Utah. After a good stint of skiing, climbing, and adventures to Alaska, Josh returned to academia on the Colorado Plateau at Northern Arizona University. It was here in Flagstaff that Josh became fascinated with ecology. He spent the next two years naturalizing in Arizona and Mexico. Following his graduation, Josh again packed up and hit the road—but this time with his kayak. He spent 4 months kayaking the Gulf of California, and it was there where Josh was properly introduced to islands. Josh then headed to Panama where he studied marine invertebrates on a fellowship with the Smithsonian. After his first tropical experience, Josh headed to Santa Cruz for a M.A. at University of California, where he spent the next five years doing ecology and conservation on islands in Mexico—and became a scientist. Josh packed his bags once again and headed to Ithaca, via southern Africa, to Cornell University. During his five-year tenure at Cornell University, Josh conducted research in the Galápagos Islands, New Zealand, Tasmania, Chile, Mexico, and the mountains of southeastern Arizona. Josh is now continuing that conservation work, while balancing it by returning to those foundational activities of skiing, climbing, hiking, and paddling in wild places.

This dissertation is dedicated to four of four different decades: all whose wisdom of nature, life, and what it all means I will keep with me until I'm compost.

Thanks Jesse, Gary, Harry, and Paul.

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The past five years have been monumental in my personal and professional progress as an ecologist, environmentalist, and student of nature. I started my Cornell tenure with a one-month long river trip on the Grand Canyon, one of our country's last wild places, and last year, I went to eight countries a couple different times for "work"—I'm a lucky guy. Many have played influential and important roles in that progress. I've had a lot of help.

First and foremost are my committee and advisors. Alex Flecker provided keen ecological advice, and constantly brought a different and often wet perspective to my largely terrestrial endeavors. He always seemed to have fun while doing so, which was also some great advice. Alex supported my research and conservation, wherever it took me. Bobbi Peckarsky provided great advice on science and other important stuff over the past five years. And our few days together at the Rocky Mountain Biological Laboratory a few years ago (along with a few hockey games) is as good as testament as any that not only is Bobbi a rock star when it comes to doing science but also when it comes to having fun. Anurag joined my committee more than halfway through my Ph.D.; however, his input has always been insightful and improved my thinking and writing. He is a frighteningly sharp thinker, and perhaps the most timely committee member I have come across in my seven-year and two-university tour of graduate school. Harry has been a great life coach over the past five years, and I have hopes he will continue to be so. He has provided and shared insights, experience, and wisdom to a student that by no means whatsoever qualifies as a herpetologist. We've had some grand times that have included a bunch of undergraduates romping around the desert, a yurt fire, a bunch of famous biologists romping around the desert, and one (re)wild experience.

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Over the past five years, I have spent many months in the Galápagos Islands working on a “side project” called *Project Isabela*. I am very proud to have played a role in the world’s largest island conservation project. My fellow *islanos* gave me more inspiration to rewild places than I could ever ask for. At the center of that inspiration was Karl Campbell. Not only can the man kill goats better than anyone alive, his determination and commitment to island conservation is unmatched. I also thank the rest of Project Isabela, particularly Felipe Cruz, who was our fearless leader and somehow always found funding when there was none to be found. I also thank Victor Carrion, Christian Lavoie, Tom Poulsom, and all the others for good times on the islands. Along with those good times, we have also been productive (Campbell et al. 2006; Campbell et al. 2005; Campbell & Donlan 2005; Campbell et al. 2004; Carrion et al. 2007; Cruz et al. 2005; Donlan et al. 2005b; Donlan et al. 2003b; Lavoie et al.

2007).

The three days I spent on the Ladder Ranch, New Mexico in August of 2004 running a workshop on ecological history was a truly incredible experience. Many of those workshop participants were my ecological and conservation heroes. And many since have become better friends. Howling wolves up by moonlight with the “Ladder 12” and red wine is a night I will not forget. I thank deeply the Ladder 12 for sharing their wisdom, insights, and time with me: Joel Berger, Carl Bock, Jane Bock, David Burney, Dave Forman, Paul Martin, Gary Roemer, Felisa Smith, Michael Soulé, Joe Truett, and Harry Greene. I also thank Steve Dobrott, Jim Estes and Mike Phillips who also played instrumental roles in the Pleistocene Rewilding project (Donlan 2007; Donlan et al. 2006; Donlan & Greene in press; Donlan et al. 2005b; Donlan & Martin 2004; Donlan et al. 2007).

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Chapter 1: Rewilding the ðeglands: Biodiversity, invasive species, and saving the world's islands

Islands, the *watered lands* once known as ðeglands in Old English, serve as models for the interactions between humans and their environment. Nowhere is this relationship better illustrated than in the current biodiversity crisis. Islands make up approximately ~3% of land area worldwide, yet they harbor a relatively high percentage of biodiversity, including many endemics such as giant Galápagos tortoises, New Caledonia geckos the size of small dogs, and the now extinct pygmy mammoth of Siberia's Wrangell Island. In fact, since the fall of the world's last mammoth some 4,000 years ago, the majority of vertebrate extinctions have been insular in nature. The islands of Oceania provide a stark example: prior to the onset of human impacts *c.* 3,000 years ago, these islands were home to over 2,000 now extinct bird species—over 20% of the extant avifauna worldwide (Steadman 2006). While in many cases humans likely played a direct role, the introduction of invasive mammals was a major driver in these island extinctions and subsequent ecosystem changes. This threat is even more pervasive today; invasive mammals are present on over 80% of the world's islands. Of the mammal and bird species on World Conservation Union's red list of threatened species, nearly half occur on islands (Figure 1).

Unique evolutionary histories predispose island flora and fauna to impacts by invasive mammals. Terrestrial mammalian predators and large herbivores are rare on islands, and thus insular species generally lack behavioral, physical, and life history defenses against mammalian herbivory and predation. Thus, introduced herbivores, such as feral goats (*Capra hircus*) and donkeys (*Equus asinus*), devastate island plant communities by overgrazing and impact island fauna through habitat destruction. As omnivores, feral pigs (*Sus scrofa*) feed on fruits and plants, prey on vertebrates, and

raid nests of birds and reptiles. Invasive predators, such as rats (*Rattus* spp.) and feral cats (*Felis catus*), have decimated rodent, reptile, and bird populations, and extirpated numerous seabird colonies on islands around the globe. Invasive rats alone are responsible for at least 50 documented extinctions (Towns et al. 2006), including the world's only flightless songbird (*Xenicus lyalli*).

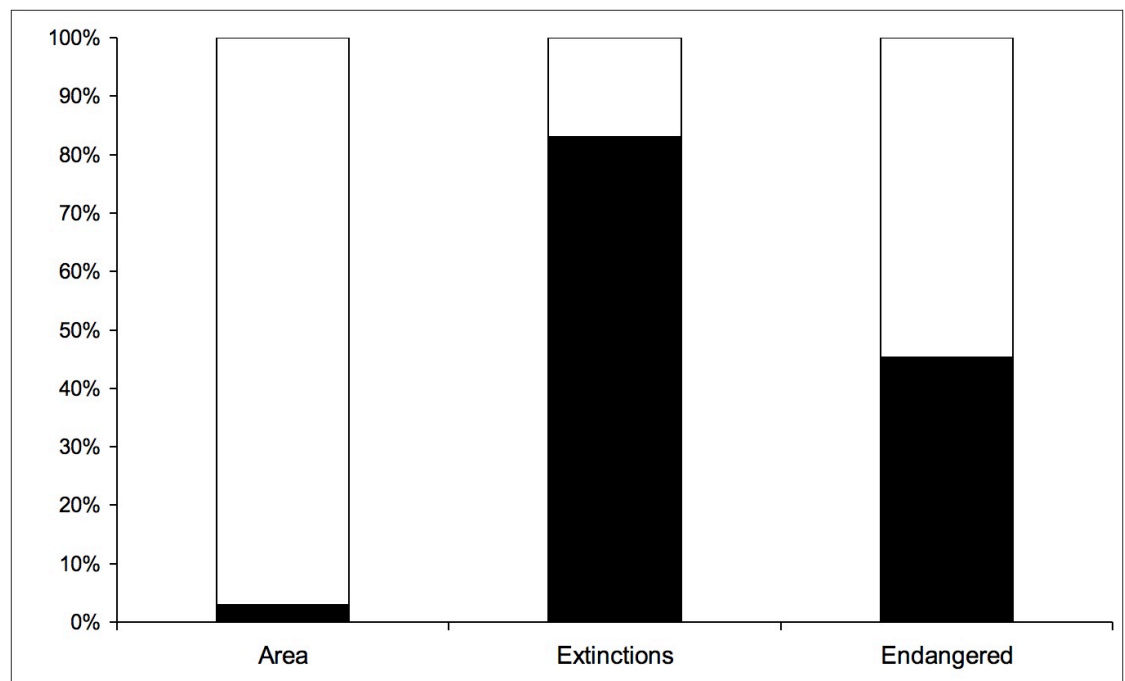


Figure 1. Global percent comparisons of islands (black) versus continental (white) for total area, and extinct and endangered species of mammals and birds combined. Species come from the World Conservation Union's Red List (www.redlist.org). I classed Red List categories EX and EW as extinct, and CR, EN, and VU as endangered.

Rats drove this wren to extinction on the main islands of New Zealand, and in 1894, a single cat belonging to the lighthouse keeper of Stephen's Island provided the only specimens known to science while single-handedly killing the last individuals of the species.

Some seven decades later, rats invaded a small island of southern New Zealand wiping out the last population of yet another wren (*Xenicus longipes*). But this time, some New Zealanders fought back, attempting to save the wren and other species under threat (Veitch & Clout 2002). The “kiwis” failed for most, but managed to save the South Island Saddleback (*Philesturnus c. carunculatus*), raising the question could the onslaught of New Zealand’s biodiversity by invasive mammals be stopped? In 1960, hundreds of dead white-faced storm petrels (*Pelagodroma marina*) were found dead after Norway rats invaded Maria Island (0.01 km²), a small island off New Zealand the size of a football field. In response, biologist Don Merton, along with members of the Forest and Bird Protection Society, spread rodenticide around the island in an effort to control the rat population. When they returned a few years later, much to their amazement, the rat population had been eradicated. A decade later, biologist Dick Veitch and others with the Department of Internal Affairs Wildlife Branch conducted a similar rat-control program on the slightly larger Titi Island (0.3 km²) in an effort to protect breeding seabirds. The rat population was significantly reduced but not eradicated. A symposium then convened with over 50 of New Zealand researchers and conservation practitioners to discuss the possibility of controlling invading rats populations on New Zealand’s hundreds of satellite islands, the country’s last biodiversity stronghold. In 1976, They came to the calamitous conclusion that “We have control methods, and methods for reducing populations, but complete extermination on islands is remote or at least a very very difficult thing indeed” (Thomas & Taylor 2002). Luckily, a handful of kiwis were not willing to settle for such a calamity. Phil Moors, Ian MacFadden, and others continued testing new rodenticides and techniques on small islands in northern New Zealand. Bait stations were developed, which could be systematically placed over an entire island

and armed with rodenticide. Meanwhile in the far south, two other biologists Bruce Thomas and Rowley Taylor had begun another research program building on previous knowledge. Their aim was to “develop a system of dispensing a proven rodenticide into a territory of every rat on an island, in a way that would minimize non-target poisoning, and monitor the effectiveness of the campaign as it progressed” (Thomas & Taylor 2002). By 1983 they had succeeded and rats had been intentionally eradicated from a number of islands in New Zealand, but all them small ($< 0.5 \text{ km}^2$). The prospect of reversing the impacts from invasive rats had evolved from dismally remote to guardedly optimistic. But most, including those intimately involved in New Zealand conservation, were still skeptical on scaling up to large islands, leading to the commonly held view “Once rats have established on an island, it is generally not feasible to remove them unless the island is very small” (Thomas & Taylor 2002).

But Bruce Thomas, Rowley Taylor, and others kept at it. In 1988, they led an effort that placed 743 bait stations on Breaksea Island (1.70 km^2) in New Zealand’s famous Fiordland. In 21 days, the rats were eradicated (Taylor & Thomas 1993). This effort created the largest predator-free island in Fiordland, critical for endangered species translocations such as the last remaining individuals of the critically endangered kakapo (*Strigops habroptilus*)—the world’s only nocturnal parrot. They showed to the world that islands, small and large, could be saved from the impacts of invasive rats.

Today, twenty years after Breaksea, the removal of rats and other invasive mammals from islands has become a powerful tool for biodiversity conservation. Alongside and concurrently with the New Zealanders, Australian conservationists developed rat eradication techniques removing rats from 41 islands (Veitch & Clout 2002). In New Zealand alone, rats have now been eradicated from 116 islands. Over the past decade, conservation practitioners from around the globe have successfully

adopted these techniques: 332 successful invasive rodents eradications have been undertaken (Howald et al. in press).

New technology and techniques have drastically improved the ability to remove invasive mammals from islands. Aerial broadcast of rodenticide by helicopter, with the aid of GPS technology, has become the common method used in rodent eradications. This has led to successful rat removals on larger and larger islands, and more cost-effective eradication campaigns. In 2001, Norway rats (*R. norvegicus*) were removed from Campbell Island, New Zealand (113 km²), which is the largest rat eradication to date, an area slightly smaller than Washington D.C. (McClelland & Tyree 2002). The Campbell Island Teal (*Anas nesiotis*), driven to near extinction by rat predation, survived only in captivity and on a tiny rat-free islet adjacent to Campbell Island. This emblematic, flightless duck has been reintroduced to Campbell Island where it is recovering. Twenty years ago, eradicating rats from an island the size of a football field was a risky and daunting challenge. Today, eradicating rats from a remote subantarctic island the size of Washington D.C. is a reality.

Other tools and techniques have improved the ability to mitigate for potential non-target impacts of native island species during eradication campaigns. In 2002, black rats (*R. rattus*) were removed from Anacapa Island, California using an aerial broadcast of rodenticide (Howald et al. 2005). The project presented novel challenges since an endemic rodent (Anacapa deer mouse, *Peromyscus maniculatus anacapae*) was also present on the island and equally susceptible to the rodenticide. Prior to the bait application, a genetic study was conducted and formed the basis of the mitigation. Mice across Anacapa's three islets were found to be genetically similar and functioning as a metapopulation. A captive population of ~1000 mice would be necessary to maintain the observed genetic diversity. To insure that there were two viable populations of mice at all times, in addition to the captive population, the

broadcast of rodenticide was staggered over two years so that a free ranging population was always present on one or more of the Anacapa islets. The eradication and mitigation was a success; after a series of translocations between islands and reintroductions from the captive population, native mouse populations recovered to pre-eradication densities or higher within six months following the rat eradication. Seabirds have benefited as well. Once heavily impacted by rat predation, the endangered Xantus' murrelet (*Synthliboramphus hypoleucus*) and other seabirds are now successfully breeding in record numbers on the island.

Similar conservation gains have been achieved on islands around the globe by eradicating other invasive predators and herbivores. To date, there have been at least 629 successful invasive mammal eradications (Campbell & Donlan 2005; Howald et al. in press; Nogales et al. 2004; Veitch & Clout 2002). These conservation actions have stopped extinctions and restored island ecosystems, safeguarding seabirds and insular species on dozens of island archipelagos. Historically, systematic island conservation programs and the eradication of invasive mammals have been largely limited to small and medium-sized islands, particularly in Australasia. This is no longer the case; restoration is now taking place on islands large and small throughout the world.

Foxes, seabirds, and the Aleutian islands

Alaska's Aleutian Islands are one the world's last wild places. The 2500+ islands that make up the U.S. Fish and Wildlife Service Alaska Maritime National Wildlife Refuge encompass 1.9 million hectares and provide nesting habitat for over 40 million seabirds. Yet, the Aleutians have not been spared the impacts of non-native mammals; introductions began after Russians discovered the islands more than 200

years ago. Black rats were accidentally introduced, and arctic and red foxes (*Alopex lagopus*, *Vulpes vulpes*) were intentionally released on more than 450 islands for fur and food. Foxes subsequently severely reduced populations of waterfowl, shorebirds, seabirds, and ptarmigan by preying on eggs, nestlings, and adults (Bailey 1993). The endemic Aleutian Cackling Goose (*Branta hutchinsii leucopareia*) was extirpated from all but three islands. Foxes also precipitated ecosystem impacts: by preying on seabirds, foxes indirectly reduced nutrient transport from the ocean to land via seabird guano, transforming grasslands to tundra (Maron et al. 2006).

A dedicated refuge staff, led and inspired by Ed Bailey and Vernon Byrd, have been eradicating foxes from the Aleutian archipelago since 1949. Since 1983, foxes have been removed from at least one island a year. Within the refuge, foxes have been eradicated from 40 islands, totaling over 5,000 km² (Veitch & Clout 2002). Recovery of waterfowl, shorebird, and ptarmigan populations has been widespread and dramatic, and nesting seabird populations have increased four to five-fold (Byrd et al. 1994). The combination of the archipelago-wide fox removal program and a translocation program saved the Aleutian Cackling Goose from extinction; numbers have increased from less than 1,000 birds in 1975 to more than 80,000 in 2006. Introduced foxes remain on just nine islands that are being targeted for removal, and managers are now turning toward removing rat populations from the archipelago. These conservation actions are grand strides in protecting the northern hemisphere's most important seabird nesting grounds.

Feral cats and the islands of western Mexico

The islands of western Mexico are celebrated laboratories of evolution and beacons of biodiversity. Historically, these islands were protected from direct human

perturbations by aridity, isolation, and low human population densities on the adjacent mainland. Today, most of the islands are government owned and legally protected from many forms of land conversion. However, invasive mammals were introduced to many of these islands starting in the late 1800s, and introductions continue to take place. As seen elsewhere, feral cats are responsible for widespread biodiversity impacts in the region, including wholesale reductions or extirpations of breeding seabird colonies and the extinction of eight endemic rodents.

Since 1994, the conservation organizations Island Conservation and Conservación de Islas A.C. have been working in collaboration with the Mexican government, Centro de Investigaciones Biológicas del Noroeste, Universidad Nacional Autónoma de México, and others to remove invasive mammals from islands in western Mexico. Led by seabird biologist Bernie Tershy and retired trapper Bill Wood, these collaborations have resulted in the removal of forty-two populations from 26 islands, including cats from 17 islands—a third of the successful cat eradications worldwide (Veitch & Clout 2002). These successes were a product of a holistic conservation model that included integrating research, public education, policy work, capacity building, on-the-ground conservation action, and monitoring. Cost-effective conservation gains have resulted: 88 endemic terrestrial vertebrates and 201 seabird colonies have been protected for less than \$50,000 per taxon/colony.

With sufficient capacity and political support, and now with proven success in the region, all of the remaining islands in western México are feasible conservation targets. Feral cats are present on three of western Mexico's most important islands for biodiversity conservation: Guadalupe, Socorro, and the Tres Mariás. All are large enough to present unprecedented challenges with respect to cat eradication; however, recent research and advances in Australia, particularly the development of aerial-

broadcasted cat baits, make eradication on these islands feasible (Algar & Burrows 2004). Funding, rather than technical capacity and island size, may now be limiting factors in preventing extinctions on the remaining islands in western Mexico. These islands will be challenging and expensive, but will yield dramatic conservation benefits and bring this unique and diverse archipelago one step closer back to a balanced and wild ecosystem.

Introduced herbivores and the Galápagos islands

Both Wallace and Darwin witnessed the destruction of St. Helena Island by goats in the 19th century. Introduced in the 1200s, goats are responsible for at least eleven plant extinctions; the real number is unknown since the first botanical survey occurred 300 years after goats arrived. Unfortunately, goats also beat Darwin to the Galápagos. They have been introduced onto thirteen islands causing widespread habitat destruction in every case. While goats still roam the transformed landscape of St. Helena, many Galápagos islands are now recovering from introduced herbivory, and the entire archipelago is on its way to becoming goat-free.

In 1961 goats were removed from the small island of Plaza Sur (0.12 km²), the first eradication in the Galápagos. Between then and 2000, the Galápagos National Park and Charles Darwin Foundation have removed goat populations from seven islands in the archipelago. Early eradication campaigns were opportunistic, and involved ground hunting without specialized techniques or monitoring programs in place. In the late 1990s, the National Park and Charles Darwin Foundation received funding from the Global Environmental Facility and others to develop an ambitious program to remove goats from the largest islands in the archipelago. Led by Felipe Cruz and Victor Carrion, both born and raised in the Galápagos, and Australian Karl

Campbell, *Project Isabela* was an eradication program of unprecedented scale. First, feral pigs and goats would be eradicated from Santiago Island (580 km²), an island three times larger than the largest eradication to date. After refining and developing techniques on Santiago, the goat eradication program would move to Isabela Island. At 4,590 km², Isabela would be largest conservation action ever attempted in terms of scale and complexity.

Removing goats from an island the size of Rhode Island required leveraging new technology, hunting, and monitoring techniques. This massive effort included the integration GPS and GIS technology into all facets of the campaign, a large-scale aerial hunting effort by helicopter, ground-based hunting with specialized dogs, and Judas goats techniques (Lavoie et al. 2007). Judas goats, radio-collared individuals that are released and associate with the remaining feral goats at low densities, aid in removing the final goats (Campbell & Donlan 2005). Both projects were successful: pigs, goats, and donkeys were removed from Santiago and goats from Isabela, over 140,000 goats were removed between the two islands (Carrion et al. 2007; Cruz et al. 2005; Lavoie et al. 2007). These two islands double the area worldwide where goats have been eradicated. Widespread ecosystem recovery has been swift; entire plant communities are recovering, benefiting Galápagos fauna such as giant tortoises and endemic rails. Once impacted by pig predation and habitat destruction by goats, densities of Galápagos rails (*Laterallus spilonotus*) have increased by over a magnitude on Santiago Island. Galapagos National Park is currently working toward removing goats from the last four islands where they remain. After hundreds of years, the long-standing biodiversity impacts of introduced herbivores on the Galapagos flora and fauna are coming to an end.

The Aleutians, Galápagos, and the islands of western Mexico are just three examples of successful island conservation programs. From the Indian Ocean to the

Subantarctic to the Tropical Pacific, conservation practitioners are following the lead of those stubborn New Zealanders who were not willing to lose the last of their wilds (Veitch & Clout 2002). Stopping extinction is at the center of biodiversity conservation. The removal of invasive mammals from islands is no longer rare event; rather, it is becoming routine, and is one of society's most powerful tools to prevent extinctions and restore ecosystems. And with the recent successes of Campbell and Isabela Island, island size may no longer be the limiting factor in our efforts. But, those kiwis already knew that decades ago when they were struggling to accomplish the “impossible”: eradicating rats from an island the size of a football field. From a football field to Washington D.C. to Rhode Island—it is not the size that is limiting, it's the attitude. The burning desire to rewild those places we can.

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Chapter 2: Recovery of The Galápagos Rail (*Laterallus Spilonotus*) following the removal of invasive mammals

“Rails are the most intriguing and tragic family of birds in Oceania if not the world...If not for human impact, more species of rails would be alive today than of any other family of birds.” –David Steadman, 2006

Abstract

Rails (family Rallidae) are vulnerable to the impacts of invasive mammals, and this is particularly true for species on oceanic islands. The endemic Galápagos rail (*Laterallus spilonotus*) is no exception; previous studies suggested that Galápagos rail populations were heavily impacted due to predation by pigs (*Sus scrofa*) and habitat degradation by goats (*Capra hircus*). Following recent conservation actions that have eradicated pigs and goats from Santiago Island, changes in rail abundance were observed. Estimated densities have increased by over an order of magnitude between 1986/87 and 2004/05. Limited data on rail densities from two additional islands over the same time period provide further support to the notion that the eradications spurred recovery. On Fernandina Island, where there is no history of invasive mammals, rail density changed little between 1986/87 and 2004/05. In contrast, on Isabela Island where invasive mammals were present both in 1986/87 and 2004/05, rail densities declined at one site between those two time periods. While the Galápagos rail is vulnerable to invasive mammals, the observed changes following goat and pig removal is encouraging for Rallidae conservation.

Introduction

Insular endemic birds in general and rails (Rallidae) in particular are vulnerable to non-native mammals and other anthropogenic impacts (Harding et al. 2001; Innes et al. 1999; Miller & Mullette 1985; Owens & Bennett 2000; Steadman 2006). The late Quaternary fossil record documents an unprecedented avian extinction event in Oceania: roughly 1000-2000 species, most of them rails, were lost on tropical Pacific islands after the arrival of humans (Steadman 2006). Those extinctions were presumably the result of predation and habitat degradation by humans and their commensals, such as rats (*Rattus* spp.) and pigs (*Sus scrofa*). More recently, seventeen species of insular rails have gone extinct in the Pacific since 1600 (Greenway 1958), and one third of the 142 extant rail species are threatened (Bennett & Owens 1997).

The Galápagos Islands were uninhabited by humans prior to European discovery in the mid-sixteenth century, and consequently the fauna suffered little extinction until recently. However since European arrival, extinction and extirpation have become increasingly common trends (Cruz & Cruz 1987; Dowler et al. 2000; Steadman 1986; Steadman & Ray 1982). Invasive mammals, including pigs, rats, goats (*Capra hircus*), and cats (*Felis catus*) are the primary agents driving those biodiversity impacts (Cruz & Cruz 1987; Hamann 1979; Loope et al. 1988; Steadman 1986). The endemic Galápagos rail (*Laterallus spilonotus*) is no exception, with populations suffering from the adverse effects of invasive mammals.

The Galápagos rail originally occurred on seven islands; nest predation by pigs, habitat destruction by goats, and the indirect impacts of invasive plants have caused rail populations to decline throughout the archipelago (Coblentz & Baber 1987; Franklin et al. 1979; Gibbs et al. 2003; Rosenberg 1990). During 1986/87 surveys, only 25 rails were detected on Santiago Island (Rosenberg 1990), where both goats and pigs were abundant. Considering the impacts by goats and pigs (Hamann 1993b;

Schofield 1989), Rosenberg (1990) speculated that the eradication of those invasive species would benefit rail populations.

Here, we report on recent Galápagos rail surveys. Between 1998 – 2006, pigs, goats, and donkeys were eradicated from the island: over 17,000 pigs and 70,000 goats were removed from the island (unpublished data, Carrion et al. 2007; Cruz et al. 2005; Donlan et al. 2005). In an effort to quantify the consequences of invasive mammal eradications, we repeated surveys conducted in 1986/87 by Rosenberg (1990) on three islands: Santiago, Fernandina, and Isabela. Fernandina Island has remained free of invasive mammals since the initial surveys (Table 1). Goats, pigs, and donkeys remain on many parts of Isabela Island (as was the case in 1986/87). Thus, distinct differences exist among the three islands with respect to the presence of invasive mammals in 1986/87 and in 2004/05 (Table 1). Those differences provide an opportunity to compare rail abundance between two time frames, enabling us to draw some inference with respect to potential causes of rail population changes. While we lack data on other environmental aspects that have may have changed during the 20-year period including natural variation of rail numbers through time, the three islands provide an opportunity to compare rail abundance between two time frames, enabling us to draw some inference with respect to potential causes of rail population changes.

Methods And Results

We conducted rail surveys on Isabela (December 2004, February 2005), Santiago (December 2004, February 2005), and Fernandina (December 2004) Islands. Our field methods and statistical analyses are identical to those of the only available historical survey of Galápagos rails in 1986/87 (Rosenberg 1990), which enables us to make direct temporal and spatial comparisons. We sampled sites during the same time

of the year as the original surveys (within 8 weeks) to remove seasonal bias in

Table 1. Non-native mammals and dominant invasive woody plants present on three Galápagos Islands where rails were surveyed (X = Present, E = Eradicated). On Isabela Island, the distribution of non-native species differs depending on the location.

	Mice ^a	Rats	Cats	Goats	Pigs	Donkeys/Horses	Cattle	Plants
Isabela								
Ecuador, Wolf, Darwin	X	X	X	E ^b				
Volcanoes								
Alcedo Volcano	X	X	X	E ^b		E ^b		
Sierra Negra Volcano	X	X	X	X	X	X	X	X ^c
Fernandina								
Santiago	X	X		E	E	E		

a: *Mus musculus*, *Rattus rattus*, *Felis catus*, *Capra hircus*, *Sus scrofa*, *Equus* spp. *Bos* sp.

b: Eradicated after rail surveys

c: Guava (*Psidium guava*) dominant over large areas

response of rails to playbacks (Conway et al. 1993). Sites were located approximately in the same location, based on the survey site descriptions (see Table 2 and Rosenberg 1990). Surveys were replicated at each site and consisted of 25m radius circular plots (0.20 ha), with approximately 100m spacing between plots. We used a playback system (recording obtained from Cornell Lab of Ornithology), playing rail calls for 1 minute (15 seconds in 90 degree rotations); we scored responding rail calls for a total of 3 minutes (1 minute of playback + 2 minutes following). We scored only those rails within the 25m radius, and we attempted to count individual rails only once. We characterized plot vegetation structure using two categories: high (>25% cover of forbs and grass >30cm tall) or low (<25% cover of forbs and grass >30cm in height and >25% cover in forbs and grass <30cm in height; sensu Rosenberg 1990). We also recorded the presence or absence of standing water within the survey plot. We also

surveyed seven additional sites on Isabela Island for the first time to provide baselines for future surveys (Table 2).

Table 2. Galápagos rail surveys conducted in 2004/05. Number of rails detected and density (per hectare) at 12 sites on three islands in the archipelago. Chi square and p-value columns show temporal comparisons from surveys in 1986; Sierra Negra sites declined, Santiago sites increased (see text and Figure 2).

Island (<i>Site</i>) ^a	# of rails	density	# of survey plots	chi sq.	p-value
Fernandina	11	1.8	31		
<i>highlands</i>	11	3.4	16		
<i>mangrove</i>	0	0.0	15		
Isabela	13	0.2	247		
<i>highlands - Ecuador</i>	0	0.0	16		
<i>highlands-Wolf</i>	10	1.4	37		
<i>highlands-Darwin</i>	0	0.0	18		
<i>mangroves - Puerto Chino</i>	0	0.0	20		
<i>highlands-Alcedo</i>	0	0.0	85		
<i>mangroves-Punta Alfaró</i>	0	0.0	14		
<i>highlands - NE Sierra Negra</i>	0	0.0	29	1.9	0.16 (0.341 ^b)
<i>highlands - SE Sierra Negra</i>	3	0.5	28	10.7	0.005
Santiago	279	13.2	92		
<i>highlands-Central</i>	233	17.9	65	77.2	< 0.001
<i>woodlands-La Chosa</i>	46	8.5	27	44.6	< 0.001
Total	303		370		

a: Site locations: Fernandina-highlands S 00.4075 W 91.5493; Fernandina-mangrove S 00.2646 W 91.4487; Isabela-Ecuador S 00.0278 W 91.5553; Isabela-Wolf S 00.0216 W 91.3716; Isabela-Darwin S 00.1977 W 91.3168; Isabela-Puerto Chino S 00.4258 W 90.9588; Isabela-Alcedo S 00.4492 W 91.1063; Isabela-Punta Alfaró S 00.3535 W 91.2800; Isabela-NE Sierra Negra S 00.7967 W 91.0910; Isabela-SE Sierra Negra S 00.8458 W 91.1052; Santiago-highlands S 00.2375 W 90.7581; Santiago woodlands S 0.2768 W 90.7604

b: p-value for Fisher's Exact Test

We detected a total of 303 rails (n = 370 surveys at 12 different sites; Table 2). Rail density varied from 0 – 17.9 rails per hectare (Table 2). Overall, rails showed a significant affinity for high vegetation compared to low ($\chi^2 = 19.05$, d.f. = 3, $p < 0.001$, n = 326, four categories: 0, 1, 2, >2 rails at each plot compared across vegetation score). Rails also showed a significant affinity for the presence of water in the survey

plot ($\chi^2 = 38.48$, d.f. = 3, $p < 0.001$, $n = 326$, four categories: 0, 1, 2, >2 rails at each plot compared across presence of water). We did not detect rails at the three mangrove sites surveyed.

On Santiago Island, we identified 279 rails in 92 survey plots (Table 2). Mean density increased significantly by over an order of magnitude at both survey sites compared to 1986/87 (four categories: 0, 1, 2, >2 rails at each plot compared across year; categories used for comparison with Rosenberg 1990; Table 2; Figure 2). In the highlands of Santiago Island, only 16 rails were located in 113 survey plots compared to 233 rails in 2004/05 in 65 survey plots (Table 2). In the lower elevation woodland habitat (La Chosa), rails were not detected during 1986/87; 46 rails were detected in December 2004.

In the highlands of Fernandina Island, which has remained free of invasive mammals, we found eleven rails on the south-southwestern slope. Rosenberg (1990) failed to detect rails on the southeastern rim of Fernandina with surveys ($n = 29$ plots); however, he did detect a small number of free-calling rails on the south-southwestern slope during the same time period. We detected only three rails at the two sites on Sierra Negra Volcano, Isabela Island, a significant decline from the surveys in 1986/87 (Table 2; Figure 2). We detected rails on Wolf Volcano, but not at the remainder of sites surveyed on Isabela Island (Table 2). However, they have been observed on Alcedo Volcano (V. Carrion and K. Campbell, personal observations).

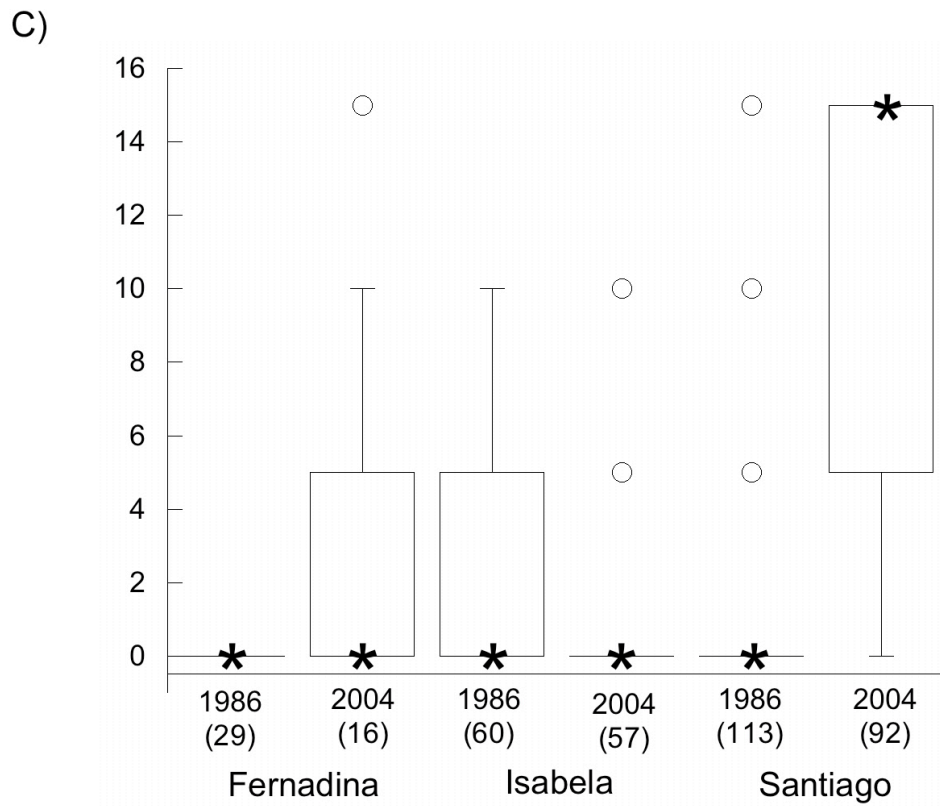
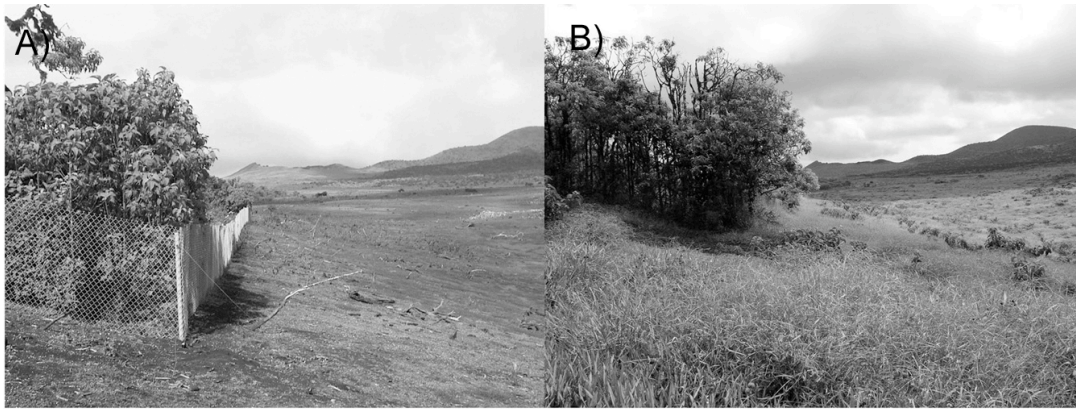


Figure 2. Habitat recovery on Santiago Island and the Galápagos rail. A) An enclosure and surrounding area in the highlands of Santiago Island before (March 1999) and B) after non-native pig and goat removal (March 2005). C) Box plots of Galápagos rail surveys showing the median rails per hectare (*) on three islands sampled in 1986/87 and 2004/05. Total number of survey plots for each year is shown in parenthesis. Non-native mammals were continuously present and absent on Isabela and Fernandina Island respectively during the two survey periods. Feral pigs and goats were removed from Santiago between 1998-2006.

Discussion

The changes in rail densities on Santiago Island between 1986/87 and 2004/05 is impressive, and a comparison of rail abundance among the three islands surveyed in this study provides inference that these changes are likely attributed to eradication of invasive mammals on Santiago. A total of thirteen rails were detected in 1986/87 island compared to 279 rails in 2004/05 with similar effort (113 vs. 92 survey plots respectively). On Fernandina Island (free of invasive mammals), survey results were similar between the two periods, with rails relatively rare during both periods. On Sierra Negra, Isabela Island, where invasive mammals have been present since the original survey, survey results were similar between the two periods with some evidence of decline at one site (Table 2). In a separate study, rail surveys on Santa Cruz Island in 2000, where goats and pigs are present, detected a minor declines compared to surveys in 1986/87 (Gibbs et al. 2003). The cause of the declines on Santa Cruz are unknown; however, habitat changes via invasive plants is suspected (Gibbs et al. 2003). The plant communities on Santiago Island are recovering following pig and goat removal campaigns (Figure 2; Cruz et al. 2005), following a pattern similar to what has been documented on other Galápagos islands where goats have been removed (e.g., Pinta Island; Campbell et al. 2004; Hamann 1979, 1993a). While it remains to be seen how the Santiago rail population will respond as plant communities continue to recover, the initial changes in rail density are encouraging.

While many insular rail species have suffered extinction due to invasive mammal impacts, populations of this and other insular species have recovered following eradication campaigns. On Pinta Island, Galápagos, rails were not observed in 1970 when goats were present in high densities (Franklin et al. 1979). In contrast, rails were common three years later after the initiation of a goat control program and the vegetation began to recover (Franklin et al. 1979; Kramer & Black 1970). In New

Zealand, a massive conservation intervention spanning over fifty years, including the control of non-native red deer (*Cervus elaphus*), has prevented the extinction of the takahe (*Poryphyrio hochstetteri*); over 200 birds are now in the wild (Lee & Jamieson 2001). On Lowe Howe Island, Australia, an endemic woodhen (*Tricholimnas sylvestris*) was on the brink of extinction; however, pig eradication and a captive-breeding program have now restored this species (Miller & Mullette 1985; NSW National Parks and Wildlife Service 2002).

While pig and goat removal appear to have facilitated the Santiago Galapagos rail recovery, additional abiotic and/or biotic factors may also play roles in the species distribution and demography. For example, it is unclear why rail densities are low on Fernandina where there is no history of non-native predators and herbivores, invasive woody plants are not present, and the appropriate highland vegetation is present. Due to large areas of bare lava on Fernandina, rail populations may be low as a consequence of fragmentation effects. There are also historical records of rails from coastal mangrove sites on Fernandina (Franklin et al. 1979; Salvin 1876), but there have been no observations among mangrove sites in this study or the three others over the past 20 years (Franklin et al. 1979; Gibbs et al. 2003; Rosenberg 1990). In 2004 rails were detected in mangrove habitat on Genovesa Island (T. Grant and G. Estes, personal communication).

Previous evidence suggests that egg predation by pigs and habitat degradation via invasive woody plants and goats threaten the persistence of Galápagos rail populations (Coblentz & Baber 1987; Franklin et al. 1979; Gibbs et al. 2003; Rosenberg 1990). As has been documented elsewhere (Wanless et al. 2002), predation by cats and rats likely also threaten Galápagos rails where they are sympatric. However, this study and others suggest that insular rail populations can respond positively to restoration actions (Lee & Jamieson 2001; Miller & Mullette 1985; NSW

National Parks and Wildlife Service 2002; Wanless et al. 2002; Witteman et al. 1990). However, as demonstrated for the Lord Howe Woodhen, recovering rail populations should be managed with close attention to other potential demographic threats, such as catastrophes and disease, as well as invasive species (Brook et al. 1997). In general, insular rails may be useful as a focal species (Landres et al. 1988) on islands where direct and indirect impacts of invasive mammals are apparent, and they may be useful as a restoration and recovery gauge once invasives are removed.

Globally, thousands of species or populations of insular rails have gone extinct due to anthropogenic impacts, including those of invasive mammals, and many remained threatened today (Bennett & Owens 1997; Steadman 2006). Twenty-two of the 33 threatened rail species currently listed by the World Conservation Union occur on islands, and 86% of those insular species are threatened by invasive mammals (data compiled from BirdLife International's World Bird Database, and includes IUCN categories *VU*, *EN*, *CR*, and *EW*). Invasive mammal eradications from islands are now commonplace (Campbell & Donlan 2005; Howald et al. in press; Nogales et al. 2004). Targeted eradications, along with proposed reintroductions and translocations (Steadman 2006), would likely benefit endangered rail populations. Before the turn of the century, Darwin commented on the great number of rails on Santiago Island (Darwin 1896). Their recovery a century later is encouraging for Rallidae conservation.

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CHAPTER 3: Nested communities, invasive species and Holocene extinctions:

Evaluating the power of a potential conservation tool

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Abstract

General ecological methods and models that require a minimum amount of information yet are still able to inform conservation planning are particularly valuable. Nested subset analysis has been advocated as such a tool for the prediction of extinction-prone species and populations. However, such advocacy has not been without skepticism and debate, and in the majority of published examples assessing extinction vulnerability, actual extinctions are based on assumptions rather than direct evidence. Here, we empirically test the power of nested subset analysis to predict extinction-prone species, using documented Holocene insular mammal extinctions on three island archipelagos off the west coast of North America. We go on to test whether the introduction of invasive mammals promotes nestedness on islands via extinction. While all three archipelagos were significantly nested before and after the extinction events, nested subset analysis largely failed to predict extinction patterns. We also failed to detect any correlations between the degree of nestedness at the genus-level with area, isolation, or species richness and extinction risk. Biogeography tools, such as nested subset analysis, must be critically evaluated before they are prescribed widely for conservation planning. For these island archipelagos, it appears detailed natural history and taxa-specific ecology may prove critical in predicting patterns of extinction risk.

Introduction

Conservation planning and policy often demand that decisions about the fates of specific species and communities be made on the basis of a limited amount of information, gathered in a limited amount of time (Soule 1985). As a result, ecologists have sought organizing principles of ecology that can be broadly applied to conservation problems (Doak & Mills 1994; Soulé & Terborgh 1999). General methods and models that can be applied to a variety of conservation scenarios, require a minimum of information, and provide critical predictions are especially valuable. At the top of the list of such key predictions are the immediate and medium-term vulnerability to extinction of populations and species (Doak & Mills 1994; Terborgh & Winter 1980). Since its initial application by Patterson and Atmar (1986), the use of nested subset analysis of species occurrence patterns has become an increasingly common tool in community ecology and many have advocated its use in conservation planning, particularly in reserve design and predicting species susceptibility to extinction (Patterson 1987; Cutler 1991, McDonald and Brown 1992; Fleishman et al. 2000; Kerr et al. 2000; Fleishman and McNally 2002; and many others). However, such advocacy has not been without substantial skepticism, concern, and debate (Boecklen 1997; Doak & Mills 1994; Quinn & Harrison 1988; Simberloff & Martin 1991; Skaggs & Boecklen 1996). Here, we investigate the relationship between nestedness patterns and extinction risk, using data on the mammalian faunas and extinction patterns of three island groups off the coasts of California, USA, and Baja California, Mexico.

A perfect nested pattern results when all species that occur on islands (or habitat fragments) containing n species also occur on all islands (fragments) containing $n + 1$ species (Darlington 1957; Patterson & Atmar 1986). Many, if not most, islands or fragments are significantly nested in a statistical sense; however, few

are even close to perfectly so (Wright et al. 1998). Similar to how species compositions of islands/fragments can be nested, incidence distributions of individual species can also be nested. Thus, both sites (islands/fragments) and species can possess nested qualities. Studies of nestedness have evolved from the elucidation of patterns and the refinement of statistical models to exploring the mechanisms that generate such patterns (Atmar & Patterson 1993; Cutler 1991; Lomolino 1996; Patterson 1987; Patterson & Atmar 1986; Wright et al. 1998). Both abiotic and biotic processes have been implicated in generating nested distributions, including area, selective extinction, differential colonization, environmental variables, distribution of resources, and anthropogenic disturbance (Cook & Quinn 1995; Fernandez-Juricic 2002; Hecnar et al. 2002; Wright et al. 1998).

Nestedness analysis is often portrayed as a tool to predict the order in which extinctions are likely to occur at a suite of sites in response to habitat reduction, fragmentation, or other types of disturbance (Bolger et al. 1991; Cutler 1991; Kerr et al. 2000; McDonald & Brown 1992). The general idea behind these predictions is that populations that are close to the predicted edge of likely occurrence on a particular island are more at risk of extinction, particularly as the nestedness of a system decreases or species or population turnover (i.e., extinction) increases (Atmar and Patterson 1993). However, such predictive power is based on inferred extinctions (e.g., faunal relaxation of Pleistocene land-bridge islands), and these hypothesized extinctions rely on a number of assumptions that are not necessarily valid (Simberloff & Martin 1991; Skaggs & Boecklen 1996). Further, the presence of a nested pattern does not necessarily implicate ordered extinction probabilities. Differences in colonization ability, among other possible factors, can also lead to such a pattern (Darlington 1957; Kadmon 1995). While the interacting effects of area and disturbance on extinction risk has a long history (Diamond 1972; Terborgh 1974), in

an alarming fraction of published examples assessing extinction vulnerability, evidence of patterned extinctions are based on statistical extrapolations with questionable assumptions, rather than direct evidence. Furthermore, direct observations of idiosyncratic species loss and subsequent species interactions with fragmentation suggest that such assumptions may not be valid (Terborgh et al. 1997).

Here, we empirically test the relationship between predicted extinction risks from nestedness analyses and the actual extinction and endangerment status of populations. Specifically, we test the power of nested subset analysis to predict the relative extinction risks of different species and populations, using documented Holocene insular mammal extinctions on islands off the west coast of North America. Given the large role invasive species play in global extinctions (Groombridge et al. 1992) and their complex interactive effects with biodiversity (Roemer et al. 2002; Vitousek & Walker 1989), we also ask whether extinctions caused by introduced species strengthen or weaken nestedness patterns, as has been inferred elsewhere (Hecnar & McCloskey 1997). At the core of this paper is an attempt to evaluate whether biogeography tools, such as nested subset analyses, are useful in predicting species endangerment, or whether knowing the autecological details of a species and their community interactions is necessary to correctly gauge risks of extinction and endangerment.

Materials And Methods

Study System

This study includes data on nonvolant mammals (all those but bats) on islands off the coasts of central California, USA south to the tip of Baja California, Mexico, including the Gulf of California (Figure 3). Islands were broken into three groups according to location, biogeographical history, and island type (oceanic or land-

bridge). The California Channel Islands (henceforth, *California*) have not been connected to mainland California during the Quaternary, while the islands off the Pacific side of Baja California (*Baja*) were connected to the Baja peninsula during the Pleistocene (Case et al. 2002; Junger & Johnson 1980). Due to the small number of oceanic islands in the Gulf of California, only islands (henceforth, *Gulf*) that were connected either to the Baja peninsula or mainland Mexico during the Pleistocene are included in the analysis (Case et al. 2002). For all archipelagos, only islands with native mammals present historically were included. Overall, each island group shares a common biogeographic history, a shared ancestral species pool, and to a certain extent similar environmental gradients, all assumptions of nested subset analysis (Atmar & Patterson 1993).

The insular mammal fauna of western North America is well studied (Huey 1964; Lawlor et al. 2002; Álvarez-Castañeda & Patton 1999). The majority of these islands have a documented history of introduced mammals, resulting in several recent extinctions. Seabirds and nonvolant mammals have suffered the greatest impact; here we concentrate on the latter. While up to seven species of exotic mammals occur on some islands in the region, feral cats (*Felis catus*), and to a lesser extent non-native rats (*Rattus* spp.) are responsible for the majority of extirpations and extinctions (Table 3; Tershy et al. 2002; Wood et al. 2002).

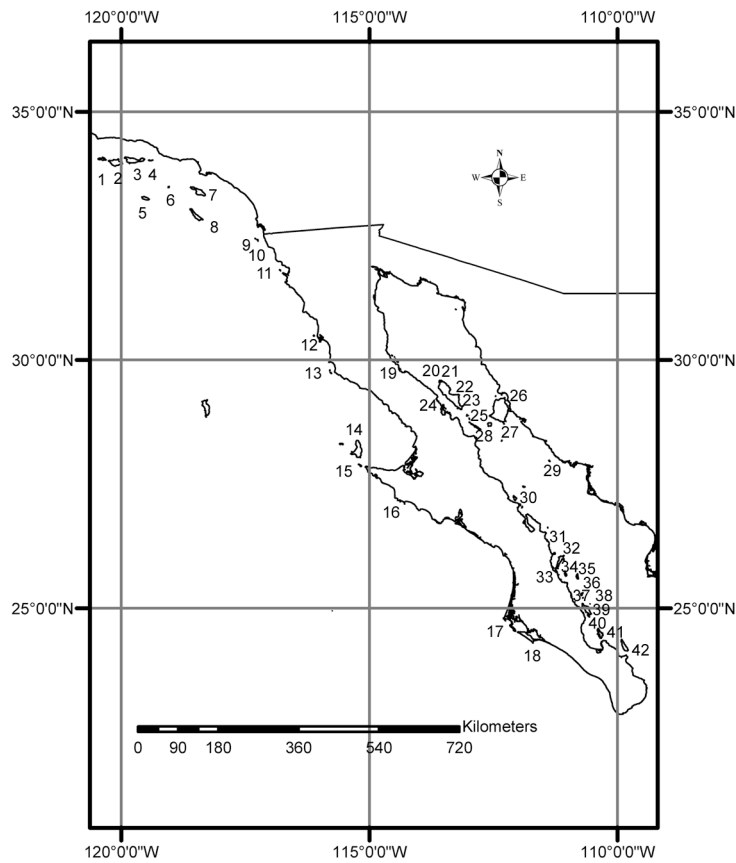


Figure 3. Three island archipelagos off the coasts of California, USA and Baja California, Mexico. California: 1: San Miguel, 2: Santa Rosa, 3: Santa Cruz, 4: Anacapa, 5: San Nicolas, 6: Santa Barbara, 7: San Catalina, 8: San Clemente, Baja California-Mexico: 9: Coronado North, 10: Coronado South, 11: Todos Santos South, 12: San Martin, 13: San Geronimo, 14: Cedros, 15: Natividad, 16: San Roque, 17: Magdalena, 18: Margarita, Gulf of California-Mexico: 19: Willard, 20: Granito, 21: Meija, 22: Angel de la Guarda, 23: Estanque, 24: Smith, 25: Salsipuedes, 26: Tiburon, 27: Turner, 28: San Lorenzo, 29: San Pedro Nolasco, 30: San Marcos, 31: Carmen, 32: San Jose, 33: Danzante, 34: Montserrat, 35: Santa Catalina, 36: Santa Cruz, 37: San Diego, 38: Animas, 39: San Jose, 40: San Francisco, 41: Espiritu Santo, 42: Cerralvo. Only islands included in the analysis are shown; island names correspond with numbers.

Table 3. Taxa of nonvolant mammals considered extinct (E) or likely extinct (LE) on islands off the west coast of North America. Likely causes and estimated date of extinction are shown (C=cats, R=rats, P=pigs, UN=Unknown, LP=Late Pleistocene, R=1950-present). Other approximate or ranges of dates during the Holocene range from 11,000 YrBP to the late 1800s.

Island Group	Extinct Taxon	Cause	Est. Date	Ref.
<i>Baja CA Pacific – Land-bridge</i>				
San Roque (E)	<i>Peromyscus maniculatus cineritus</i>	C/R	R	1,2
San Martin (E)	<i>Neotoma martinensis</i>	C	R	3
Todos Santos (E)	<i>Neotoma anthonyi</i>	C	R	2,4
<i>CA Channel Islands – Oceanic</i>				
San Miguel (E)	<i>Mammuthus exilis</i> ^a	UN	11,030 YrBP	5
San Miguel (E)	<i>Microtus</i> sp. nov.	UN	11,000 YrBP	6
San Miguel (E)	<i>Spilogale gracilis</i> ^b	UN	Late 1800s (?)	7
San Miguel (E)	<i>Sorex ornatus cf. willetti</i> ^c	UN	1,000 BP – 1800s	6
San Miguel (E)	<i>Peromyscus nesodytes</i>	UN	8,000 YrBP	6,7
San Miguel (E)	<i>Urocyon littoralis littoralis</i> ^d	P	R	8
Santa Catalina (LE)	<i>Sorex ornatus willetti</i> ^e	UN	R	9
Santa Cruz (E)	<i>Mammuthus exilis</i> ^a	UN	11,030 YrBP P	5
Santa Rosa (E)	<i>Mammuthus exilis</i> ^a	UN	11,030 YrBP	5
Santa Rosa (E)	<i>Peromyscus nesodytes</i>	UN	LP	10
Santa Rosa (E)	<i>Urocyon littoralis santarosae</i> ^d	P	R	8
Anacapa (E)	<i>Peromyscus anyapahensis</i>	UN	LP	10
<i>Gulf of California – Land-bridge</i>				
San Pedro Nolasco	<i>Peromyscus pembertoni</i>	R	R	11
Coronados (E)	<i>Neotoma bunkeri</i>	C	R	11,12
Granito (E)	<i>Peromyscus guardia harbitsoni</i>	R	R	11,13
Meija (E)	<i>Peromyscus guardia mejia</i>	C	R	11,13
Estanque (E)	<i>Peromyscus guardia subsp.</i>	C	R	13
San Jose (E)	<i>Dipodomys insularis</i>	C	R	11
Montserrat (E)	<i>Chaetodipus baileyi fornicatus</i>	C	R	11,14
Turner (LE)	<i>Neotoma varia</i> ^f	UN	R	11,15

a: estimated date of extinction on all three islands are based on the youngest radiocarbon date of pooled specimens; b: based on a fossil cranium and unpublished field notes of trapped skunks ~1893; c: abundant in the fossil record; may have gone extinct sometime in the 19th century due to land transformation by introduced sheep overgrazing; d: extinct in the wild; captive populations exist; e: last specimen collected in 1983; extinction may be due to habitat destruction from introduced herbivores and cats; f: single specimen trapped in 1977, despite trapping efforts in 1976 and 1997 (536 trap-nights) and small island size

References: 1 - Alvarez-Castaneda & Cortes-Calva 1996; 2 - Donlan et al. 2000; 3 - Cortes-Calva et al. 2001; 4 - Mellink 1992; 5 - L. Agenbroad, pers. comm.; 6 - Guthrie 1993; 7 - Walker 1980; 8 - Roemer et al. 2002; Roemer et al. 2004; 9 - Williams 1983; Collins & Martin 1985; 10 - White 1966; 11 - Alvarez-Castaneda & Ortega-Rubio 2003; 12 - Smith et al. 1993; 13 - Mellink et al. 2002; 14 - Alvarez-Castaneda & Cortes-Calva 2002; 15 - Bogan 1997

Other introduced mammals, including European rabbits, goats and pigs, have also had detrimental indirect impacts (Coblentz 1978; Donlan et al. 2002; Moran 1996; Roemer et al. 2002). Prompted by these losses, regional island conservation programs are underway that document and remove invasive mammals from islands off California (Donlan & Comendant 2003; Halvorson 1994; Schuyler et al. 2002) and Mexico (Donlan et al. 2003b; Tershy et al. 2002).

At least 21 mammal extinctions or extirpations have occurred from the islands included in our study (henceforth we refer to all local population losses as extinctions). All the extinctions on the Baja and Gulf archipelagos are recent (last 50 years), and all but one (10/11) can be attributed wholly or partially to the presence of introduced predators (see Table 3 and references therein). In contrast, of the 11 extinctions on the California Islands, 9 took place earlier in the Holocene and thus their causes are less clear (11,000 YrBP – 1800s; Table 3). These early Holocene extinctions, as well as those of a number of avian and non-avian reptiles, are coincidental or occur after the arrival and establishment of Native Americans on the Channel Islands (12,020 - 10,700 BP; Guthrie 1993; Orr 1968). The early Holocene (or Late Pleistocene) extinction of two species of *Peromyscus* (*P. nesodytes* and *P. anyapahensis*) were replaced by congeners (*P. maniculatus* ssp.), the latter possibly introduced by Native Americans (Guthrie 1993). The dwarf mammoth, *Mammuthus exilis*, occurred on Santa Rosa, Santa Cruz, and San Miguel Islands beyond the limit of radiocarbon dating (41,000 YrBP). Prior to c. 13,000 YrBP, all three islands, along with Anacapa Island, formed the larger island, Santarosae (Agenbroad 2001). Mammoth populations survived after the inundation of Santarosae and the forming of the current islands, with the youngest bone being dated at 11,030 RCBP (radiocarbon years, L. Agenbroad, personal communication), and thus they were included as three separate populations in the analysis. A single tooth of *M. exilis* has been reported from

San Nicolas Island; however, it is excluded from the analysis due to doubts of the validity and origin (e.g., human transport) of the fossil (L. Agenbroad, personal communication). The records of *M. exilis* on the other islands are based on multiple specimens (Agenbroad 2003a, 2003b).

In our analysis, we also include as extinctions two insular species that are only remotely likely to still exist. On the small island of Turner (189 ha), *Neotoma varia* has not been documented since 1977, despite at least two trapping efforts; however, a specific survey has been recommended to confirm extinction (Alvarez-Castaneda and Ortego-Rubio 2003). On Santa Catalina Island, *Sorex ornatus willetti* was last collected in 1983. This shrew is likely extinct due to habitat destruction from introduced herbivores and predation from feral cats (Collins & Martin 1985; Williams 1983). We repeated all analyses described below twice, counting three other endangered populations as either extant or extinct. The island fox (*Urocyon littoralis*), endemic to the California Channel Islands, is endangered or extinct on five of the six islands it occurs: extinct in the wild with captive populations on San Miguel and Santa Rosa Islands and endangered on Santa Catalina, Santa Cruz, and San Clemente Islands due to apparent competition induced by introduced pigs, introduced disease, and mismanagement (Roemer et al. in press; Roemer & Wayne 2003).

Nested Subset Analysis

Nested subsets analysis is based on a matrix of occurrences of species (or, as here, genera: see below) on different islands. In these matrices, each cell indicates either the occurrence or absence of a species on a particular island. Species are ordered from those with the most to the least number of occurrences, while islands are ordered from most to least species rich. This results in a matrix with solid occurrences in the

upper left, and no occurrences in the lower right. The strength of this pattern of discrete blocks of occurrences and non-occurrences in the matrix, as opposed to a random array of occurrences, indicates the degree of nestedness.

We performed six nested subset analyses for native mammals, using separate analyses for historical and current species occurrence data for each of the three island groups. Species presence/absence data for both native and exotic mammals, as well as geographical data, were obtained from a regional conservation database (Donlan et al. 2000) and published literature (Case et al. 2002; Guthrie 1993; McChesney & Tershy 1998; Álvarez-Castañeda & Ortega-Rubio 2003; Álvarez-Castañeda & Patton 1999). Given the presence of congener endemic species/subspecies that are arguably ecological analogs, all analyses were conducted at the generic level. A total of 19 genera occur or occurred on 42 islands in our study area, with only seven islands harboring two species within the same genus (all *Peromyscus* and *Chaetodipus*). In four of these cases, one of the conspecifics is now extinct. The strength of the nestedness pattern for each occurrence matrix was evaluated using the methods of Atmar and Patterson (1993; 1995), with “temperature” (T, 0° indicating maximum nestedness and 100° complete disorder) giving a relative measure of nestedness compared to a null model estimated using a Monte Carlo simulation (1000 iterations). This method arranges the island-species matrix to minimize the unexpectedness of occurrences. This index is matrix-size independent, allowing for spatial and temporal comparisons (Patterson & Atmar 2000). In particular, we use the temperature before and after Holocene extinctions to determine the impact of extinctions caused by introduced species on the strength of nestedness patterns.

We estimated risk of extinction using two approaches, both of which have been advocated in the literature (Hecnar et al. 2002; Kerr et al. 2000; Patterson & Atmar 2000). First, we compared the recent extinctions of populations to their position in the

historical occurrence matrix. Patterson and Atmar (2000) suggest that the populations near the boundary line between largely unoccupied and mostly occupied cells are at the greatest risk of extinction; further, the nestedness temperature method calculates the probability of each matrix cell being occupied, thus quantitatively assessing the stability of various populations.. To test qualitatively for an association between extinction and these risk measures, we categorized risk estimates as high or low, using a conservative probability occurrence (< 50%) as indicating high risk. To test quantitatively for an association between extinction and predicted risk, we performed a logistic regression of risk score (i.e., median of the range of probability of occurrence outputted by the nested analyses), archipelago, and their interaction on extinction versus persistence of populations. To test more generally whether there were any deviations in distributions of the risk ratings between extinct and extant populations, we also used Kolmogorov-Smirnov 2-sample tests for data from each archipelago, and overall. Note, however, that risk values for each matrix cell depend on the entire pattern of occurrences. Thus, these values are not independent and statistical results based upon them should be viewed with some caution.

Second, we asked whether the strength of historical nestedness for individual genera correlated with extinction. For each genus and island group, we first separately evaluated whether occurrence patterns were well ordered by area, isolation (i.e., distance from mainland), or species richness. For each of these ordering variables, we produced a vector of occurrences/non-occurrences and used a Wilcoxon 2-sample rank-sum statistic test (i.e., Mann-Whitney U-test) to assess orderedness, or nestedness (Simberloff & Martin 1991). To compare among genera and across archipelagos, we report the chi-square approximation (1 d.f.) and respective probabilities rather than the magnitude of the U-score, given that the latter is sample size dependent (Zar 1996). To ask if the degree of ordering predicts extinction risk, we report Spearman rank

correlations between the nestedness scores of genera (i.e. chi-square test statistic) and the fraction of original populations that have become extinct, for each island group and ordering variable. Statistical analyses were conducted in Systat 10.0 and SPSS 11 with an α -level = 0.05 (Wilkinson 1998).

Results

Mammals in all island groups exhibited significant nestedness before and after recent extinctions (Table 2). Historically, California and Gulf islands were more nested than Baja islands; while the Gulf islands are presently more nested than Baja and California islands (Table 2). However, nestedness was similar on all archipelagos. Extinctions resulted in inconsistent changes in nestedness for the three island groups. The California and Baja island groups decreased slightly in nestedness, while the Gulf islands hardly changed as a result of extinctions (Table 2). There was no clear pattern between introduced species, extinction, and nestedness. All but one extinction on the Gulf islands (7/8) were caused by introduced predators, resulting in little change in degree of nestedness, and all three extinctions on the Baja islands (3/3) were caused by introduced predators, resulting in a slight decrease in nestedness (Tables 1 and 2). The twelve extinctions on the California Islands, for many of which the cause is uncertain (10/12), also resulted in a decrease in degree of nestedness (Tables 1 and 2).

Table 4. Nestedness of nonvolant mammal communities on islands off the Pacific coast of North America before and after recent mammal extinctions. Islands are broken into oceanic and land-bridge, the latter being connected to the mainland during the Pleistocene. The lower the index (Atmar and Patterson's Temperature) the more nested the community; p-values in parenthesis are the result of a null model comparison via a Monte Carlo simulation (1000 iterations).

	Historical	Current
Land-bridge		
Baja	9.06 (0.009)	10.8 (0.02)
Gulf	6.84 (<0.001)	6.75 (<0.001)
Oceanic		
California	6.26 (0.001)	8.10 (0.02)

Qualitatively, the models predicted four of the 23 extinctions: one species of *Sorex* with a probability of occurrence of <20% and three species of *Peromyscus* with a probability <40% (Figures 4 and 5). In some cases, populations in the upper-left corner of the matrix went extinct, although under a nested framework these should be the species most resistant to extinction (Figure 4; Paterson and Atmar 2000).

Quantitatively, the logistic regression of the extant and extinct populations yielded no significant results (Log-likelihood $\chi^2 = 2.09$; factor: p-value; risk: 0.261; archipelago: 0.338; risk \times archipelago interaction: 0.221, N = 114). Results did not change when archipelagos were pooled (p = 0.980) or when endangered species were included (p > 0.194). Distributions of the probability of occurrence resulting from the nested analyses between extinct and extant populations were not different for each archipelago (Kolmogorov-Smirnov Test, p > 0.120) or across all archipelagos (p = 1.00, N_{extinct} = 23, N_{extant} = 91; Figure 6).

Part of the rationale behind the prediction of extinction risk from nestedness patterns comes from the assumption that populations on islands with more species

will, on average, have lower extinction risk; however, the alternative could also be the case depending on the effects of species interactions, island area, and colonization (MacArthur and Wilson 1967; Atmar and Paterson 1993; Cook and Quinn 1995; Lomolino 1996). Using logistic regression with data from all island groups, we found no effect of richness in a model that included island group (Log-likelihood $\chi^2 = 2.16$, $p = 0.14$, $N_{\text{extinct}} = 23$, $N_{\text{extant}} = 91$). We also tested for an influence of richness on each island group separately. Richness had significant influence on extinction in the Baja group (Log-likelihood $\chi^2 = 4.22$, $p < 0.034$, $N_{\text{extinct}} = 3$, $N_{\text{extant}} = 24$), with probability of extinction declining with increasing richness. For both of the other island groups, there were substantial, but marginally significant trends towards richness effects ($\chi^2 = 3.54$, $p < 0.060$, $N_{\text{extinct}} = 12$, $N_{\text{extant}} = 14$; and $\chi^2 = 3.76$, $p < 0.052$, $N_{\text{extinct}} = 8$, $N_{\text{extant}} = 54$, for the California and Gulf groups, respectively). The trend in the Gulf islands was also for decreasing risk of extinction with increasing species richness. However, the trend was opposite for the California islands, with high risk on more species-rich islands.

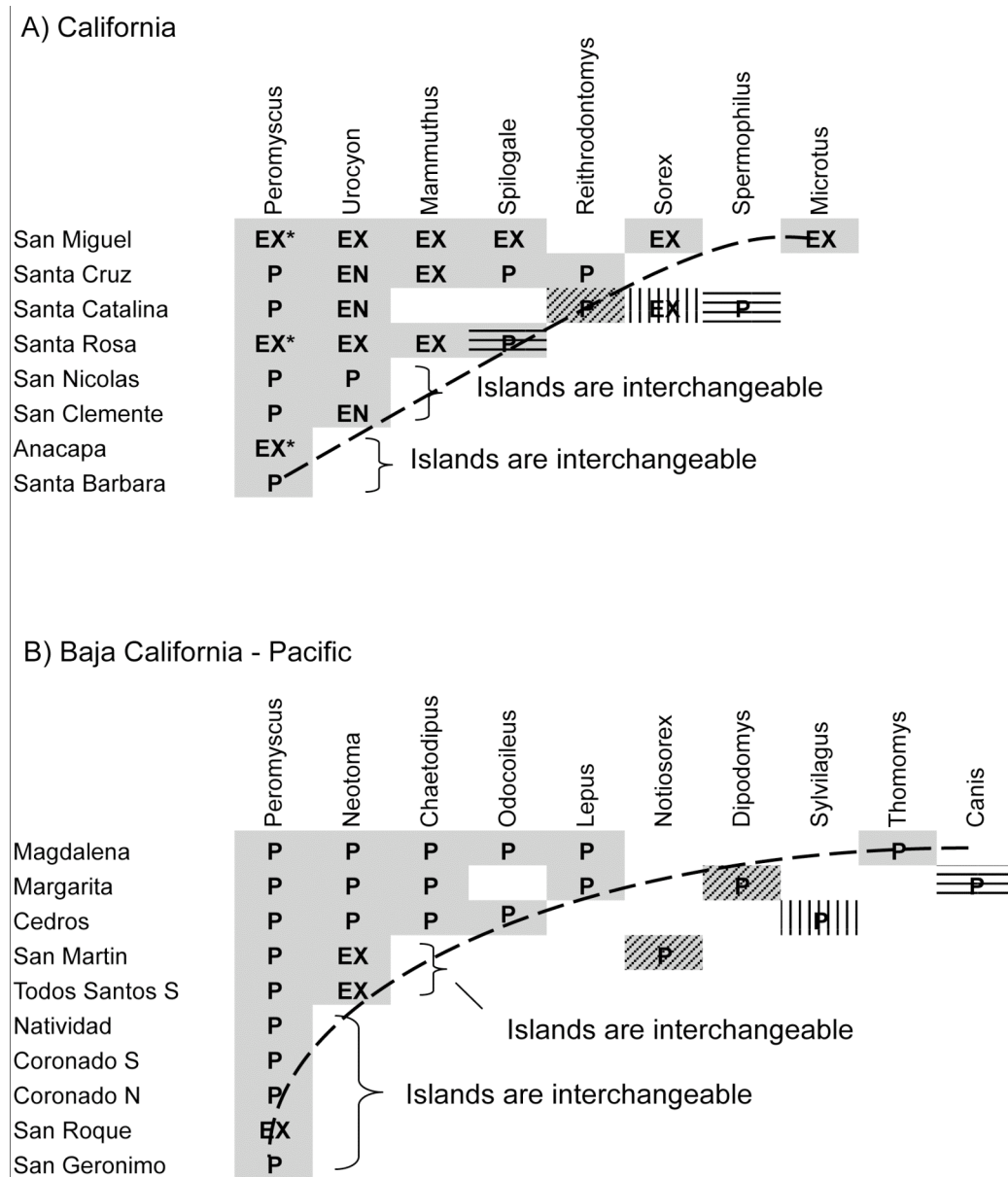


Figure 4. Nested nonvolant mammal communities on islands off A) California, USA and B) the Pacific side of Baja California, Mexico. P indicates species presence, EX recent extinctions, and EN endangered taxa. EX* indicates an extinction that was replaced by a congener. The dotted line illustrates the *boundary layer*. Certain islands are interchangeable in the arranged matrix due to identical species occurrences. Shaded boxes indicate probability of occurrence (see text): horizontal lines: 0-10%; vertical lines: 10-20%; diagonal lines: 20-30%; grey with diagonal: 30-40%; grey with horizontal stripes: 40-50%; grey: >50%.

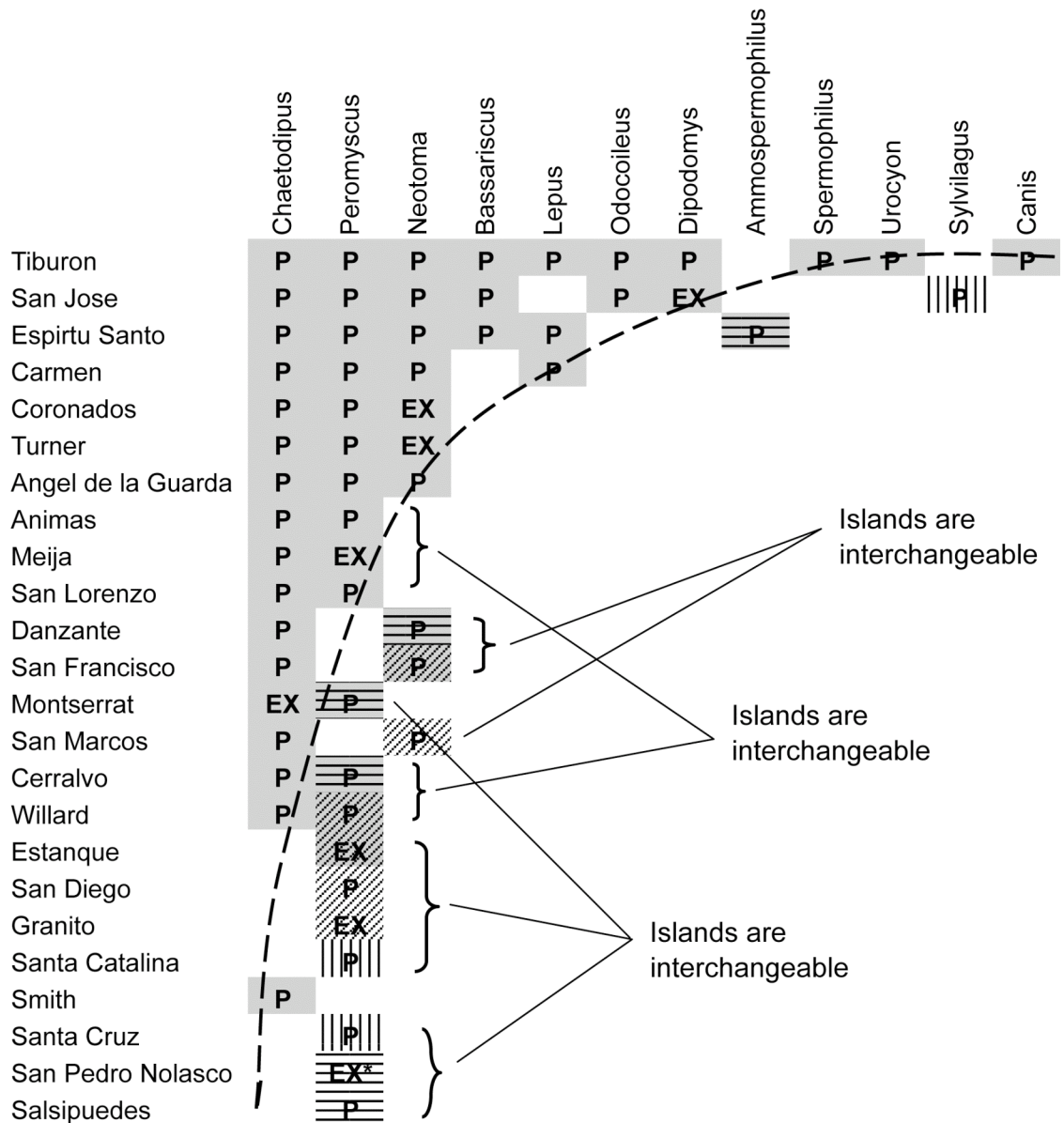


Figure 5. Nested nonvolant mammal communities on land-bridge islands in the Gulf of California, Mexico. P indicates species presence, EX recent extinctions, and EN endangered taxa. EX* indicates an extinction, but a congener remains extant. The dotted line illustrates the *boundary layer*. Certain islands are interchangeable in the arranged matrix due to identical species presence. Shaded boxes indicate taxa with a probability of occurrence (see Figure 4 caption).

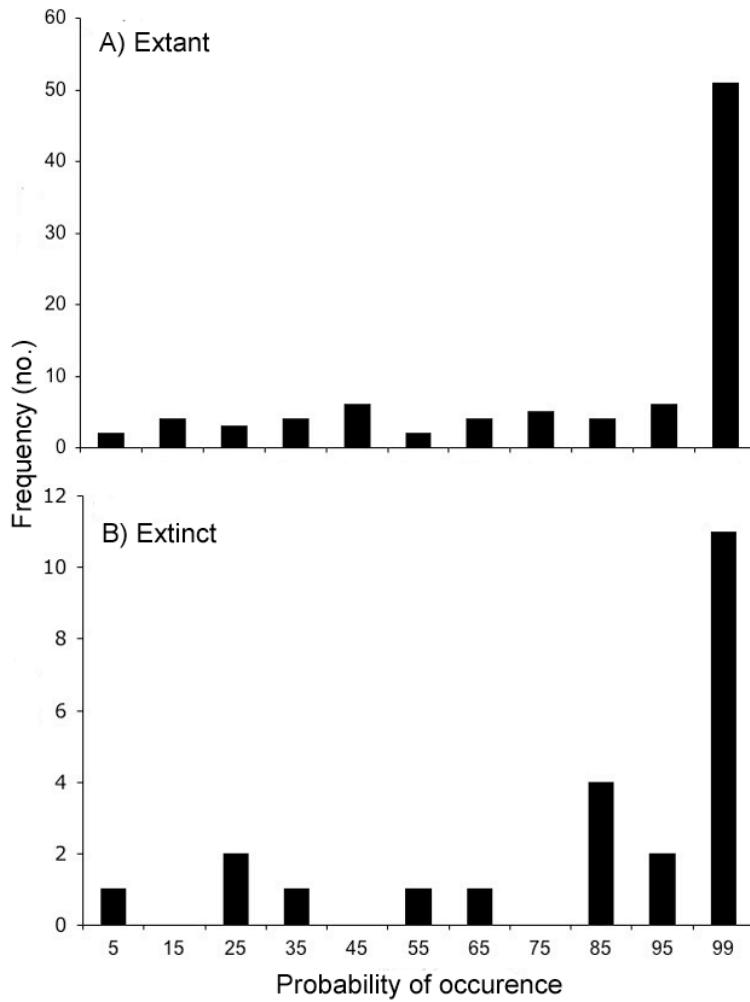


Figure 6. Distributions of the probability of occurrence from nested subset analysis of A) extant and B) extinct populations. Probabilities are reported as median percentages, as outputted from the analysis. No differences exist when populations are pooled across all three archipelagos: Kolmogorov-Smirnov 2-Sample Test, $p = 1.00$, $N_{\text{extinct}} = 23$, $N_{\text{extant}} = 91$.

Wilcoxon 2-sample rank-sum tests revealed complex patterns of nestedness at the level of individual genera. In general, few taxa were significantly nested in relation to species richness, area, or isolation (Table 3). On the Baja Islands, *Chaetodipus*, *Neotoma*, and *Odocoileus* (area only) were significantly nested when islands were ordered by species richness and area. *Lepus* was significantly nested when islands were ordered by species richness. On the California Islands, only *Urocyon* was significantly nested (ordered by species richness, area, and isolation). In the Gulf of California, a number of rodent genera (*Chaetodipus*, *Neotoma*, *Peromyscus*, and *Dipodomys*), and *Odocoileus* and *Bassariscus* were nested when ordered by one or more of the variables. None of the ordering variables (island richness, distance or size) correlated with the fraction of extinctions across genera (Table 3). When the island archipelagos were pooled, ordering by species richness produced a significant weak correlation with extinction ($S_r = 0.50$, $p = 0.03$), while ordering by the other variables showed no correlation with risk (Table 3).

Discussion

On the islands off west coast of California and Mexico, where recent mammal extinctions are well documented, nested subset analysis does a poor job of predicting observed extinctions. We could not find any statistically significant predictions of extinction risk. The utility of nested analysis in providing insights into nature reserve design and predicting extinction risk has been debated (Boecklen 1997; Doak & Mills 1994; Fleishman et al. 2002; Fleishman et al. 2000; Patterson 1987; Patterson & Atmar 2000; Simberloff & Martin 1991).

Table 5. Individual orderedness of mammal genera on three island archipelagos. Ordering variables include mammal species richness, island area, and isolation (i.e., distance to nearest mainland). Wilcoxon 2-sample rank-sum tests were used and the chi-square approximation values (1 d.f.) are reported; statistical significance is shown with ** ($p < 0.01$) and * ($p < 0.05$). *Peromyscus* spp. were not included (NI) in the analysis on the Baja and California archipelagos since they occur on every island. Spearman rank correlations (for each archipelago and for all islands pooled) are shown between chi-square statistics and fraction of original populations that are now extinct in each genera.

Genus	Baja Islands			California Islands			Gulf Islands		
	Rich	Area	Isolation	Rich	Area	Isolation	Rich	Area	Isolation
<i>Ammospermophilus</i>							0.1	0.8	0.1
<i>Bassariscus</i>							2.7	5.6*	2.7
<i>Canis</i>	2.2	0.7	0.7				2.2	2.7	2.2
<i>Chaetodipus</i>	6.5**	5.7*	0.3				13.4**	7.8**	7.5**
<i>Dipodomys</i>	2.2	0.75	0.3				2.8	4.7*	2.8
<i>Lepus</i>	5.0*	2.4	0.1				2.2	4.8*	2.2
<i>Microtus</i>				2.4	0.4	0.4			
<i>Mammuthus</i>				3.3	1.8	1.8			
<i>Neotoma</i>	7.8**	3.9*	17.0				4.8	5.8*	4.8*
<i>Notiosorex</i>	0.3	0.03	0.2						
<i>Odocoileus</i>	3.3	4.3*	0				2.8	4.7*	2.8
<i>Ovis</i>							2.2	2.7	2.2
<i>Peromyscus</i>	NI	NI	NI	NI	NI	NI	3.8*	0.1	3.8*
<i>Reithrodontomys</i>				1.8	2.7	2.7			
<i>Sorex</i>				3.4	0	0			
<i>Spermophilus</i>				0.7	0.4	0.4	2.2	2.7	2.2
<i>Spilogale</i>				3.3	0.4	1.8			
<i>Sylvilagus</i>	0.8	2.5	2.4				0.6	1.8	0.6
<i>Thomomys</i>	2.2	1.4	2.4						
<i>Urocyon</i>				4.1*	4.0*	4.0*	2.2	2.7	2.2
Spearman Rank Correlation (S_r)	0.65	0.29	0.71	0.56	-0.37	-0.37	0.55	-0.01	0.55
Bonferroni p-value	0.34	1.0	0.19	1.0	1.0	1.0	0.32	1.0	0.32
N	9	9	9	7	7	7	13	13	13
Archipelagoes Pooled									
S_r	0.50	-0.17	0.13						
Bonferroni p-value	0.03	1.0	1.0						
N	29	29	29						

However, in the majority (if not all) of past studies, extinction predictions have been inferred from unobserved historical events, such as relaxation events on land-bridge islands formed in the Pleistocene or habitat fragmentation (Bolger et al. 1991; Fleishman & Murphy 1999; Patterson & Atmar 1986; Soule 1991). In this effort to confirm the utility of nestedness predictions with documented extinction data, we come away without any evidence that this methodology can or should be used for predicting extinction risk.

The *temperature* method of Atmar and Patterson (1993; 1995) asserts that the topmost island or fragment in a packed matrix is the most hospitable, while the leftmost species is most resistant to extinction (i.e., holds the widest niche breadth, Patterson & Atmar 2000). The islands deemed the *most hospitable* in the three archipelagos were Magdalena and Margarita (Baja); San Miguel and Santa Cruz (California); Tiburon and San Jose (Gulf; Figures 4 and 5). On these islands, eight extinctions have occurred and an additional species is critically endangered (Table 4, Figures 4 and 5). Of the genera deemed most extinction-resistant (*Peromyscus*, *Neotoma*, *Chaetodipus*, and *Urocyon*), twelve populations have gone extinct and three are endangered (Table 4; Figures 4 and 5). On all three archipelagos, a single taxon occurs on the *least hospitable* islands; of these fifteen islands, five have suffered an extinction. On all three archipelagos, several extinct populations were located near the boundary line of occurrence matrices. However, this visual pattern was offset by the presence of other observed extinctions with strong predicted occurrences and the overall poor performance of the analysis to predict observed extinctions. For example, the island fox (*Urocyon littoralis*) is highly endangered or extinct in the wild (Roemer et al. in press; Roemer & Wayne 2003), while occupancy probabilities from the nested analysis were 97-100%. Of the 23 populations conservatively deemed threatened with

extinction, with a probability of occurrence <50%, only four suffered extinction.

Individual nestedness scores can be useful for determining which species or genera do and do not conform to an observed nested pattern. Taxa differ greatly to the degree they conform to their orderedness of an expected variable such area, isolation, or species richness (Table 5; Hecnar et al. 2002; Simberloff & Martin 1991). However, the ability to elucidate a mechanism to explain an observed species occurrence patterns relies on additional biological knowledge such as abundance, habitat requirements, or strength of species interactions. In addition, a species orderedness or lack thereof is a result of a number of possible mechanisms, and these mechanisms hold different conservation implications (Simberloff & Martin 1991). On all three archipelagos, species orderedness differed greatly with some genera being nested across all ordering variables (*Urocyon*), others being significantly ordered with just one variable, and many others showing no ordered pattern. The genus-level degree of orderedness failed to give insight into extinction risks; rather, detailed natural history and ecology are likely to hold the answers to such patterns.

Overall, nested subset analysis provided little qualitative or quantitative insight in predicting extinction risk. A number of prior studies have suggested a link between extinction and nestedness. However, such linkages have been based on inferences of extinction events based on assumptions about Pleistocene relict faunas or fragmentation-induced extinctions rather than direct evidence (Bolger et al. 1991; Cutler 1991; Kerr et al. 2000; Patterson 1987). While species loss may have occurred due to such events, other mechanisms are equally likely such as habitat requirements, colonization, or strong species interactions, and thus could have contributed to the observed species occurrence patterns. In this study with documented extinctions, the majority were not predicted. While a few of the predicted extinctions were corroborated by observed trends, these results could have been attained solely from the

information needed to conduct the analysis in the first place. Thus, it appears detailed natural history and taxa-specific ecology may prove critical in predicting even broad-scale patterns of extinction risk (e.g., Bennett & Owens 1997; Owens & Bennett 2000). In our opinion the best approach to making conservation and management decisions is the careful consideration of multiple ecological factors as they apply to individual taxa, rather than the application of a highly general model such as nested analysis. At the least, further research is needed in the utility of nested subset analysis before it is prescribed widely as a useful conservation tool.

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Chapter 4: Diversity, invasive species, and extinctions in insular ecosystems

Our ultimate theory of species diversity may not mention area, because area seldom exerts a direct effect on a species' presence – MacArthur & Wilson 1967

Abstract

Species invasions are a primary driver of species additions and deletions in ecosystems. Understanding the intricacies of invasions and their consequences is central to ecology and conservation. Extinctions are rarely random and often influenced by a suite of factors. We explore abiotic and biotic factors that correlate with and help provide proximate explanations for insular extinctions driven by invasive predators in western Mexico. A number of factors that were hypothesized *a priori* to explain the observed extinction patterns performed better than island area alone. Alternative prey available to invasive predators was negatively correlated with extinction, with twice the number of alternative prey species present on extinction-free islands compared to islands with extinctions. Carrying capacity estimates of extant populations were 27 times that of extinct populations. An aggregate model that included alternative prey, carrying capacity, and seasonal precipitation was the best performing model. Those factors, which are also supported by theory and empirical evidence, are informative to conservation decision makers. By focusing regionally on a specific threat, we provide a framework to practitioners that aids in prioritizing invasive predator eradications to halt insular extinctions.

Introduction

Understanding the causes and impacts of species additions and deletions in ecosystems is a central focus of ecology and conservation biology. The composition of local biotic communities arises via a series of successful invasions from a larger species pool, and subsequent species interactions with resident species such as predators, competitors, and prey (Ricklefs & Schluter 1993; Terborgh et al. 2001). A suite of factors, including body size, life history, and geographical range affect the dynamics of species invasions and extinctions; while some are well documented, many remain unknown and elusive (Fisher & Owens 2004; McKinney 1997). Invasions often cause species declines and extinction, particularly in insular ecosystems (Atkinson 1989; Towns et al. 2006). But invasions and extinctions are rarely random, and are usually caused by multiple factors and their interactions (McKinney 1997; Roemer et al. 2002; Terborgh et al. 2001). Nonetheless, an emerging generality of anthropogenic global change is invasive species replacing native species with extensive biodiversity impoverishment (Lockwood & McKinney 2001).

Comparative methods are important tools in conservation biology, and the techniques are particularly useful for searching for mechanisms that underlie patterns of extinction risk (Terborgh 1974; Wilson & Willis 1975). Comparative methods also often hope to inform on-the-ground conservation planning and interventions, yet this goal is arguably more difficult to achieve for at least three reasons. First, many studies combine correlation analyses across multiple species with phylogenetic independent contrasts to test evolutionary hypotheses with respect to changes in ecological factors (e.g., the effect of a life history trait on extinction risk, see Fisher & Owens 2004 for a

review). Contrasting species with independent phylogenies is critical to control for similarities that might be caused by phylogeny; however, the approach gives priority to phylogeny over ecology, and the unit of analyses is evolutionary events within a clade rather than the unit of extinction (Sullivan et al. 2006; Westoby et al. 1995). Thus, additional and complimentary approaches are likely provide a useful risk assessment tool to decision makers, whose goal is to manage a suite of species (or populations) in a focal community (Sullivan et al. 2006).

Second, most studies seeking factors underlying extinction risk fail to explore the role of extrinsic factors such as interactions with the environment and other species (but see Blackburn & Gaston 2002; Fisher et al. 2003). Invasive species and habitat destruction, two primary threats to biodiversity, commonly trigger novel, complex interactions within species assemblages, often resulting in population declines or extinctions (Norbury 2001; Roemer et al. 2002; Terborgh et al. 2001).

Third, most comparative studies exploring extinction threats have been global in scope, covering broad taxonomic groups or using worldwide datasets, and pooling data on different extinction risks across suites of locales and species (Fisher & Owens 2004). Since current extinction threats can be taxon- or context-specific (Owens & Bennett 2000), such analyses may be of limited utility for conservation planning or in elucidating the natural history of extinctions. While global models are vital for exploring general patterns, given the idiosyncratic nature of extinctions, regional models focusing on specific taxa and/or specific extinction drivers may be the most instructive in informing on-the-ground conservation interventions (Fisher & Owens 2004).

Regional extinction studies on islands are particularly informative. Of the threatened mammal and bird species listed by the World Conservation Union, 43% are insular (Aguirre-Muñoz et al. in review). Invasive species are the primary driver of

extinction and ecosystem change on islands (Towns et al. 2006). Invasive predators, such as cats (*Felis catus*) and rats (*Rattus spp.*), are present on over 80% of the world's islands and new introductions persist (Atkinson 1985). However, invasive mammals can now be removed from islands: over 700 successful eradications have taken place over the past three decades (Donlan in press). Prioritizing islands for eradication to halt extinctions of native species should thus be an important focus for conservation science. For example, a certain amount of resources are available to remove feral cats from three islands in an archipelago; based on the available data, which islands should be targeted to maximize the probability of preventing extinctions?

Here, we use the islands off the western coast of Mexico, known for their endemism and biodiversity, to explore patterns of small mammal extinctions and how intrinsic and extrinsic factors interact in ways that might predispose populations to extinction by invasive predators. Feral cats and rats have recently caused a number of extirpations and extinctions on some of these islands (Donlan et al. 2005; Knowlton et al. in press; Álvarez-Castañeda & Ortega-Rubio 2003; Álvarez-Castañeda & Patton 1999). Yet, on other islands off the western coast of Mexico with invasive predators biodiversity loss has not occurred. Using theory and empirical evidence, we test eight *a priori* hypotheses that may have contributed to insular extinctions (Table 6).

Table 6. Geographical, autecological, and synecological variables, proposed proxy, and their potential contribution to extinction risk of small mammals on islands where invasive predators are present.

Variable (proposed proxy) [+ or - correlation with population decline / extinction risk]	Possible Mechanism	Support
Geographical		
max. elevation (habitat heterogeneity) [-]	spatial structure promotes population persistence, including within predator-prey systems	1-5
rainfall (<i>in situ</i> primary productivity) [-/+]	low or variable productivity results in proneness to demographic perturbations or stochastic, or the reverse trend via the <i>paradox of enrichment</i>	7-10
perimeter-area ratio (allochthonous input) [-/+]	depending on the subsidy magnitude and prey preference, donor-controlled resources could stabilize or destabilize food web interactions or predatory-prey interactions	11-14
Autecological		
Kmax (carrying capacity) [-]	small populations are prone to demographic perturbations and stochastic	1, 15-17
Rmax (population growth rate) [-]	populations with low intrinsic growth rates may lack the ability to recover from disturbances	18-20
σ -r (variance in population growth rate) [+]	populations with greater temporal variation are more prone to extinction	15, 16, 18, 21
Synecological		
mammals and lizard richness (alternative prey) [+/-]	alternative prey could stabilize strong predator-prey interactions or destabilize them via apparent competition	2, 22-25
snake and carnivore richness (presence of predation pressure) [-]	many islands lack predators, thus prey lack anti-predator defenses making them more vulnerable to predation	26, 27, 28
References: 1-MacArthur & Wilson 1967; 2-Holt 1977; 3-Boecklen 1986; 4-Ricklefs & Lovette 1999; 5-Elmer et al. 2001; 6-Rosenzweig 1971; 7-O'Conner 1991; 8-Abrams & Roth 1994; 9-O'Conner 1991; 10-Braithwaite & Muller 1997; 11-Bustamante et al. 1995; 12-Huxel & McCann 1998; 13-Sabo & Power 2002; 14-Polis et al. 2004; 15-Leigh 1981; 16-Brown 1995; 17-Fisher & Owens 2004; 18-Pimm 1991; 19-Owens & Bennett 2000; 20-Bodmer et al. 1997; 21-Diamond 1984; 22-Elton 1927; 23-Holt et al. 1994; 24-Hanski et al. 2001; 25-Roemer et al. 2002; 26-Stone et al. 1994; 27-Bowen & Van Vuren 1997; 28-Buckley & Jetz 2007		

We do so with a limited dataset that serves as proxy for proposed mechanisms. This data-poor scenario is representative of most conservation planning exercises. We explore geographical (i.e., habitat heterogeneity and productivity), autecological (i.e., carrying capacity and population growth rate), and synecological (i.e., presence of predators and alternative prey) factors that potentially correlate with and, thereby, help provide proximate explanations for extinctions driven by invasive predators.

Materials And Methods

Using an island biodiversity database for the region (Donlan et al. 2000), we collated biotic and abiotic information for all the islands off the Pacific coast of Baja California ($n = 23$) and in the Gulf of California ($n > 135$) where feral cats and rats are present or recently removed after extinctions occurred (Figure 7; Table 9). We recorded the extant ($n = 58$) and extinct ($n = 9$) native, nonvolant mammals occurring on the 25 islands with invasive predators. Two carnivores (ringtail, *Bassariscus astutus* and coyote, *Canis latrans*) were excluded since predation by cats or rats is not a threat (these species are included in the native predation index below).

Taxa included in the analysis were from the following genera (number of populations): *Ammospermophilus* (2), *Chaetodipus* (16), *Dipodomys* (2), *Lepus* (5), *Neotoma* (13), *Notiosorex* (1), *Peromyscus* (25), *Sylvilagus* (2), and *Thomomys* (1). The biodiversity and extinctions on the islands are well documented, with species losses attributed to the impacts of cats and/or rats (Donlan et al. 2005; Espinosa-Gayosso & Álvarez-Castañeda 2006; Knowlton et al. in press; Vázquez-Domínguez et al. 2004; Álvarez-Castañeda & Cortes-Calva 1996, 2002; Álvarez-Castañeda & Ortega-Rubio 2003; Álvarez-Castañeda & Patton 1999). On Meija Island, *Peromyscus guardia* was recently observed (A. Samaniego, pers. comm., 2005). However, it is

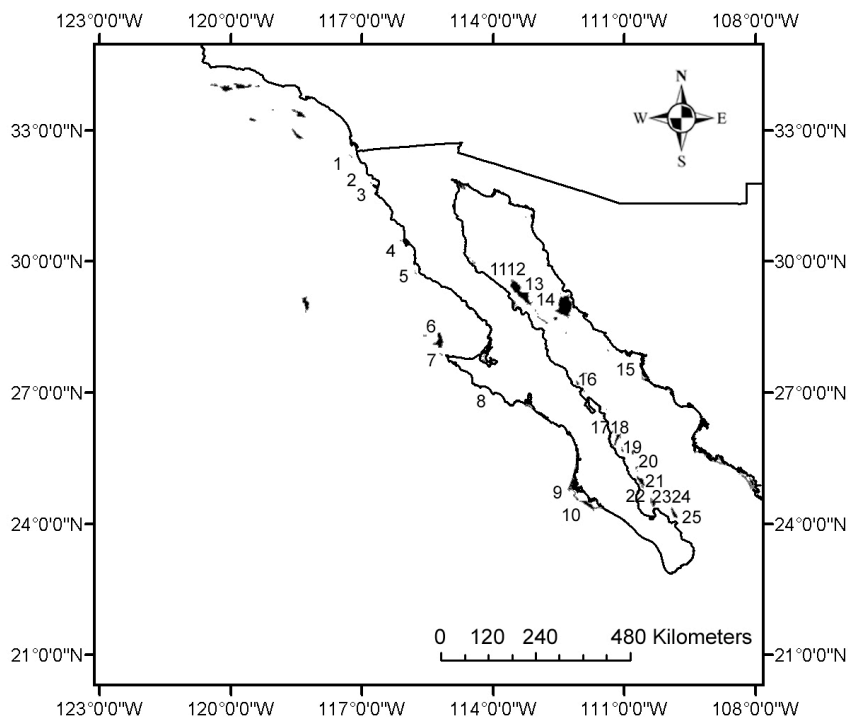


Figure 7. The islands of northwest Mexico that have (or recently had) feral cat and/or invasive rat populations and native nonvolant small mammals. Baja California: 1 Coronado North, 2 Todos Santos South, 3 Todos Santos North, 4 San Martin, 5 San Geronimo, 6 Cedros, 7 Natividad, 8 San Roque, 9 Magdalena, 10 Santa Margarita, Gulf of Mexico: 11 Granito, 12 Meija, 13 Angel de la Guarda, 14 Estanque, 15 San Pedro Nolasco, 16 San Marcos, 17 Coronados, 18 Carmen, 19 Monserrate, 20 Santa Catalina, 21 San Jose, 22 San Francisco, 23 Partida, 24 Espiritu Santo, 25 Cerralvo

unclear whether the individuals observed are from this is the same population that was last collected in 1973 and declared extinct after substantial trapping efforts (Álvarez-Castañeda & Ortega-Rubio 2003), or a new population that either immigrated from two islands nearby (~570m). Introduction by fishermen during camping activities is also a possibility. Given the trapping effort, the small size of the island (3.3 km²), and the reality of stow-away introductions (Hafner et al. 2001), we assumed the populations is newly arrived.

Island area (range: 0.6–951 km²), perimeter (range: 3.5–278 km), and

maximum elevation (range: 15-1318 m) were calculated from a geospatial database (Donlan et al. 2000) and the literature (e.g., Case et al. 2002). Perimeter-area ratio is a demonstrated proxy for the amount of allochthonous resource input from the marine environment to island ecosystems in the region (Polis & Hurd 1996). Climatic parameters were calculated from long-term weather data from the islands directly or from a nearby station on the adjacent mainland (Hastings & Humphrey 1969). The islands are dominated by two climatic regimes: a monsoonal pattern moving north from the tropics and a Mediterranean pattern moving south. To capture those patterns, means and the coefficients of variation were calculated for annual, January, and September rainfall; the latter two months represent bi-modal peaks for precipitation in the region (Figure 8).

Adult body mass was recorded directly ($n = 46$) or estimated from closely-related species/subspecies ($n = 21$) from the literature (Lackey 1991; Wilson & Ruff 1999; Álvarez-Castañeda & Patton 1999). Autecological parameters were estimated using allometric relationships. The potential maximum rate of increase (r_{\max}) was estimated from the equation $r_m = 1.375W^{-0.315}$, where W is the estimated mean mass and r_m = the maximum instantaneous, intrinsic rate of increase over a year (Sinclair 1996). The standard deviation of instantaneous rate of change (σ_r) was estimated from the equation $\sigma_r = 0.805W^{-0.316}$ (Sinclair 1996). Population density (number km^{-2}) was estimated from mass, based on an <100kg herbivorous mammal-specific allometric relationship [$\log(\text{density}) = 1.38(\log W^{-0.75})$] (Silva & Downing 1995). Carrying capacity (K_{\max}) was estimated by multiplying population density by island area.

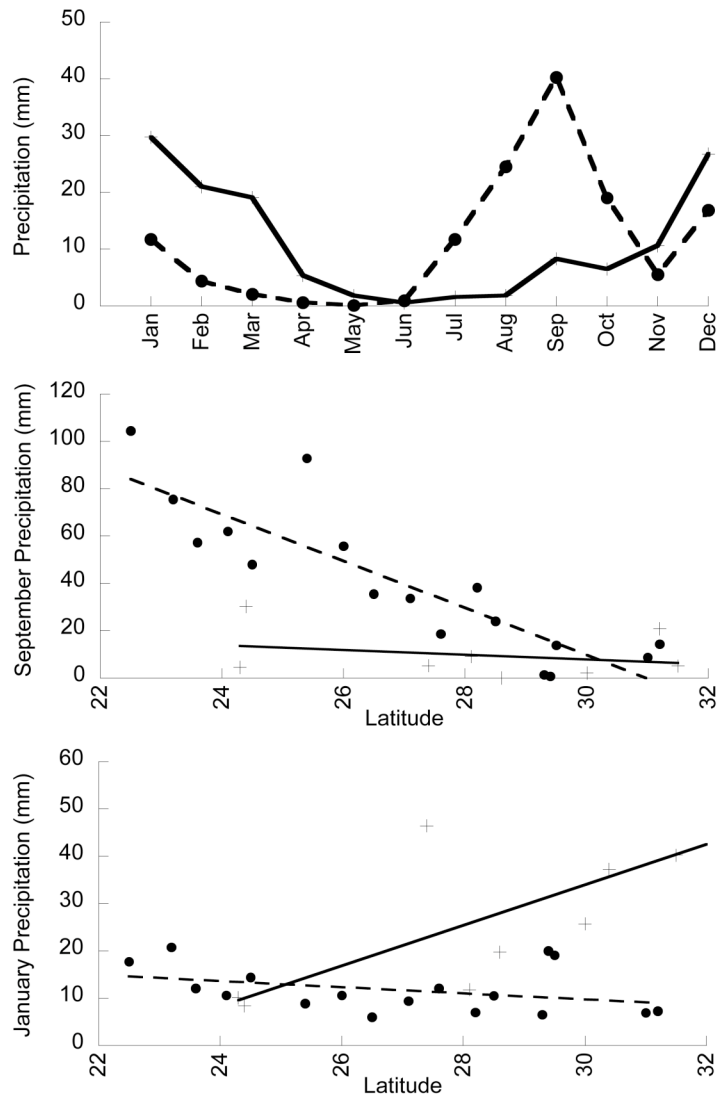


Figure 8. Precipitation on the islands of northwest Mexico. (A) Mean monthly rainfall for the Gulf of California (dotted line) and of the Pacific side of Baja California (solid line). (B) Mean September and (C) January rainfall for the Gulf of California and Baja California. Data is based on a long-term monthly rainfall records averaging 23 years (range: 2-54 years).

Our index for alternative prey available to invasive predators included all additional nonvolant, native mammal and lizard taxa. This is an underestimate for two reasons. First, both cats and rats feed on terrestrial and intertidal invertebrates (Catling

1988; Reed & Bowen 2001; Towns et al. 2006). Second, cats and rats are known to prey on seabirds and their eggs when available, and land birds to a lesser extent (Keitt et al. 2002; Reed & Bowen 2001; Towns et al. 2006). Neither birds nor invertebrates were included due to incomplete data. However, tenebrionid beetle and breeding land bird diversity correlates with island area in the region (Case et al. 2002), and therefore their diversity is expected to correlate with our index.

Number of native mammalian carnivores and snake species known to feed on small mammals was used as an index of presence of predation pressure. Densities of predators was not available; thus we used species richness as a proxy for predation strength (Buckley & Jetz 2007). Raptor diversity was not included due to incomplete data; however, it too correlates with island area in the region (Case et al. 2002). Ringtail cats (*Bassariscus astutus*) and coyotes (*Canis latrans*) are present on four islands; known prey items include invertebrates, small mammals, and lizards (Rodriguez-Estrella et al. 2000; Rose & Polis 1998). Snake diet was based on island-specific data and/or inferred based on closely-related populations or taxa (Grismer 2002). Our index is conservative in the sense that only snakes that prey regularly or solely on small mammals were included (i.e., *Crotalus*, *Lichanura*, *Masticophis*, *Pituophis*, and *Trimorphodon*).

Certain variables (K_{\max} , PA ratio, and $CV_{\text{annual rain}}$) were log transformed to meet criteria necessary for statistical analyses. All abiotic and biotic factors (Table 6) were standardized [(observation-mean)/standard deviation] to allow for comparisons. We combined two statistical approaches for inference (Stephens et al. 2005). First, we used 1-way ANOVAs allowing both F-values and p-values to inform our *a priori* hypotheses regarding parameters that influence extinction (Table 6). Abiotic and biotic parameters were the independent variables. Our binomial response variable was extinction probability, with populations considered to be replicates. Partial Bonferroni

corrected p-values were adjusted for correlated variables, and are reported with a family wide α -level of 0.05 (Sankoh et al. 1997).

Second, we assessed the *a priori* hypothesis using logistic regression, exploring a range of functional forms for each hypothesis. Abiotic and biotic parameters were the independent variables; extinction probability was the dependent variable. The best performing models for each *a priori* hypothesis were selected based on Akaike's Information Criteria values (AIC, Burnham & Anderson 2002). We then used multivariate stepwise model selection to pick the best aggregate model from all possible sets of best performing forms for each *a priori* hypothesis. Our *a priori* approach, along with exploring all possible model subsets, controls for the possibility of spurious results due to multicollinearity (Graham 2003).

While from ecological and conservation perspectives, populations are the unit of extinction and the motivation for this analyses, using population as the replicate could be potentially viewed as pseudoreplication from two perspectives. First, geographical and synecological parameters are a function of both the target population and the island. Secondly, due to the regional focus and thus small sample size, we were not able to control for the possibility of phylogenetic non-independence among species. Thus, autecological parameters could potentially be non-independent. To explore these potential biases, we repeated the univariate analyses twice: once with island as the replicate using the entire dataset, and again restricting the data to the genus *Peromyscus*, collapsing 26 *Peromyscus* populations to 5 independent groups according to their known mainland phylogenetic affinity (Hafner et al. 2001; Lawlor et al. 2002). The *Peromyscus*-specific analysis provides some insight with regard to the potential evolutionary role of the autecological parameters on extinction.

Lastly, since island is often the focus of island biogeography and extinction analyses, and that many of our *a priori* factors were estimated by and correlate with

island area, we tested the performance of the logistic regression models with and without the inclusion of island area. Analyses were conducted in the statistical programs SPSS and R (R Development Core Team 2005; SPSS 1999).

Results

With the univariate analysis, alternative prey explained the most variance between extant and extinct populations, followed by native predators, perimeter-area ratio, and carrying capacity (Figure 9). Alternative prey was negatively correlated with extinction, with extinction-free islands having on average over twice the alternative prey than islands with extinctions (non-standardized means: 10.4 vs. 4.3; 1-way ANOVA with island as the replicate: $F_{1,23} = 6.64$, $p = 0.017$). Alternative prey also had the lowest AIC value of the *a priori* models (Table 7). Native predators were three times greater on extinction-free islands (non-transformed means: 2.88 vs. 0.89; 1-way ANOVA with island as the replicate: $F_{1,23} = 7.00$, $p = 0.014$). Carrying capacity estimates of extant populations were 27 times that of extinct populations (Figure 9; non-standardized means: 5.2×10^4 vs. 1.9×10^3). Of autecological parameters, carrying capacity had the lowest AIC value (Table 7). There were no differences in r_{\max} or σ_r (Figure 9). Perimeter-area ratio had the lowest AIC of the *a priori* geographical parameters, and negatively correlated with extinction (Figure 9; Table 7; non-transformed means: 2.02 vs. 3.44; 1-way ANOVA: $F_{1,23} = 4.62$, $p = 0.042$). Extinctions occurred on islands with lower perimeter-area ratios compared to islands where extinctions did not occur. Despite the small sample size ($n = 7$), the *Peromyscus*-specific analysis on autecological variables revealed similar patterns compared to the analysis that included the entire small mammal community, but with marginal or no statistical significance (Table 8).

Table 7. Comparison of models for probability of small mammal extinctions from invasive predators. Alternative prey, carrying capacity, and January rain made up the best performing aggregate model relative to the single parameter *a priori* models (see Table 6). For synecological, autecological, geographical parameters, the best performing model was selected from all possible models. ΔAIC is the difference between AIC values for each model and the lowest AIC value. A lower AIC value indicates a better fitting model; W is the model's Akaike weight, the relative probability that the model is the best fit to the data tested.

Proposed factor(s)	Parameter(s)	Best Model - Parameter(s)	AIC	Δ AIC	W
Synecological + Autecological + Geographical					
	all parameters	alternative prey + log K_{max} + Jan. rain	39.07	0.00	0.68
Synecological					
alternative prey	mammal and lizard richness	alternative prey	41.02	1.95	0.26
native predation / history	mammal and snake predators				
Autecological					
carrying capacity	$\log K_{max}$				
population growth rate	r_{max}	$\log K_{max}$	46.49	7.42	0.02
variance in population growth rate	σ_{r-max}				
Geographical					
island area	$\log km^2$	$\log km^2$	45.03	5.96	0.03
allochthonous input	$\log PA$ ratio	$\log PA$ ratio	47.11	8.04	0.01
habitat heterogeneity	max. elevation	maximum elevation	49.45	10.38	<0.01
<i>in situ</i> primary productivity	mean and CV [annual rain, Sept. rain, Jan. rain]	Jan. rain	54.36	15.29	<0.01

Combining the best *a priori* single parameter models, the best performing aggregate model included three parameters: alternative prey, carrying capacity and January rain (Table 7). The three-parameter model was nearly twenty times more likely to explain variation in extinctions among small mammal populations than island area (Evidence Ratio = $W_{alt\ prey + K_{max} + Jan.\ rain} / W_{island\ area}$). The best performing aggregate model did not include island area. As a single parameter, island area performed best compared to other geographical parameters; however alternative prey alone was better performing (Table 7). Island area was different on islands with and without extinctions (non-transformed mean: 4.8 vs. 146.7 km²; 1-way ANOVA on log area: $F_{1,23} = 6.098$, $p = 0.021$).

Table 8. Insular *Peromyscus* populations (n = 25) collapsed to mainland phylogenetic affinity groups (n = 5). Means of autecological parameters for each group are shown, along with means of extinct and extant populations collapsed to group.

Phylogenetic Grouping (mainland affinity)	No. of populations (extinct)	log K_{max}	Γ_{max}	σ_{r-max}
<i>Peromyscus boylii</i>	1 (0)	3.2	4.2	2.5
<i>Peromyscus eremicus</i>	11 (3)	4.1	4.3	2.6
<i>Peromyscus fraterculus</i>	2 (0)	4.3	4.3	2.5
<i>Peromyscus maniculatus</i>	10 (1)	3.4	4.6	2.7
<i>Peromyscus merriami</i>	1 (1)	3.2	4.4	2.6
Phylogenetic Independent Extant Mean	4	3.9	4.3	2.5
Phylogenetic Independent Extinct Mean	3	2.8	4.6	2.6
$F_{1,5}$		5.71	0.605	0.606
p-value		.062	0.47	0.47

Discussion

Over the last 500 years, feral cats and invasive rats are likely responsible for more documented vertebrate extinctions worldwide than any other agent (Aguirre-Muñoz et al. in review; Atkinson 1989; Towns et al. 2006). Cats are present on 24 of

the 25 islands in this study (or were recently removed, Tershy et al. 2002), and are responsible for eight of the observed extinctions (see refs. in Methods). Rats, present on five islands, are known to compete with and suppress insular rodent populations (Harris et al. 2006). They are presumed to be responsible for the additional extinction and may have contributed to others. Our results suggest that the interplay of autecological, synecological, and geographical traits may predispose small mammals to extinction via feral cat predation.

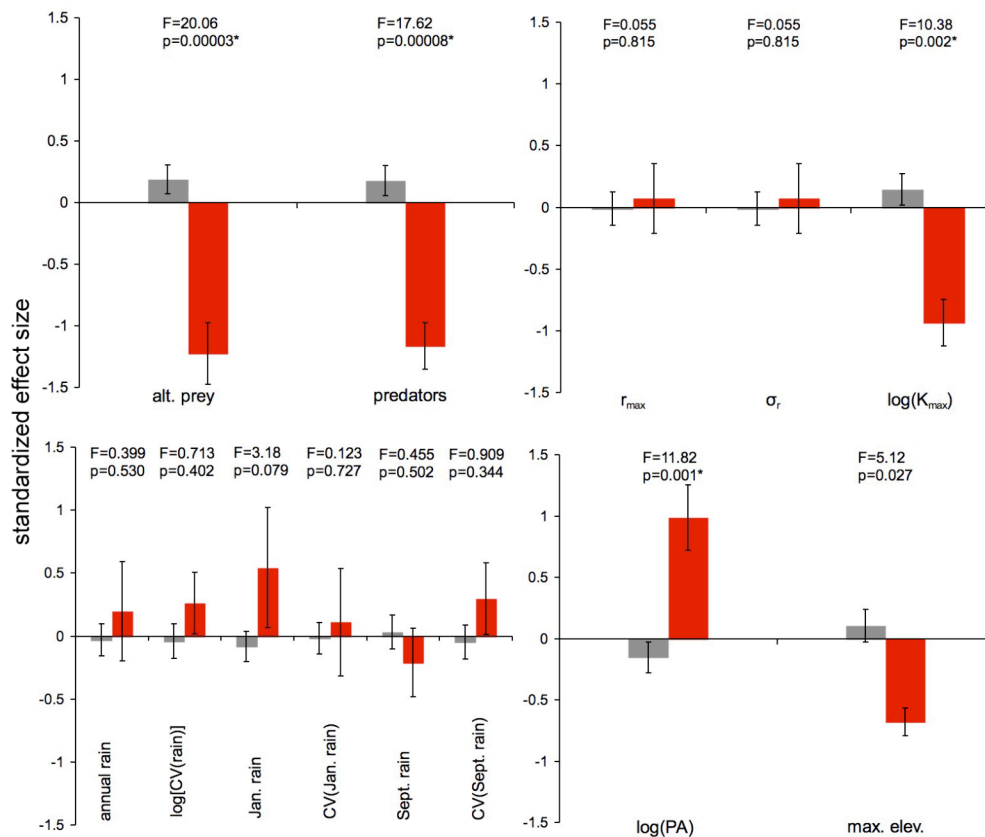


Figure 9. Differences in synecological, autecological, and geographical traits between extant (grey) and extinct (red) insular populations in western Mexico [mean (SE); $n = 67$ populations]. Asterisks (*) indicate significant differences with a family-wide Bonferroni corrected α -level of 0.05.

Synecological Factors

Alternative prey was consistently the most powerful explanatory variable between extant and extinct populations. Feral cats are generalist and opportunistic predators, with small mammals commonly making up a large percentage of their diet (Bloomer & Bester 1990; Molsher et al. 1999; Paltridge et al. 1997). Cats are also known to prey on seabirds and lizards, particularly when mammals are in low abundance or absent (Bloomer & Bester 1990; Keitt et al. 2002; Paltridge et al. 1997). With high prey densities, prey-switching in generalist predators can lead to Type III functional responses (Hanski et al. 1991). In Australia, cats commonly show evidence of a Type III functional response to their preferred prey species (i.e., rabbits), with prey consumption following primary prey abundance and prey switching when that prey declines (Catling 1988; Molsher et al. 1999; Reed & Bowen 2001). As originally hypothesized by Elton (1927), in a community with diverse prey, this predator functional response can have stabilizing effects on prey abundance (Hanski et al. 2001). Alternatively in less diverse communities, a generalist predator could feasibly destabilize prey populations and increase the extinction probability of the preferred prey species.

Long-term empirical studies on rodent predator-prey dynamics in other systems support the hypothesis of context-dependent community response from predators. In Fennoscandia and arctic Canada, specialist predators show a delayed numerical response to changes in rodent prey populations, which results in unstable prey population dynamics due to delayed density-dependent mortality of rodents (Hanski et al. 2001). In contrast, generalist predators in the same high latitude ecosystems stabilize (i.e., inhibit population oscillations) rodent demography (Erlinge et al. 1984; Hanski et al. 2001; Reid et al. 1995). Similarly, systems like islands with low prey diversity, could necessarily limit prey switching for generalist predators such

as feral cats, which in turn could lead to extinction. Our results are consistent with the hypothesis that similar dynamics are occurring on the islands of western Mexico.

Autecological Factors

Low mean abundance, which often correlates with extinction, is a function of intrinsic traits (i.e., survival and reproduction) interacting with extrinsic abiotic and biotic factors. Our carrying capacity estimate likely errs toward its upper bound because it assumes populations are saturated in the habitat, and the estimate is based on an intrinsic trait and a single bounded abiotic factor: maximum available habitat (i.e. island area). In contrast to others (Duncan et al. 2002; Owens & Bennett 2000), we found no evidence that slow life history attributes (i.e., r_{\max} and σ_r) correlate with extinction by invasive predators. While theory predicts that species with slow life histories should be more vulnerable to exploitative forces (Pimm 1991), results of empirical studies have been mixed (Fisher & Owens 2004).

For autecological traits, population size (and percent change) may be the best predictor of extinction risk (O'Grady et al. 2004); however, it is often unavailable. While imprecise, carrying capacity estimated by body size and available habitat (data that is commonly available) may be a useful proxy of population size to help predict extinction vulnerability by invasive mammals. When combined with alternative prey, it was more informative than using island area alone and provides insights into possible mechanisms. In contrast, area is multi-factorial, a proxy for a suite of correlated factors (MacArthur & Wilson 1967; Ricklefs & Lovette 1999). Further, island area does not always correlate linearly with ecological factors. For example, populations of *Peromyscus* are often found at high densities on very small islands (Stapp & Polis 2003).

Geographical Factors

In western Mexico, we suspect primary productivity via precipitation influences the probability of extinction by invasive predators in complex ways by interacting with island-specific factors. While the entire arid region is heavily influenced by rainfall, precipitation differs between the islands in the Gulf of California and off the Pacific side of Baja California. In the Gulf of California, September rainfall from tropical storms decreases moving northward. The Pacific islands receive the majority of their rainfall during the winter, with a decreasing trend moving southward away from the Mediterranean climate of California (Figure 8). The role of January rain in invasive predator-driven extinctions is equivocal. While the inclusion of January rain in the aggregate model is consistent with a *paradox of enrichment* hypothesis (Rosenzweig 1971), it is unclear whether this effect is general, or alternatively heavily influenced by two extinctions that have occurred on northern islands with greater January rainfall compared to the rest of the region. When those two (2 of 9) extinctions are removed from the analyses, January rain is not included in the aggregate model.

Precipitation is known to heavily influence island dynamics in the region, particularly high rainfall events and subsequent prolonged droughts associated with the El Niño Southern Oscillation (ENSO, Donlan et al. 2002; Polis et al. 1997). While the details of how introduced predation and precipitation interact at the landscape scale are unclear, empirical studies with insular *Peromyscus* in the region suggest the interaction may be important (Stapp & Polis 2003).

Of the nine extinctions, *Peromyscus* spp. were the most frequent (5 out of 25 populations), followed by woodrats (*Neotoma* spp., 3) and pocket mice (*Chaetodipus baileyi*, 1). With the exception of one population, all *Peromyscus* extinctions have occurred on islands where it was the only native mammal present. Insular *Peromyscus*

populations are dynamic, with drastic fluctuations driven by ENSO-related rainfall events (Stapp & Polis 2003). Populations show precipitous declines with a return to arid conditions following ENSO-rains, and often become restricted to near-shore habitats due to a reliance on littoral resources (Stapp & Polis 2003). During prolonged droughts, the large numerical responses of *Peromyscus* to bottom-up forcing coupled with a reliance on allochthonous resources may make them more vulnerable to novel top-down forces (Rosemond et al. 1993).

Feral cats, and other predators, are known to heavily utilize near-shore habitats in search of both terrestrial and littoral prey (Rose & Polis 1998; Tidemann 1994, CJD personal observation). Significant allochthonous inputs from the marine environment to island ecosystems have been documented (Polis et al. 2004). Subsidy effects in predator-prey systems are predicted to be positive or negative on a target consumer depending on the preference of allochthonous versus autochthonous sources and the level of allochthonous input (Huxel & McCann 1998). Both positive effects driven by a consumer's functional response and negative effects driven by a consumer's numerical response have been reported in other systems (see refs in Table 6). While our study was consistent with a negative effect (Figure 9) and it has been hypothesized elsewhere (Power et al. 2004), whether marine subsidies increase predation pressure on native, island species by invasive predators via a numerical response remains to be seen.

Informing Conservation Interventions

Information that is both relatively accessible and instructive to conservation planning is in high demand. While some information may be universal, most may end up being geographically or situationally dependent (Donlan et al. 2005). Models that require a minimum amount of data will be more useful, since the majority of

conservation planning scenarios are data poor (Doak & Mills 1994). Data such as population abundance and predator density are preferable over carrying capacity estimated by body size and predator richness; however, the former are more often than not unavailable. For western Mexico's islands, alternative prey and carrying capacity are two factors that could help guide the prioritization invasive predator eradication campaigns. Our analysis demonstrates that those parameters are more informative to conservation decision makers than island area alone. Influences of precipitation appear more complex, which highlights the challenge of elucidating relationships that balance the search for mechanism and utility to conservation decision-making. The approach used here could be used as a template for other archipelagos in informing conservation programs.

Table 9.Small mammal records used in the analyses. Variables include Mass (grams), Area (km²), perimeter-area ratio(PA), maximum elevation (meters), alternative prey (AP), native predators (NP), annual rain (AR), coefficient of variation of annual rain (CV(AR)), and September (SR) and January (JR) rain and coefficient of variation.

Taxon	Extinct	MASS	AREA	PA	ME	AP	NP	AR	CV(AR)	SR	CV(SR)	JR	CV(JR)
Ammospermophilus insularis	No	106.5	87.0	0.77	181	19	5	179.1	1272.7	62	88.98	10.60	94.97
Ammospermophilus insularis	No	106.5	20.3	1.61	30	14	5	179.1	1272.7	62	88.98	10.60	94.97
Chaetodipus arenarius albus	No	13	303.3	0.92	118	12	4	73.7	192.2	4.5	11.34	10.10	12.03
Chaetodipus arenarius amphilus	No	13	236.9	0.45	173	16	4	73.7	192.2	4.5	11.34	10.10	12.03
Chaetodipus arenarius siccus	No	13	145.9	0.48	234	10	5	211.0	1019.0	57.3	74.77	12.10	33.06
Chaetodipus baileyi fornicatus	Yes	13	18.8	1.12	69	7	3	141.1	1025.8	55.8	103.45	10.60	31.20
Chaetodipus fallax anthonyi	No	19.5	378.7	0.32	367	13	3	65.5	193.6	9.1	40.65	11.80	36.13
Chaetodipus spinatus bryanti	No	15.5	0.7	5.28	12	16	6	95.3	1079.8	48	188.81	14.40	27.23
Chaetodipus spinatus evermanni	No	15.5	3.3	2.45	79	5	1	73.6	357.7	24	107.89	10.50	14.52
Chaetodipus spinatus guardia	No	15.5	951.3	0.22	402	11	3	73.6	357.7	24	107.89	10.50	14.52
Chaetodipus spinatus lambi	No	15.5	87.0	0.77	181	19	5	179.1	1272.7	62	88.98	10.60	94.97
Chaetodipus spinatus lambi	No	19.5	20.3	1.61	30	14	5	179.1	1272.7	62	88.98	10.60	94.97
Chaetodipus spinatus latijugularis	No	19.5	4.6	2.26	76	9	1	95.3	1079.8	48	188.81	14.40	27.23
Chaetodipus spinatus macrosensis	No	15.5	30.9	0.86	83	13	5	104.5	993.7	33.7	29.08	9.40	30.39
Chaetodipus spinatus magdalenae	No	19.5	303.3	0.92	118	12	4	73.7	192.2	4.5	11.34	10.10	12.03
Chaetodipus spinatus margaritae	No	19.5	236.9	0.45	173	16	4	73.7	192.2	4.5	11.34	10.10	12.03
Chaetodipus spinatus occultus	No	15.5	144.8	0.64	146	14	3	141.1	1025.8	55.8	103.45	10.60	31.20
Chaetodipus spinatus pullus	No	15.5	10.0	1.55	86	14	2	141.1	1025.8	55.8	103.45	10.60	31.20
Dipodomys insularis	No	43.15	0.7	5.28	12	16	6	95.3	1079.8	48	188.81	14.40	27.23
Dipodomys merriami margaritae	No	43.15	236.9	0.45	173	16	4	73.7	192.2	4.5	11.34	10.10	12.03
Lepus californicus magdalenae	No	2300	303.3	0.92	118	12	4	73.7	192.2	4.5	11.34	10.10	12.03
Lepus californicus magdalenae	No	2300	236.9	0.45	173	16	4	73.7	192.2	4.5	11.34	10.10	12.03
Lepus californicus sheldoni	No	2300	144.8	0.64	146	14	3	141.1	1025.8	55.8	103.45	10.60	31.20
Lepus insularis	No	2300	87.0	0.77	181	19	5	179.1	1272.7	62	88.98	10.60	94.97
Lepus insularis	No	2300	20.3	1.61	30	14	5	179.1	1272.7	62	88.98	10.60	94.97
Neotoma anthonyi	Yes	145	1.3	4.33	95	5	0	256.6	1578.8	20.9	157.74	40.20	25.92
Neotoma bryanti	No	145	378.7	0.32	367	13	3	65.5	193.6	9.1	40.65	11.80	36.13
Neotoma bunkerii	Yes	145	10.0	1.55	86	14	2	141.1	1025.8	55.8	103.45	10.60	31.20
Neotoma lepida abbreviata	No	145	4.6	2.26	76	9	1	95.3	1079.8	48	188.81	14.40	27.23
Neotoma lepida insularis	No	145	951.3	0.22	402	11	3	73.6	357.7	24	107.89	10.50	14.52
Neotoma lepida macrosensis	No	145	30.9	0.86	83	13	5	104.5	993.7	33.7	29.08	9.40	30.39
Neotoma lepida nudicauda	No	145	144.8	0.64	146	14	3	141.1	1025.8	55.8	103.45	10.60	31.20
Neotoma lepida perpallida	No	145	0.7	5.28	12	16	6	95.3	1079.8	48	188.81	14.40	27.23
Neotoma lepida pretiosa	No	145	303.3	0.92	118	12	4	73.7	192.2	4.5	11.34	10.10	12.03
Neotoma lepida pretiosa	No	145	236.9	0.45	173	16	4	73.7	192.2	4.5	11.34	10.10	12.03
Neotoma lepida vicina	No	145	87.0	0.77	181	19	5	179.1	1272.7	62	88.98	10.60	94.97
Neotoma lepida vicina	No	145	20.3	1.61	30	14	5	179.1	1272.7	62	88.98	10.60	94.97
Neotoma martinensis	Yes	145	3.0	2.68	12	4	1	137.7	847.5	0.3	3.00	46.90	127.33
Notiosorex crawfordi	No	145	3.0	2.68	12	4	1	137.7	847.5	0.3	3.00	46.90	127.33
Peromyscus boylii glasselli	No	29	4.2	2.40	96	6	0	235.2	1462.9	18.6	128.93	12.10	26.51
Peromyscus caniceps	No	27	18.8	1.12	69	7	3	141.1	1025.8	55.8	103.45	10.60	31.20
Peromyscus eremicus avius	No	27	145.9	0.48	234	10	5	211.0	1019.0	57.3	74.77	12.10	33.06
Peromyscus eremicus cedrosensis	No	27	378.7	0.32	367	13	3	65.5	193.6	9.1	40.65	11.80	36.13
Peromyscus eremicus insulicola	No	27	87.0	0.77	181	19	5	179.1	1272.7	62	88.98	10.60	94.97
Peromyscus eremicus insulicola	No	27	20.3	1.61	30	14	5	179.1	1272.7	62	88.98	10.60	94.97
Peromyscus eremicus polypoli	No	27	303.3	0.92	118	12	4	73.7	192.2	4.5	11.34	10.10	12.03
Peromyscus eremicus polypoli	No	27	236.9	0.45	173	16	4	73.7	192.2	4.5	11.34	10.10	12.03
Peromyscus eva carmen	No	27	144.8	0.64	146	14	3	141.1	1025.8	55.8	103.45	10.60	31.20
Peromyscus guardia guardia	No	27	951.3	0.22	402	11	3	73.6	357.7	24	107.89	10.50	14.52
Peromyscus guardia harbonsonii	Yes	27	0.7	5.60	26	2	0	73.6	357.7	24	107.89	10.50	14.52
Peromyscus guardia meija	Yes	27	3.3	2.45	79	5	1	73.6	357.7	24	107.89	10.50	14.52
Peromyscus guardia sp.	Yes	27	1.0	4.75	37	4	1	73.6	357.7	24	107.89	10.50	14.52
Peromyscus maniculatus assimilis	No	20	0.8	4.97	152	6	0	256.6	1204.6	5.1	29.40	50.80	33.74
Peromyscus maniculatus cineritius	Yes	20	0.8	6.12	5	1	0	95.8	752.4	5.2	27.23	46.40	126.50
Peromyscus maniculatus dorsalis	No	20	10.3	1.80	49	2	1	65.5	193.6	9.1	40.65	11.80	36.13
Peromyscus maniculatus dubius	No	20	0.6	5.59	17	3	0	256.6	1578.8	20.9	157.74	40.20	25.92
Peromyscus maniculatus dubius	No	20	1.3	4.33	95	5	0	256.6	1578.8	20.9	157.74	40.20	25.92
Peromyscus maniculatus exiguus	No	20	3.0	2.68	12	4	1	137.7	847.5	0.3	3.00	46.90	127.33
Peromyscus maniculatus geronimensis	No	20	0.7	5.28	12	2	0	95.0	847.5	0.3	3.00	46.90	127.33
Peromyscus maniculatus magdalenae	No	20	303.3	0.92	118	12	4	73.7	192.2	4.5	11.34	10.10	12.03
Peromyscus maniculatus margaritae	No	20	236.9	0.45	173	16	4	73.7	192.2	4.5	11.34	10.10	12.03
Peromyscus pembertoni	Yes	25	4.2	2.40	96	6	0	235.2	1462.9	18.6	128.93	12.10	26.51
Peromyscus pseudocricitius	No	18	10.0	1.55	86	14	2	141.1	1025.8	55.8	103.45	10.60	31.20
Peromyscus slevini	No	54.4	30.8	0.92	143	7	1	141.1	1025.8	55.8	103.45	10.60	31.20
Sylvilagus bachmani cerrosensis	No	54.4	378.7	0.32	367	13	3	65.5	193.6	9.1	40.65	11.80	36.13
Sylvilagus mansuetas	No	54.4	0.7	5.28	12	16	6	95.3	1079.8	48	188.81	14.40	27.23
Thomomys bottae magdalenae	No	714	303.3	0.92	118	12	4	73.7	192.2	4.5	11.34	10.10	12.03

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Chapter 5: Pleistocene Rewilding: An optimistic agenda for 21st 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 America 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, locality-by-locality basis. Pleistocene Rewilding would deliberately promote “K-selected” 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. From Bolson tortoises to Holarctic lions, Pleistocene Rewilding can begin immediately and continue through the coming centuries. 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 U.S. are likely to first implement this restoration. Risks of Pleistocene Rewilding include the possibility of disease transmission and associated human health implications, and unexpected ecological and sociopolitical consequences of reintroductions. Monitoring programs that characterize 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, whereas social challenges will include acceptance of predation as an overriding natural process and the incorporation of pre-Columbian ecological frameworks into conservation strategies.

Introduction

Far more than any other species in the history of life on Earth, humans alter their environments by eliminating species, changing ecosystem function, and affecting the very future of evolution (Flannery 2006; Meyer 2005; Myers & Knoll 2001; Sala et al. 2000; Smith 2003; Thomas et al. 2004a; Thomas et al. 2004b). We will surely continue to do so for the foreseeable future, either by default or design (Western 2001; Wilson & Willis 1975). Earth is now nowhere pristine in the sense of being substantially free from human influence, and indeed most major landmasses have sustained many thousands of years of human occupancy and impacts (Burney & Flannery 2005; Flannery 1995, 2001; Heckenberger et al. 2003; Mason 2004; Vitousek et al. 1997). Human economics, politics, demographics, and chemicals pervade every ecosystem. Even the largest parks thus require active management to prevent extinction (Berger 2003; Newmark 1995). Human-induced environmental impacts are now unprecedented in their magnitude, cosmopolitan in their distribution, and show alarming signs of worsening.

Human influences on the environment take a variety of well-known and often inter-related general forms, including habitat alteration and fragmentation, pollution, and resource reductions from 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 they are often the foci of human exploitation (Burney & Flannery 2005; Cardillo et al. 2005; Flannery 1995).

Substantial loss of megafaunal biodiversity has already occurred in Europe, Australia, the Americas, and large continental islands. In Africa and Asia, the only places where a diverse megafauna remains relatively intact, many large mammals are threatened with extinction (Balmford et al. 2001; Blake & Hedges 2004; Goossens et al. 2006; Marchant 2001; Musters et al. 2000; Vogel 2000), especially in regions where war, corruption, and political turmoil wage over increasingly scarce resources (André & Platteu 1998; Diamond 2004; Smith et al. 2003c).

In the Americas, most large mammals along with their commensals were lost by *c.* 13,000 years ago (Burney & Flannery 2005; Martin 1958; Martin 2005b). 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 (Donlan et al. in press; Janzen & Martin 1982; Terborgh 2005). The prehistoric, historic, and contemporary extinction of large vertebrates and their associated ecological roles thus hold paramount but still underappreciated implications for biodiversity conservation (Donlan et al. in press; Estes 1996; Flannery 2001; Jackson et al. 2001; Martin 1999, 2005b; Martin & Burney 1999; Ray et al. 2005; Springer et al. 2003; Terborgh et al. 1999).

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 in press). Prior to the onset of human impacts *c.* 3,000 years ago, these islands were home to over 2,000 now extinct bird species—over 20% of the extant avifauna worldwide (Monroe & Sibley 1993; Steadman 1995; Steadman & Martin 2003). Over the past three decades,

conservation practitioners have developed techniques to halt insular extinctions and restore island ecosystems (Donlan et al. 2003; Veitch & Clout 2002), 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 these losses are unknown and even unimagined.

Pleistocene history along with 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*—re-instituting 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, Martin and Burney 1999, Martin 2005b). The events and processes underlying our proposal apply not only to North America (Donlan et al. 2005; Flannery 2001; Martin & Burney 1999), but to most other island archipelagos and continental ecosystems. This proposed program for 21st century conservation, which is both optimistic and defensible on multiple grounds, echoes and expands on similar proposals for eastern Siberia (Stone 1998; Zimov 2005), South America (Galetti 2004), and certain island archipelagos (Atkinson 2001; Burney 2003; Burney et al. 2002; Lazell 2002; Steadman & Martin 2003).

The intent of this paper, which follows a preliminary and much shorter version (Donlan et al. 2005), is to lay out a more substantive argument for Pleistocene Rewilding. We first present ecological arguments for the proposal, 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 further inform 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 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 function (Terborgh 2005). If these influences were important, would an attempt to partially restore the 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 just species but species interactions (Soulé et al. 2003; Soulé et al. 2005). A variety of evidence indeed indicates that the functional roles of large carnivores and megaherbivores are often significant (Berger et al. 2001; Estes et al. 1998; Jackson et al. 2001; Owen-Smith 1988; Ray et al. 2005; Sinclair et al. 2003; Soulé et al. 1988; Terborgh et al. 1999; Terborgh et al. 2001), and that degraded systems may both cause and result from the loss of these species (Springer et al. 2003; Terborgh & Feeley in press; Terborgh et al. 2006). It follows that many now extinct large mammals must have shaped the life histories of extant species and ecosystem characteristics through the selective forces of strong species interactions (Barlow 2000; Byers 1997; Greenwood & Atkinson 1977; Janzen & Martin 1982; Zimov et al. 1995). The likely

consequences of so much large vertebrate-induced change in functionality is ecosystem dysfunction (Jackson 1997; Pandolfi et al. 2003; Terborgh and Feeley in press), driven in part by anachronistic attributes of the surviving species (Janzen and Martin 1982) and ecological chain reactions that lead to further extinctions (Donlan et al. in press; Koh et al. 2004; Springer et al. 2003; Terborgh et al. 2006).

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 & Schoener 1994); fish in lakes (Carpenter & Kitchell 1996); seastars 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 influences through their evolutionary effects on other species (Janzen 1986; Janzen & Martin 1982). Various North American species have characteristics that appear to be anachronistic on modern landscapes, 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 proboscidians 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 1986, but see Howe 1985 for an alternative viewpoint; Janzen & Martin 1982). When dozens of large herbivores in the Americas went extinct in the late Pleistocene, important ecological and evolutionary interactions such as frugivory and herbivory were disrupted, and subsequently seed dispersal and subsequent distributions of many plant species were altered. While such ideas were brought to the forefront of evolutionary ecology more than two decades ago (Janzen 1986; Janzen & Martin 1982), 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 four 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 (*Micracinonyx 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 (Barlow 2000; Eskildsen et al. 2004; Greenwood & Atkinson 1977; Janzen & Martin 1982; Springer et al. 2003). Gray wolves (*Canis lupus*) provide 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 (Berger et al. 2001; Hebblewhite et al. 2005; Ripple & Larsen 2000; Ripple et al. 2001; Soulé et al. 2003). 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 & Beschta 2004). These 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 biodiversity to climate change (Smith et al. 2003a; Willmers & 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 we describe below (Figure 10, e.g., Bond et al. 2004; Eskildsen et al. 2004).

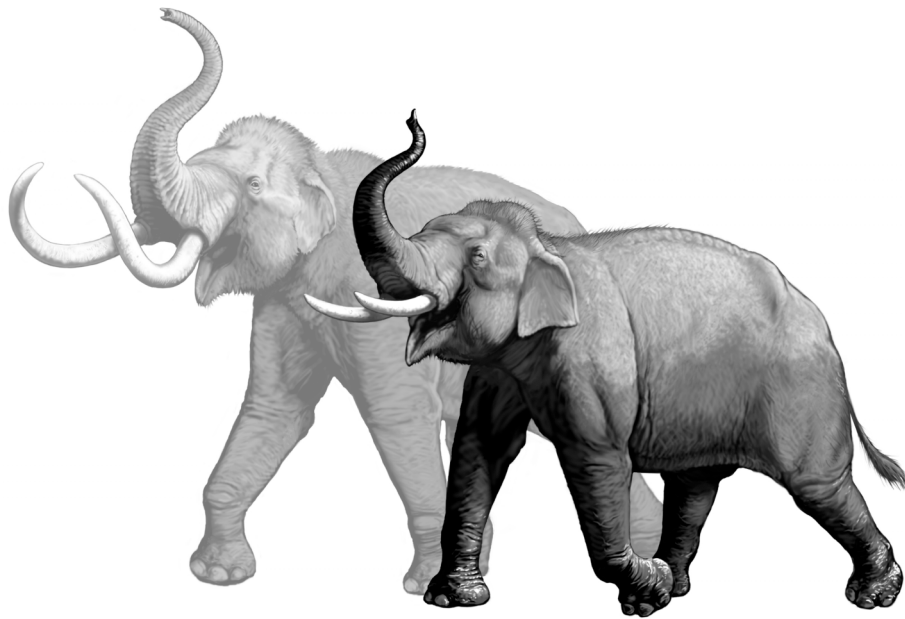


Figure 10. Could the Asian elephant serve as an ecological proxy for North American mammoths in an effort to restore megaherbivore function back to North America? Illustration by Carl Buell.

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 prior to 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 likely 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 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 & Holt 2004). Many diseases are carried by rodents (Ostfeld & 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—combined with 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 into their visions for restoration ecology. Pleistocene Rewilding offers an experimental framework to better understand the biology of a continent that vanished *c.* 13,000 years ago with the conquest of the Clovis cultures 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 & Martin 2004; Martin 2005a). In North America, we routinely turn to the Columbian landfall of A.D. 1492 as a *de facto* restoration baseline (Leopold et al. 1963), thereby discounting significant earlier ecological impacts by humans (Kay & Simmons 2002; Martin & Szuter 1999). The arrival of the first Americans (Haynes 2002) and the contemporaneous late Pleistocene extinctions constitutes a less arbitrary benchmark that is justifiable from multiple perspectives. Ever more evidence points to early humans precipitating the late Pleistocene extinction events across multiple landmasses (Barnosky et al. 2004; Burney & Flannery 2005; Lyons et al. 2004; MacPhee 1999; Martin 2005b; Miller et al. 2005; Robinson et al. 2005). Such attestation also raises important ethical questions regarding our conservation benchmarks and strategies.

Prior to 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 (Figure 11, 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 (Donlan et al. in press; Guix et al. 2005; Janzen & Martin 1982; Purvis et al. 2000; Terborgh 2005).

While evolutionary perspectives have been raised in conservation planning (Erwin 1991; Frankel & Soulé 1981), they have usually emphasized conserving existing processes (Ashley et al. 2003; Woodruff 2001) rather than restoring recently extinct interactions (Atkinson 2001; Burney et al. 2002; Martin 1999; Martin & Burney 1999). The bold actions needed to preserve evolutionary potential in the wake

of the drastic decline in biodiversity and global change have generally 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; Blake & Hedges 2004; Gros 2002; Marchant 2001; Thomas et al. 2004a). The widespread disruptions of population dynamics and of the potential for adaptive responses to climate change suggest that absent 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 this evolutionary potential, regional rewilding (Foreman 2004; Soulé & Noss 1998) carries global conservation implications.

The most straightforward conservation advantage of Pleistocene Rewilding would be enhancing the persistence of endangered large vertebrates with a multi-continent 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 re-introduction of Przewalski horses (*Equus caballus przewalski*) from North American and European zoos to the semi-wild state in to their native habitats in central Asia. Additional viable populations could also enlarge the possibilities for adaptation to global change for target species, 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.

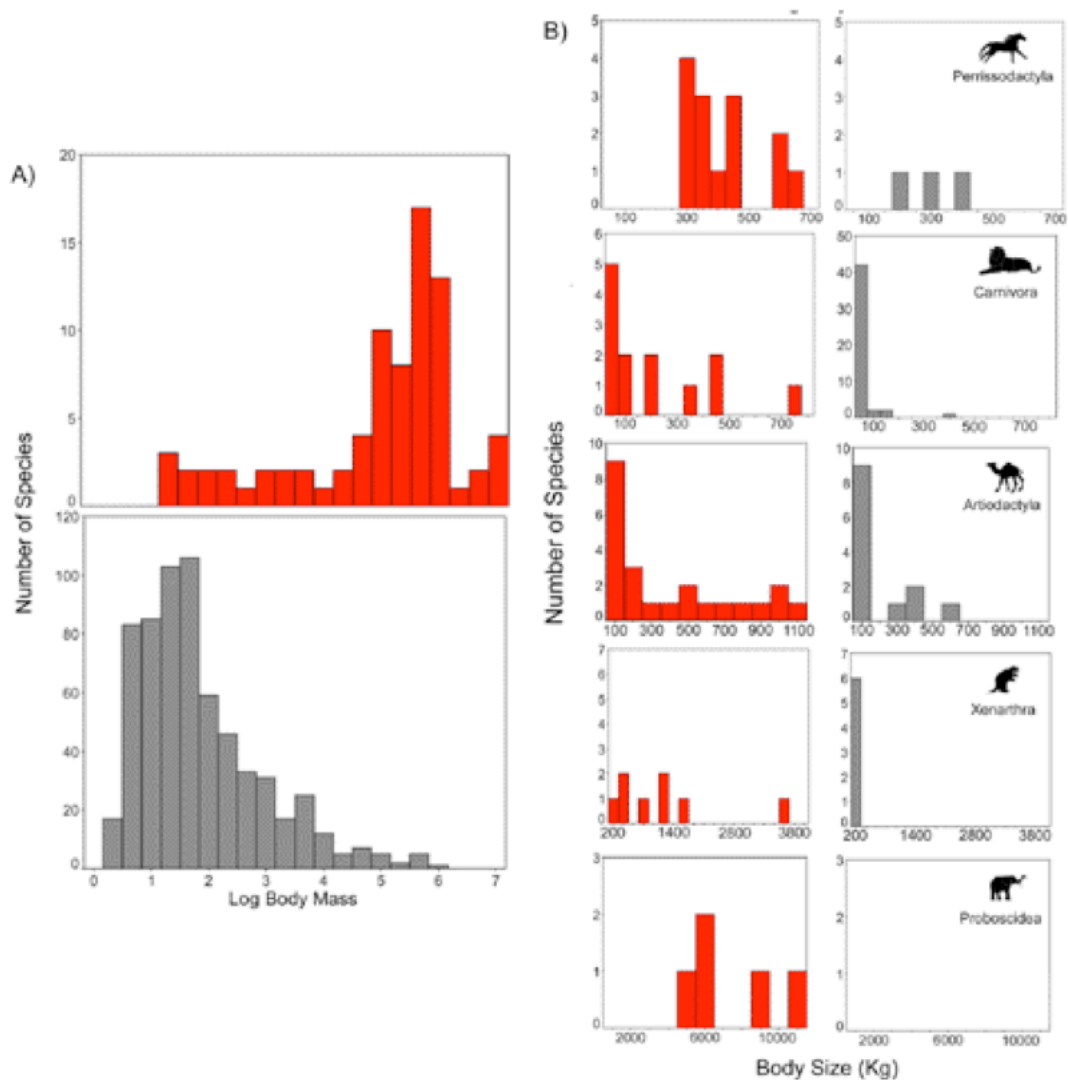


Figure 11. (A) Body size distributions (log body mass) of terrestrial North American mammals (including bats) before (red) and after (grey) late Pleistocene (LP) extinctions (north of the Isthmus of Tehuantepec). (B) Body size distributions (kg) of four large-bodied (over 44 kg) taxonomic groups before and after LP extinctions. Extant distribution of Perissodactyla includes Old World horses and burros. Modified from Lyons et al 2004.

In a general sense, Pleistocene Rewilding could be part of a movement to transform conservation biology, which is currently too easily characterized as a ‘doom and gloom’ discipline (Anonymous 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 & Sanjayan 2003). Moving away from managing extinction and toward actively restoring ecological and evolutionary processes with 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 (Burney & Flannery 2005; Lyons et al. 2004; Martin 1966; Martin 2005b; Martin & Steadman 1999; 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, due to persecution, habitat fragmentation, and their subsequent effects 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 extend back into the Pleistocene and reach forward to contemporary times (Peacock & Peacock in press; Quammen 2003; Shepard 1998). 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 1999-2004, more than 1.5 million people annually visited San Diego Zoo's Wild Animal Park to catch a glimpse of large mammals (C. Simmons, personal communication). Only 12 U.S. National Parks received over 1.5 million visitors in 2000 (National Park Service 2000). Alarming, per capita visitation to U.S.

National Parks has been declining since 1987—the first time since the 1930s (Pergams et al. 2004).

Pleistocene Rewilding would likely 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 compared to an estimated annual cost of \$0.5-0.9 million to society (Duffield & 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 esthetic 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 10). All differ in their potential costs and benefits, and all are already present in the U.S. either as free-roaming populations or in a captive setting. All potential restoration programs would be experimental, science-driven, and evaluated within a cost-benefit perspective. We start our discussion with two taxa that have already been successfully reintroduced to North America, move on to species that are already present in North America but viewed as non-native species, and end with potential proxy species that could replace some of our lost Pleistocene megafauna. While not exhaustive, 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*) was saved from near extinction due to DDT contaminants (Cade & 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 eastern and mid-western U.S. and parts of Canada came from captive stock of seven subspecies from North America, Europe, South America, and Australia, totaling more than 2500 birds (Tordoff & 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 & Redig 2001). Falcons from four continents now serve as a collective proxy for the mid-western peregrine population that went extinct in the 1960s. The Peregrine Falcon not only serves as a testament that species recovery can succeed at continental scales, but also demonstrates that at least in some cases taxon substitutions are culturally acceptable as a powerful conservation tool.

Table 10. The magnitude of biodiversity loss of North America megafauna (north of the Isthmus of Tehuantepec) and potential benefits and costs of Pleistocene rewilding (+ represents an increase in respective qualitative category). Late Pleistocene (LP) and current diversity of continental large-bodied North American mammalian orders/families, along with some potential species proxies.

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 Human conflict	++	+++
			Lion	Predation	?	Tourism; hunting		++	+++
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							
Artiodactylidae	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*, *Lama guanicoe*, *Vicugna vicugna* equid: *Equus caballus*, *Equus przewalskii*, *Equus hemionus* cheetah: *Acinonyx jubatus* lion: *Panthera leo* elephant: *Elephas maximus*, *Loxodonta africana* Bolson tortoise: *Gopherus flavomarginatus*.

^b Predation on mink 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.

Giant Vultures

The California condor (*Gymnogyps californianus*) was present throughout North America until the late Pleistocene, then disappeared across most of its range along with the megafauna upon which it fed. Condors survived solely along the West Coast, relying heavily on carcasses of marine mammals (Chamberlain et al. 2005), and last roamed over the Grand Canyon *c.* 10,000 years ago, where they scavenged on mammoths (*Mammuthus* sp), horses, camels, and other extinct taxa (Emslie 1987). Condors may have returned briefly to the southwest U.S. in the 1700s in response to the introduction of domesticated cattle, horses, and sheep, but the validity of those records is unclear (S. Emslie, personal communication; L. Kiff, personal communication, Federal Register 1996); nonetheless, by the time of European arrival *Gymnogyps* was restricted to 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 (Beissinger 2001; Snyder & Snyder 2000). 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 (Bury et al. 1988; Van Devender et al. 1976). 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 restricted to a small area in central Mexico (Morafka 1982; Morafka & McCoy 1988). Chelonians were part of the exploited Pleistocene megafauna in the American southwest and elsewhere (Moodie & Van Devender 1979; Stiner et al. 1999; Taylor 1982). Harsh winters could have played a contributing role to their decline (Moodie & Van Devender 1979; Van Devender et al. 1976), but *G. flavomarginatus* is relatively cold-tolerant, as evidenced by a reproducing captive population in southeast Arizona (Appleton 1978).

A previous reintroduction proposal for Big Bend National Park (Aquirre & Adest 1991) was rejected by the National Park Service on the basis that *G. flavomarginatus* is a non-native species, its endangered status notwithstanding (Houston & Schreiner 1995). This conclusion is counter to ecological and historical insights, and inconsistent with subsequent restoration of California Condors to the Grand Canyon (Donlan & Martin 2004). Along with conservation benefits for the species, tortoise reintroductions to the southwestern U.S. might increase local biodiversity by promoting landscape heterogeneity via burrow construction (Kaczor & 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 10).

Equids

Feral equids (*Equus caballus*, *E. 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: they were present there 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 (MacFadden 1992; Oakenfull & Clegg 1998; Stebbins 1981). Today feral horses and burros in North America are widely viewed as ecological pests (Houston & 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 end of the Pleistocene (Vilà et al. 2001; Weinstock et al. 2005). Based on molecular systematic studies (Weinstock et al. 2005), *E. caballus* is arguably as similar to late Pleistocene North American horses as are the abovementioned peregrine falcons from five continents and the contemporary coastal and late Pleistocene interior populations of California condors. Both horses and burros, and perhaps other extant Old World equids, are plausible taxonomic and ecological proxies for extinct New World taxa (Donlan & Martin 2004; Martin 1970).

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; Janzen 1982; Janzen & Martin 1982). Moreover, wild asses (e.g., *E. hemionus*) and Przewalski’s horse 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 prior to 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 (Beaver & Brussard 2004; Kuiters 2003; Levin et al. 2002; Zalba & Cozzani 2004; Zervanos 1998). A potentially important factor in the overall context for free-ranging horses is the presence of

predators (Turner et al. 1992), including 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 (Honey et al. 1998; Kurtén & Anderson 1980; Smith et al. 2003b). Today, two species of Old World camelines and four species of South American lamalines are extant globally. Wild Bactrian camels (*Camelus bactrianus*) are on the verge of extinction, with less than 1000 free-living animals remaining in Asia (Hare 2001). Domestic or captive-bred camelids could be introduced to parts of North America, further assuring their semi-wild persistence and serving as ecological proxies for extinct late Pleistocene lamalines (e.g., Camelops, Honey et al. 1998; e.g., Camelops, Webb 1965).

Camelids potentially offer biodiversity benefits to arid and semi-arid North American ecosystems by browsing on woody species that now often dominate areas that formerly were mixed desert scrub and grassland (Table 10, Martin 1969; Mengli et al. in press; Van Auken 2000). In the 1850s, when Lt. 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). While evidence is largely anecdotal, large numbers of feral camels appear to be having unfavorable ecological impacts in the Northern Territory, Australia 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 U.S. 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 *c.* 13,000 years ago (Stebbins 1981).

Camelids might bring economic benefits to North America as well: in Australia, well-managed co-grazing programs of cattle and camels produce additional markets for meat, milk, and fiber without negatively impacting cattle production (Phillips et al. 2001). Organized trekking with camelinines and lamalinines, long popular in Australia, is already present in the U.S. (e.g., www.texascamelcorps.com). Camelids thus exemplify how managed, experimental reintroductions could be used to weigh benefits and costs of Pleistocene Rewilding under carefully controlled, experimental conditions.

Cheetah

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 cheetah 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 were arguably the principal selective agent favoring speed and visual acuity in pronghorn (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 have continued 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 cheetah are unique in that the majority of the remaining individuals are located outside of protected areas, commonly on commercial livestock and game farmland (Caro 1994; Marker et al. 2003b). Most (~90%) of Namibia's cheetahs live on commercial livestock farmland, where lions (*Panthera leo*) and spotted hyaenas (*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 U.S. could potentially facilitate economic alternatives to ranchers through ecotourism with little costs to other revenue streams of ranching (Table 10). Restoring cheetah to North America could also reinstitute what must have been strong interactions with pronghorn and perhaps help save the world's fastest land mammal from extinction. An single intriguing anecdote hints that the pronghorn's speed and escape tactics from 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).

Proboscidiens

Five species of proboscidiens roamed North America in the Pleistocene (Kurtén & Anderson 1980; Smith et al. 2003b). Asian elephants (*Elephas maximus*) are more closely related to North American mammoths (i.e., *Mammuthus primigenus*) 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 keystone roles as

megaherbivores (Dublin 1995; Owen-Smith 1988), just as mastodons, mammoths, and gomphotheres surely once did in the Americas (Barlow 2000; Janzen & Martin 1982). Collectively, proboscidians 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 proboscidians occupied for millennia (Figure 10)? African elephants inhibit woodland regeneration and promote grasslands; elevated densities appear to be the primary driver of woodland loss (Western & Maitumo 2004; Whyte et al. 2003). Encroachment of woody and shrub plant species over the past century now threaten 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 (Agenbroadhowlad 2005) and recognizing that extinct proboscidians 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 10). Further, many elephant populations, particularly in Asia and West Africa, are in grave danger of extinction (Blake & Hedges 2004), and captive breeding programs are not self-sustaining for either species (Olson & Wiese 2000; Rees 2003; Wiese 2000). Proboscidians played a variety of ecologically and evolutionarily significant roles across North American landscapes for millennia (Barlow 2000; Janzen 1986; Janzen & Martin 1982). With the appropriate resources and vision, captive stock and some of the 16,000 domesticated elephants in Asia (Lair 1997) could perhaps elucidate 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 *Panthera leo (sensu lato)* was perhaps once collectively the most wide-ranging wild land mammal of all time (Kurtén & Anderson 1980).

Today, lions play a pivotal role regulating prey populations in African savanna ecosystems (Sinclair et al. 2003), as they surely once did in the Americas and Eurasia. With the estimated population dropping from 76,000 to less than 40,000 over the past twenty years (IUCN 2006), African lions are increasingly threatened by habitat degradation, human conflict, reduction in prey base, and disease (IUCN 2006; Marchant 2001; Nowell & Jackson 1996; Roelke-Parker et al. 1996). The Asiatic lion (*P. l. 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 & Jackson 1996). However, lions have been re-established or managed in African and Indian reserves of similar size to 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 public attraction to large predators, the potential esthetic and economic benefits of restoring lions to North America are obvious—as are the challenges (Table 10). 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 & Leggat 1999), local human-lion conflicts (including deaths) are serious problems in some other parts of Africa and India (Packer et al. 2005; Saberwal et al. 1994). Mitigating for human-carnivore conflict is by no means a new conservation challenge (Saberwal et al. 1994; Treves & Karanth 2003), but clearly momentous obstacles would have to be overcome with a detailed science-based management and education program (Packer et al. 2005) in advance of restoring lions to North America.

Nevertheless, models of carnivore repatriation exist even though goals vary 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 (Gittleman & Gompper 2001; Reading & Clark 1996) with at least those of cheetahs and lions being demographically successful in African reserves and re-instilling normative behavior in their ungulate prey (Hunter & Skinner 1998), just as have grizzly bears and wolves in the Yellowstone region (Pyare & Berger 2003).

Still, the critical test beyond simply returning large dangerous carnivores hinges on reserve size. If carnivore densities achieve a size that minimizes their chance of extinction, then at least a threshold for recovery will be reached. But, if reserves are small, whether fenced to protect humans or economic interests beyond reserve boundaries or unfenced, problems may persist. If carnivores are not food-supplemented, prey might be harvested at unsustainable rates and rather than restoring a functional ecological relationship, some will claim the reserve may be nothing more than a large zoo. However, differences among type of reserve—zoo, small protected area, big protected area or large functioning system—is a matter of spatial gradation and management goal. Our view of rewilding is to begin modestly. Some private

South African game parks with re-introduced lions have now attained sizes between 15,000 and 75,000 ha, whereas large ranches in southwestern North America exceed these in size.

Risks, costs, challenges, and objections to Pleistocene Rewilding

Potentially serious and legitimate objections to Pleistocene Rewilding must be faced objectively, with all available information, and within a cost-benefit context that includes the above-mentioned ecological, evolutionary, economic, esthetic, and ethical considerations. We must first ask, is a pre-1492 benchmark for conservation realistic in our current world and for the foreseeable future? There are many emerging ecological and anthropological reasons against a *de facto* Columbian benchmark (Donlan & Martin 2004; Jackson 1997; Kay & Simmons 2002; Martin 2005b), yet temporal scales of restoration and baselines have received little debate (but see Callicott 2002; but see Gobster & Hull 2000). Nonetheless, the recent restoration of condors to Arizona suggests that a late Pleistocene benchmark warrants consideration and contradicts objections that bringing back megafauna by definition would waste precious conservation dollars. Obviously, a Pleistocene benchmark is not appropriate for much of North America, but we argue it should be debated, particularly in areas where it may be a real possibility.

There are a number of key issues to be considered with 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. Old World conspecifics or ecological proxies, for example, 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,

respectively; Smith et al. 2003a). What role does nutrition play with respect to differences in observed body size differences? 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 (Calder 1984; Gwynne & Bell 1968; Murray & Brown 1993; Owen-Smith 1988)? Along with body size will come questions and objections concerning genetics. How genetically different were Pleistocene cheetahs, lions, elephants, and horses from extant populations today? With the rapidly advancing field of paleogenomics, these questions are being increasingly answered (Johnson et al. 2006; Poinar et al. 2006; Weinstock et al. 2005) and are one of multiple factors to inform decisions regarding the use of taxon substitutions. That such questions can be addressed in the context of specific conservation objectives is illustrated by the Peregrine Falcon.

Careful studies of potential proxies and their ecological role need to be undertaken (Atkinson 2001; Simberloff 1990). 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 restoration of ecological and evolutionary processes are goals of conservation (Atkinson 1998, 2001). While the idea of using taxon substitutions as a conservation tool is gaining traction (Nicholls 2006), many aspects of ecological proxies remain unfocused. Aspects such as phylogenetic relatedness, ecological function, and 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 & Martin 2003). That their value may often outweigh costs and objections is illustrated by successfully introduced ecological proxies including the Peregrine Falcon, the North African Red-necked

Ostrich (*Struthio camelus camelus*) as proxy for the Arabian Ostrich (*S. c. syriacus*) (see Sedon & Soorae 1999), night herons, and giant land tortoises.

In Bermuda, the Yellow-crowned night heron (*Nycticorax violacea*) was introduced in the mid 1970s as an proxy for a closely related endemic night heron (*Nycticorax sp.*) that was extirpated in the 17th century (Olson et al. 2005; Wingate 1982). The established breeding population subsequently exhibited top-down control on land crabs (*Gecarcinus lateralis*), which are a major prey species of night herons and were exceptionally abundant and causing economic damage prior to the heron introduction (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 the historical and present ecological states into conservation planning and action (Davenport et al. 2001).

Under a scientific experimental framework, scientists from the Mauritian Wildlife Federation are using giant tortoises from Aldabra Island (*Aldabrachelys gigantea*) as ecological proxies for the two extinct species of the Mascarene Islands (*Cylindraspis inepta* and *C. triserrata*). Tortoises were first introduced into exclosures on Ile aux Aigrettes Island (Zavaleta et al. 2001); now free-roaming tortoises are present on the island resulting in both increased seed dispersal and tourism (Vikash Tatayah, 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 a substantial reaction from diverse sectors, both positive and negative (Krtistof 2005; Nicholls 2006; Stolzenburg 2006). Criticisms thus far have generally focused on opportunity costs and uncertainty

surrounding the challenges of Pleistocene Rewilding (Chapron 2005; Dinnerstein & 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, and furthermore, conservation dollars are often non-transferable. We are not advocating Pleistocene Rewilding as a substitute for or as a priority over on-going conservation projects in Africa or North America, and conservation gains are indeed being made on those continents. Our proposal centers instead 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 & 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. Necessary precautions and protocols will be needed and implemented, as they are similarly advocated with other reintroduction and translocation programs (Cunningham 1996; Viggers et al. 1993). The temporal dynamics of habitats is well established; its 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 of contemporary ecosystems is large vertebrates. Very few plants and small mammals suffered extinction during the late Pleistocene (Jackson & Weng 1999; Lyons et al. 2004).

The taxa we discuss differ critically compared to non-native 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, in some cases were recently present in North America, and 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 (Karesh & Cook 2005; Ostfeld & Holt 2004). 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, 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 a requisite, including designs that capture multiple levels of biodiversity dynamics, spatial and temporal heterogeneity, and other holistic measures of ecosystem health. All of these concerns above hinge on insights of ecological history, from the late Pleistocene and beyond (Donlan et al. 2005; Donlan & Martin 2004; Estes 2002; Martin 1969, 1970; Terborgh 2005).

Some will argue that 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 U.S. and thus reintroduction attempts now would likely 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. Lt. 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). Not only feasible, experimental camel introductions could shed light on the possibility of camels refilling the niche that they once did 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), as yet no evidence supports that concern. International tourism receipts in 1999 and 2000 were approximately US\$10-11 billion annually, and in 1999 58% of African tourist arrivals were interregional, 38.3% European, and only 4.1% from the entire Americas (World Tourism Organization 2001). Perhaps more importantly, foreign ecotourism is beyond the economic means of most U.S. 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).

Africa has much knowledge and experience to offer efforts revolving around Pleistocene Rewilding. First, it provides an optimistic perspective in terms of the long-term feasibility of restoring megafauna to North America. The year following its declaration, Kruger National Park was hardly the celebrated mainstay of southern African biodiversity it is today. In 1903, there were zero elephants, nine lions, eight buffalo, and very few cheetahs within the boundaries of the park. Due to vision and dedication of African conservationists, 7,300 elephants, 2,300 lions, 28,000 buffalo, and 250 cheetah roamed Kruger one hundred years later—as did 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 rural, poor communities (Ashley & Roe 2002; Mahony & Zyl 2002; Spenceley & Seif 2003).

With respect to local economic, political, and cultural interests (Schlaepfer 2005; Shay 2005), we argue that local incentives for stakeholders (economic, esthetic, or otherwise) would be prerequisite for its success and that parts of the central and southwestern U.S. show special promise for Pleistocene Rewilding (Donlan et al. 2005). Nearly twenty years since anthropologists Deborah and Frank Popper proposed the Buffalo Commons (Popper & Popper 1987) – long-term restoration of native grass and wildlife – in an attempt to break the boom and bust cycles of the Midwest that started in the 1860s, residents are embracing the idea (contra Shay’s (2005) 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 Midwestern economy and biodiversity (Popper & Popper 2004).

Implementing Pleistocene Rewilding

Pleistocene Rewilding scales globally and is already underway 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. Endangered birds from Marquesas and Tongan islands are being reintroduced to nearby islands where long-term persistence is more likely, using the fossil record as a guide (Burney et al. 2002; Steadman & Martin 2003). At the 6,000

ha nature reserve *Oostvaardersplassen* in 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 (Sutherland 2002; Vera 2000). Beavers (*Castor fiber*) are being reintroduced throughout Europe to restore ecological processes and heterogeneity to landscapes, in some cases where they and their associated community interactions have been absent for thousands of years (Gamborg & Sandøe 2004). By combining science and restoration driven by history, an international team of ecologists are moving forward on a bold plan to reintroduce large herbivores back to the Siberian steppe, including Yakutian horses, wood bison, and musk ox (Stone 1998; Zimov 2005; Zimov et al. 1995). 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, with some of them already underway. 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 all ready being implemented (Popper & Popper 1999; Popper & Popper 2004). Restoration of Bolson tortoises to ranches in southern New Mexico is currently being considered by the Turner Endangered Species Fund (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 U.S. (Mittermeier et al. 2003) are potentially

appropriate for Pleistocene Rewilding, with the fossil record and carefully designed research as guideposts and safeguards. Private lands likely hold the most immediate potential: more than 77,000 Asian and African large mammals (71 species) are present on Texas ranches (Schmidly 2002), for example, although their significance for conservation remains largely unevaluated and their landscape impacts unexplored.

Other projects can also begin immediately, with the experimental maintenance on private property of small numbers of cheetah, lions, and elephants guided by experts from a variety of disciplines, such that the ecological impact and biology of these species can be carefully studied. The requisite animals are already present in the U.S. or can be readily produced by captive breeding; the primary logistical innovation at this point is 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 between zoo practitioners, animal welfare proponents, and ecologists. Presumably rewilding would be tackled on a species-by-species basis, with specialty groups for each taxon (e.g., cheetah) broadening their global scope to include evaluating and advising such activities.

A third and more ambitious scenario would be exemplified by an enormous Ecological History Park, encompassing thousands of square miles in what are already

economically depressed parts of the Great Plains (Popper & Popper 1999). Secure game fencing, which can effectively mitigate human conflict (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 on the future of biodiversity. The default scenario will surely include ever more pest-and-weed dominated landscapes, 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, one that fundamentally challenges our views of nature and transforms conservation biology from the reactive to the proactive. The potential benefits of several proposed proxies have been outlined here; while sound science can help mitigate the potential costs, 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 in the context of an arguably equal degree of uncertainty, inarguably high costs, and often obscure benefits associated with the prevailing worldview of conservation—maintaining the

status quo or at best retrieving something of the very recent past.

To those who find objections to Pleistocene Rewilding compelling, we ask, 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, cheetah, 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 indeed substantial and the risks are not trivial, we can no longer accept a hands-off approach to wilderness preservation as realistic, defensible, or cost-free. It is time to not only save wild places, but to rewild and reinvigorate them.

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