CASE STUDY

Beyond Historic Baselines: Restoring Bolson Tortoises to Pleistocene Range

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ABSTRACT

Ecological restoration in North America traditionally has strived to return ecosystems to some semblance of the early historic (post-Columbian) condition. Emerging alternative paradigms recognize the large impacts exerted by pre-Columbian peoples, the ever-changing nature of ecosystems regardless of anthropogenic effects, and the possibility of using other benchmarks. Recently, the Turner Endangered Species Fund (TESF) initiated a project to restore the endangered bolson tortoise to an area in southern New Mexico within its late Pleistocene, but not historic, range. Justifications included the likelihood that prehistoric humans extirpated it from New Mexico, the presence of habitats similar to those in its current range in Mexico, and escalating threats to the species there. Thirty tortoises long kept captive outdoors in Arizona, another part of its prehistoric range, formed the basis for the restoration effort. The TESF and the Living Desert Zoo and Gardens State Park near Carlsbad, New Mexico, maintain the adults in outdoor enclosures, and incubate eggs and rear young in smaller facilities. The TESF is initiating studies to assess whether the species can persist in the wild in New Mexico. Restoring imperiled species to prehistoric ranges has some precedent in North America and, we believe, merits increasing consideration as historic ranges of some species offer increasingly less security.

Keywords: baseline, bolson tortoise (*Gopherus flavomarginatus*), Pleistocene distribution, restoration, rewilding

Introduction

In August 2005, an article titled "Rewilding North America" (Donlan et al. 2005) appeared in the journal *Nature*. The dozen authors, mostly from North American universities, offered a startling proposal: consider restoring to North America a suite of wild megafauna resembling that lost at the Pleistocene's end some 10,000 years ago. Because most of those species no longer exist, they could be replaced, according to the authors, by closely related "proxies." Such proxies include several Old World species—Bactrian camel (*Camelus bactrianus*), cheetah (*Acinonyx jubatus*), African elephant (*Loxodonta africana*), Asian elephant (*Elephas maximus*), and lion (*Panthera leo*)—and a North American Pleistocene survivor, the bolson tortoise (*Gopherus flavomarginatus*).

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This "restoration" proposal stimulated hundreds of responses, both critical and supportive, from the scientific community (e.g., Rubenstein et al. 2006, Caro 2007) and the popular media (J. Donlan, pers. comm.). Most objections related to the proposed introduction of large non-native animals. A close reading of the "rewilding" proposal in its initial (Donlan et al. 2005) and expanded (Donlan et al. 2006) versions shows it to be less bizarre, at least conceptually, than implied by some of its critics. Most of the proxies mentioned were present-day African-Asian species, either conspecific with (e.g., lion) or slightly more distantly related to (e.g., cheetah) the forms lost from North America at the end of the Pleistocene. The close relationships arose from ancestral ranges that in the Pleistocene had spanned Asia and North America.

Reintroducing such species to North America seems outlandish to some because conservationists traditionally have used historic (i.e., post-Columbian), not prehistoric conditions as restoration baselines or benchmarks (Reid 1996, Simpson 2002, Botkin 2001). During the past few decades, however, restoration programs for some imperiled species have included releases in regions without historic records of occurrence. Prominent among these releases are California condors (*Gymnogyps californianus*) released in northern Arizona (Meretsky et al. 2000) and black-footed ferrets (*Mustela nigripes*) released in northern Chihuahua (Messing 1986, Lockhart et al. 2006). We review the rationale for and progress toward restoring the endangered bolson tortoise to an area occupied prehistorically but not historically.

Changing Paradigms

Until recently, two assumptions have justified using post-Columbian benchmarks to set restoration goals. The first assumption, based in part on Frederic Clements's (1916) "succession" theory

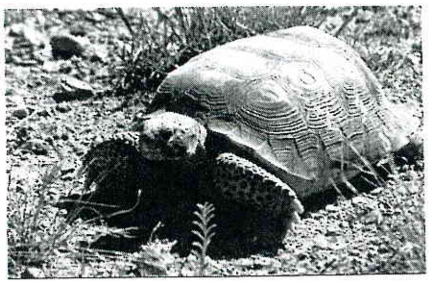

Figure 1. The bolson tortoise can weigh up to 13 kg or more and has a life span similar to that of humans. Photo by J. Truett

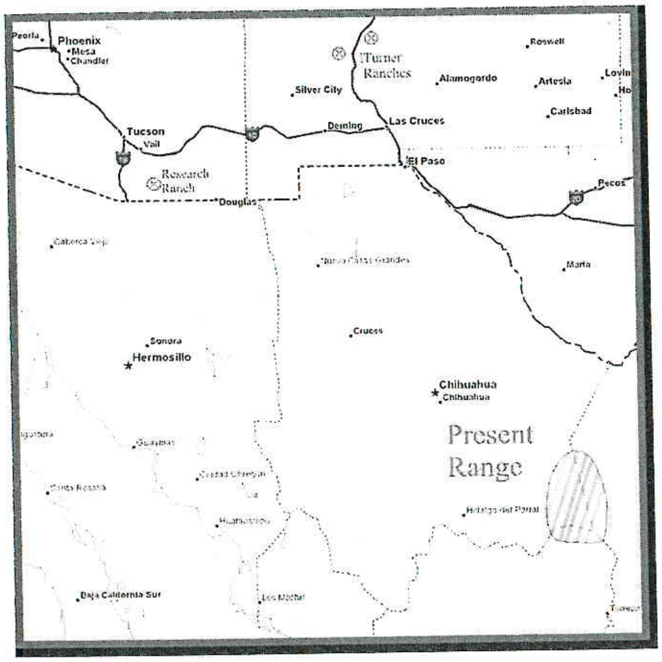

Figure 2. The historic range of the bolson tortoise is about 700 km SSE of the New Mexico ranches where this restoration project is taking place and the Appleton Research Ranch where the adults previously resided for up to 35 years.

of community development (Westman 1990, Sprugel 1991, Borman and Pyke 1994), held that natural communities consisted of coevolved members and for millennia had changed little in composition. The second assumption was that pre-Columbian peoples had exerted little influence on their environments (Diamond 1986, Wagner and Kay 1993, Reid 1996). Neither assumption now seems reliable (Diamond 1986, Hunter et al. 1988, Kay 1994, Redman 1999, O'Brien 2001).

Indeed, emerging consensus that ecosystems have always changed, with or without impacts from humans (Dickinson 1995, Hobbs and Norton 1996, Simpson 2002), suggests that the term "restoration" may have been an unfortunate choice. To complicate matters, climate change may soon alter some environments to the extent that neither historic nor present-day assemblages of species offer useful restoration goals (Graham 1988, Soulé 1990, Sprugel 1991). Given these conundrums, Pickett and Parker (1994, 75) suggest ecological restoration be viewed not as a "lasting patch or repair," but an "intervention into an ongoing process."

Should biodiversity conservationists focus on saving individual species in danger of extinction rather than trying to restore historical and supposedly coevolved communities? Perhaps. Although the past has clear relevance for planning the future, prudent restoration is unlikely to be as straightforward as, for example, reestablishing along the Missouri River the same panorama of communities Lewis and Clark observed there two centuries ago.

The Bolson Tortoise: A Pleistocene Relict

In early fall 2004, Drs. Jane and Carl Bock of the University of Colorado inquired whether the Turner Endangered Species Fund (TESF) might accept for conservation a captive group of bolson tortoises (Figure 1). The captives in question (the "Appleton tortoises") lived at the time in outdoor enclosures at the Appleton Research Ranch in southeastern Arizona. For three decades or so they had been managed by the owner of the property (see Appleton 1978, 1980, 1983).

We began to assess the feasibility of accepting the captives and, over time, developing one or more wild populations on two New Mexico properties—the Turner-owned Ladder and Armendaris ranches—in the northern reaches of the Chihuahuan Desert. No post-Pleistocene records exist for wild populations beyond the tortoise's present Chihuahuan Desert range some 700 km south-southeast of these ranches (Figure 2). No other tortoise species exists on or within several hundred kilometers of these ranches. The bolson tortoise has imperiled status both with the U.S. Fish and Wildlife Service (under the U.S. Endangered Species Act) and the Mexican government (Aguirre et al. 1997).

First described as a species by Legler (1959), the bolson tortoise in the wild occupies a series of enclosed desert basins collectively called the Bolsón de Mapimí. Its distribution, estimated to cover less than 6,090 km^2, surrounds the juncture of the Mexican states of Chihuahua, Durango, and Coahuila 150–300 km south of Big Bend National Park in Texas (Bury et al. 1988). Subsequent to the discovery of the species, studies revealed diminishing numbers and range (Bury et al. 1988, Morafka 1988, Treviño et al. 1997). The Mapimí Biosphere Reserve in northern Durango was formed in 1977 to help protect the species.

Based on remains discovered in a number of locations, the species during the late Pleistocene appears to have ranged from Arizona eastward at least as far as western Texas (Morafka et al. 1981). Bolson tortoise remains from Maravillas Cave near Big Bend National Park, Texas, for example, date from the late Wisconsin glaciation, or about 11,000 years B.P. (Van Devender and Bradley 1994).

Morafka (1988) concluded that the most likely cause of the species' relatively restricted current range was predation by humans during the Holocene epoch. North American aboriginal groups are known to have consumed other species of *Gopherus* (Schneider 1996). Present-day harvesting of desert tortoises (*G. agassizii*) by the Seri of northwestern Mexico is a long-standing tradition (Felger et al. 1981) that may explain the fewer and smaller tortoises near mainland Seri settlements compared with those on the more remote Tiburon Island. Furthermore, people still eat bolson tortoises, leading to reduced or extirpated tortoise populations in parts of their current range near human settlements and transportation corridors (Bury et al. 1988, Morafka 1988). Expanding agricultural and other developments threaten further losses.

Life History

The bolson tortoise is one of four species of land tortoise (*Gopherus* spp.) native to North America. Individuals reach weights of at least 13 kg and ages of 70 years or more (c.f. Appleton 1978, TESF unpub. data). These animals spend over 95 percent of their lives in self-dug burrows, which they use as winter hibernacula, refuges from temperature extremes during all seasons, and escape from predators (Morafka et al. 1981, Adest et al. 1989). They live in loosely organized colonies at densities of one or more per hectare. Adults occupy home ranges that cover several hectares to one square kilometer or more in habitats dominated by creosote bush (*Larrea tridentata*), mesquite (*Prosopis juliflora*), tobosagrass (*Pleuraphis mutica*), and other Chihuahuan Desert plants.

Bolson tortoises, herbivores like other tortoise species, eat mainly grasses and forbs (herbaceous leafy plants) (Morafka et al. 1981, Adest et al. 1989, TESF unpub. data). The rather low number of plant species in the arid habitats occupied by bolson tortoises, compared with plant diversity in more mesic regions, restricts their dietary breadth. Observations of captives in Arizona (Appleton 1978) and New Mexico (TESF unpub. data), coupled with the undoubtedly greater diversity of plants in the species' evolutionary range, suggest that access to greater plant diversity may expand the diversity of plants consumed.

Breeding occurs largely in late summer and early fall, coincident with monsoonal rains (Morafka et al. 1981, Adest et al. 1989), while egg laying takes place mostly in May and June (Appleton 1978, TESF unpub. data), indicating sperm sequestration at least over winter. Females usually lay one or two clutches of 1–10 eggs each year, burying them near burrows in excavations they dig with their hind feet (Appleton 1978, TESF unpub. data).

As in other tortoises (Morafka et al. 1997), the eggs and young of bolson tortoises commonly suffer high mortalities (Appleton 1980, Tom 1994). This early-stage "bottleneck" to survival in the wild suggests that reducing the losses of young should be an effective strategy for population recovery (Morafka et al. 1997), and we have focused our efforts accordingly.

The Restoration Experiment Begins

In early 2005, we asked an assemblage of tortoise specialists at the 30th Annual Desert Tortoise Symposium whether a restoration project in New Mexico was justifiable (Truett et al. 2005). All responses were affirmative, in part because of the perceived insecurity of the species in its historic range. Some of the biologists present recommended that we initiate restoration-site studies to assess habitat suitability, nutritional adequacy of forage, and potential disease threats. Several suggested that rapid reproductive augmentation of the Appleton population would require "head starting" to protect eggs, neonates, and juveniles from predators.

A year later, in early 2006 at the 31st Symposium, Dr. Lucina Hernandez, at the time administrator of the Mapimí Biosphere Reserve in Mexico, noted the post-1980s decline of efforts to conserve the species in Mexico (Hernández and Laundré 2006). She suggested that the proposed effort in New Mexico might help reverse that trend, by both augmenting numbers in the United States and encouraging greater protection in Mexico.

In June 2006, Dr. James Jarchow, a veterinarian experienced with desert (Jarchow et al. 2002) and bolson (Adest et al. 1989) tortoises, assembled a team to help capture the Appleton tortoises and assess their nutritional and disease status. Visual examinations showed the animals to be in generally good health, with no evidence of clinical infections. Blood tests per Christopher and others (1997) showed four individuals positive for antibodies to *Mycoplasma*, a causative agent for upper respiratory tract disease (URTD), which is common but often benign in the closely related desert tortoise (Berry and Christopher 2001).

In early fall 2006, TESF biologists transferred the 30 adult bolson tortoises and seven of their recently hatched offspring from Arizona to facilities in New Mexico. The move required permits from the New Mexico Department of Game and Fish. Because the tortoises had been legally imported to Arizona from Mexico prior to being listed as endangered by the U.S. Fish and Wildlife Service and the Mexican government, or were offspring of the captives, we needed no permits from the U.S. Fish and Wildlife Service (to comply with the Endangered Species Act) or from the Convention on International Trade in Endangered Species. Federal permits will be required before we release any tortoises into the wild.

The four *Mycoplasma*-positive adults (two males, two females) went to the Living Desert Zoo and Gardens State Park (Living Desert) near Carlsbad, New Mexico. Living Desert staff provided them with artificial burrows in an outdoor enclosure isolated from other animals. Like some *Mycoplasma*-positive desert tortoises (Berry and Christopher 2001), they have not exhibited clinical signs of disease.

Biologists with the TESF apportioned the 26 disease-free adults between two larger enclosures (3.5 ha each) on the Armendaris Ranch. Each enclosure contained soil textures, dominant forages, and landscape gradients selected to mimic as nearly as possible those at the Mapimí Biosphere Reserve as described by Morafka and others (1981), Lieberman and Morafka (1988), and Traphagen (2006). Elevation, precipitation (annual amount and seasonal distribution), and average summer temperatures in the Armendaris Ranch area (Wainwright 2005) are remarkably similar to those at Mapimí (Morafka et al. 1981). But New Mexico winters are colder—January temperatures at the Armendaris average about 15°C lower than those at Mapimí.

Inside the Armendaris Ranch enclosures, biologists and ranch personnel constructed "starter burrows" that angled into the ground at about 20° from the horizontal. We provided the tortoises with water but not supplemental food. Frequent visits during the first few months after releases confirmed that the animals were alive, feeding, drinking, and maintaining body weight. They dug most of the starter burrows deeper and also dug several new burrows. Since the translocation, the tortoises have lived in both kinds of burrows.

These tortoises have hibernated in their burrows during approximately December-March each year. In May and June each year we have collected some eggs for incubation indoors in electric incubators and left others outdoors to hatch. On the Armendaris Ranch, TESF personnel temporarily place gravid females (status of eggs determined by x-ray) in a 4-m × 10-m outdoor "maternity pen." We leave some eggs as they are laid and buried by the females and collect others for artificial incubation. Personnel at the Living Desert collect all eggs laid and incubate them artificially. These efforts have produced over 40 hatchlings to date, all of which are currently alive. Artificial incubation at the Living Desert has yielded a greater success rate than either of the two methods used by the TESF.

Current plans call for juvenile tortoises to be husbanded for the first several years of their lives in head-start enclosures as recommended by Morafka and others (1997). In the fall of 2007, the TESF constructed a facility for this purpose on the Ladder Ranch, and in early 2009 began constructing an additional one. In collaboration with the Living Desert, we will compare survival, weight maintenance, and health profiles of young tortoises kept under different husbandry regimes (indoors vs. outdoors, fed during winter vs. hibernated, fed different diets, etc.).

The status to date of the adult and juvenile tortoises suggests good potential for their survival and reproduction in New Mexico. All translocated adults survived except one male that died during winter 2006–2007 of unknown causes, possibly exposure given that he died aboveground. All four of the *Mycoplasma*-positive tortoises (two females, two males) at the Living Desert continue to appear healthy, and both females have produced viable eggs. Overall, annual egg production by reproducing females has substantially exceeded that reported from the wild (see Adest et al. 1989). In most cases the young have grown rapidly and, aside from minor eye infections that we treated with antibiotics, have shown few signs of malnourishment or disease.

For several more years, we will retain all tortoises in this project in captivity. The adults on the Armendaris Ranch will continue to live in a semiwild state inside the two 3.5-ha enclosures, where their densities approximate those of naturally occurring "nuclear colonies" in Mexico as described by Bury and others (1988). The adults at the Living Desert will remain in smaller outdoor enclosures. The neonates will occupy head-start facilities. We will continue to monitor the health of the tortoises, both by external examination and by blood tests for antibodies to *Mycoplasma*, *Pasteurella*, and other pathogens (see Berry and Christopher 2001). Molecular genetics analyses recently completed (T. Edwards, University of Arizona Human Origins Genotyping Laboratory, unpub. data) will help guide future matings to maximize genetic diversity in the captive population. A Mexican graduate student pursuing a Master of Science degree through an international exchange program at New Mexico State University is initiating a study of nutritional adequacy of New Mexico forage plants. Maintenance of a database that describes methods and results of monitoring and research will continue, as will publication of new information in peer-reviewed journals and elsewhere.

Is the New Mexico Habitat Suitable?

Bolson tortoises are K-selected to the extreme, first breeding when 12–17 years old (Germano 1994). Along with this life-history strategy come typically low recruitment of young into the breeding population and low population turnover. Thus it will be many years before we have a living demonstration that populations can persist in New Mexico without management assistance.

Based on problems in desert tortoises (Berry 1997, Berry and Christopher 2001), disease threats, especially URTD (caused by infection with *Mycoplasma*) and cutaneous dyskeratosis, are the greatest concerns. The apparently benign effects of *Mycoplasma* in the four individuals residing at the Living Desert are encouraging. We have seen no symptoms of cutaneous dyskeratosis in the tortoises. We will use the protocols of Berry and Christopher (2001) for annual disease evaluations, initiating more intensive tests if symptoms suggestive of potentially serious problems appear.

The tortoises' persistence and reproduction for 30-plus years in a climate regime in Arizona similar to that on the New Mexico ranches suggest the adults will be able to tolerate the climate. In time, the New Mexico climate may become even more like that in their Mexico range if global warming brings Mexico-like winter temperature regimes northward. In the meantime, Dr. James Juvik of the University of Hawaii (pers. comm.) has installed meteorological stations at Mapimí and the Armendaris Ranch to enable comparisons of parameters such as relative humidity and soil and air temperatures.

Can the eggs and young survive the predation bottleneck that is common among tortoises (Tom 1994, Morafka et al. 1997)? For the next several years we will probably not expose any young to predation, depending on the rate at which their numbers increase. But once we have produced and reared substantial numbers of young tortoises in captivity, we plan to release some into the wild and monitor rates of survival and the causes of mortality.

In-depth research during the next few years will likely focus on nutrition. Reasons for this are several. We do not want to expose the young to native predators until later. Testing for disease at this stage seems a monitoring rather than a research priority. Enhancing productivity calls for close management attention rather than new research. In keeping with this, current graduate study is investigating food selection and its implications. Do bolson tortoises choose plants and plant parts on the basis of their protein content, fiber content, and presence or absence of toxins rather than on their species identity? If so, does this imply they are not tied nutritionally to plant assemblages in their present range? Answers to such questions have strong implications for the long-term conservation of the species.

Discussion

Disagreement exists among conservation scientists about the desirability of "restoring" species to areas beyond their historic ranges. Choice of words can reduce or elevate the acrimony (Simpson 2002). For example, McLachlan and others (2007) and Hunter (2007) used the phrases "assisted migration" and "assisted colonization," respectively, for proposals to introduce species beyond their current or historical ranges in anticipation of climate change. A different response to the same proposals might have resulted if they had used instead the term "introduction of exotics." Aside from semantics and perception, the effects of moving species into new areas may range from ecologically inconsequential (Botkin 2001) to economically bothersome (Young and Clements 2005) to extirpation of natives (Savidge 1987).

What should be the basis for decision when introduction of an imperiled animal outside its historic range might save a species and not greatly alter a community? Consider that each imperiled vertebrate commonly has existed in its present form, or functionally so, for hundreds of millennia. In contrast, unique assemblages of species, that is, communities, often take shape and disappear within a few tens of millennia or less (Graham and Lundelius 1984, FAUNMAP Working Group 1996). Community composition will continue to change on relatively short time scales, not only with the climate but also with increasingly disruptive anthropogenic forces and other agents affecting dispersal, reproduction, survival, and mortality of species.

This difference in temporal durability of species and communities can be seen in the bolson tortoise and the Bolsón de Mapimí habitat it currently occupies. The bolson tortoise took shape some two to three million years ago as a grassland herbivore, and has lived not in deserts but in grasslands most of the time since (Morafka 1988). In contrast, only about 25,000 years ago at most did the present-day dominant plant in the Chihuahuan Desert, creosote bush, arrive in bolson tortoise habitat (Morafka et al. 1981). Not until the end of the Pleistocene, 10,000–12,000 years ago, did plant assemblages resembling those of today appear in the Bolsón de Mapimí (Van Devender 1990). By these lines of evidence, the bolson tortoise is at least 100–250 times as old as the plant community it presently occupies.

We suggest that conservation biologists and restorationists begin to think beyond the use of historic species assemblages and distributions as the reference points for ecological restoration. Imperiled species generally deserve conservation priority over the communities they occupy. We are applying that philosophy to our work with the bolson tortoise. Species are the building blocks that can be recycled again and again as community compositions inevitably change in future human generations under the influences of climate shifts, ecological interactions, and accidents of dispersal. Diverse communities will assemble and reassemble as long as the building blocks persist. Species, once lost, will not be coming back.

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