Native fishes, exotic mammals, and the conservation of desert springs

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Desert springs are fragile ecosystems that often harbor endemic species of fishes and other taxa. Historically, these springs experienced major disturbances from Pleistocene megafauna, aboriginal humans, and livestock. However, management practices to preserve and restore spring ecosystems and biota have led to the removal of livestock. We document changes in spring habitats and extinctions of fish populations due to management practices at two spring reserves: Ash Meadows in the southwestern United States and Dalhousie in central Australia. After springs were fenced and livestock removed, these ecosystems experienced increases in riparian vegetation, reduction of open-water habitat, and extinction of fish populations. Despite manual removal of vegetation to maintain open-water habitat, at least one pupfish population went extinct in Ash Meadows, and 18 populations, representing four of the five species native to desert springs in the Dalhousie reserve, also went extinct. To maintain the diversity of aquatic habitats and endemic biota, management of small desert springs must include substantial disturbance.

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Desert springs are among the most threatened ecosystems throughout the world. Depletion of groundwater, diversion of surface water, and introduction of exotic species are transforming their aquatic and riparian habitats and causing the extinction of native species. These problems are common in all arid regions, including wealthy, conservation-conscious countries such as the US and Australia. In these two nations, habitat changes and losses of native aquatic and riparian biota have continued to occur in recent years, despite the implementation of nature reserves and restoration and management efforts (Pister 1985; Williams *et al.* 1985; Miller *et al.* 1989; Minckley and Deacon 1991; Shepard 1993; Rinne *et al.* 1996).

Despite large differences in geology, hydrology, and flora and fauna, there are striking similarities in conservation issues facing desert springs in the southwestern US and central Australia. Threats of water diversion, habitat destruction, and exotic species introductions have been addressed by establishing nature reserves to protect springs and surrounding riparian and desert habitats. Management activities are implemented to restore habitats and stabilize populations of endangered species, including exclusion of feral livestock and removal of exotic species. Despite these measures, populations of native fish and other aquatic and riparian organisms have declined and additional extinctions have occurred.

Here, we consider the conservation history of desert springs through an examination of two examples: the Ash Meadows Springs in the Death Valley region of Nevada, USA, and the Dalhousie Springs in northern South Australia. Both systems have springs of varying sizes, which historically supported multiple populations of endemic fish species, as well as native aquatic and riparian plants, invertebrates, and amphibians. European immigrants homesteaded around both springs nearly a century ago, diverting water, modifying habitats for agricultural uses, and importing domestic livestock. In the 1980s, these springs were designated as nature reserves, in recognition of the fragility of their ecosystems and the uniqueness and endangerment of their biota. Management plans, which included efforts to reduce groundwater depletion and other human impacts, remove exotic species, and restore and maintain aquatic and riparian habitats, were implemented. One of these management activities, removal of feral livestock, although well intended, has been detrimental to the conservation of these desert springs and their biota.

We document the history and current conservation status of each spring system in some detail and then draw some general lessons for the conservation and management of desert spring ecosystems.

In a nutshell:

- Major disturbance is necessary to maintain habitat structure and native fish species diversity in desert springs
- Extinct mammalian megaherbivores, aboriginal humans, and domestic livestock historically caused such disturbances
- Removal of feral livestock has led to the extinction of fish populations in desert springs of North America and Australia
- Some substitute for mammalian impacts is necessary to restore desert spring habitats and preserve aquatic biotas

Ash Meadows, Nevada

The 97-km^2 area known as Ash Meadows, located in the Amargosa River basin of western Nevada, contains approximately 20 springs and wetlands inhabited by fish. Springs vary in size from a few square meters to 3300 m^2, and flow rate ranges from a tiny trickle to 164 L s^{-1}. When

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Figure 1. *Matched photographs of two large springs in Ash Meadows National Wildlife Refuge, Nevada. (a) Big Spring, March 1972 and (b) in March 2005. (c) Jackrabbit Spring, June 1967 and (d) in March 2005.*

first surveyed in the 1930s and 1940s, the Ash Meadows spring system contained three genera and four species of native fishes. These exhibited a nested subset community structure, with all three genera (Ash Meadows pupfish, *Cyprinodon nevadensis*; dace, *Rhinichthys osculus*; and Ash Meadows poolfish, *Empetrichthys merriami*) occurring in the largest springs, pupfish and dace occurring in intermediate-sized springs, and only pupfish (*C nevadensis* or *Cyprinodon diabolis*) inhabiting the smallest springs (Miller 1948). By the early 1970s, the endemic Ash Meadows killifish had vanished, and some local populations of dace and pupfish were also extinct or drastically reduced, apparently due primarily to the introduction of exotic fish, including mosquitofish (*Gambusia affinis*), molly (*Poecilia mexicana*), and bass (*Micropterus salmoides*), and an exotic crayfish (*Procabrus clarkii*).

Prior to the initiation of conservation activities, the springs were threatened by groundwater pumping and diversion of surface water for irrigation. The entire Ash Meadows area was also heavily impacted by livestock, especially by feral horses, which kept the aquatic and riparian vegetation of the springs at low levels (Figure 1). Conservation efforts began in the 1960s and early 1970s, with the fencing of three small springs: Devils Hole, School, and Mexican. Devils Hole, a deep cleft in the rock, never possessed emergent vegetation and fencing therefore had essentially no impact. School and Mexican Springs, however, were rapidly overgrown. Within a few weeks after the fencing of Mexican Spring, growth of *Scirpus* and other vegetation, and the resulting transpiration, caused complete drying of surface water and the extinction of pupfish (Figure 2d). School Spring, which was somewhat larger, also became densely overgrown. The population of pupfish was maintained, however, first by periodic manual removal of vegetation, and subsequently by extensive habitat modification, including installation of concrete pools.

In 1984, most of the area was designated as Ash Meadows National Wildlife Refuge. The entire reserve was fenced and all feral livestock removed. Subsequently, all of the springs have experienced dramatic increases in aquatic and riparian vegetation, and consequent reduction in open-water habitat and fish populations (Figure 1). Changes have been most pronounced in small springs (Figure 2). The current management plan recognizes the desirability of removing emergent plants and preserving open water. Although large quantities of vegetation are removed annually, human and financial resources limit the number of springs that can be treated each year. Consequently, all springs are severely overgrown, and the excessive vegetation negatively impacts pupfish populations (Kennedy *et al.* 2005). It is likely that these habitat changes have had negative effects on other aquatic and riparian species, including the endangered Amargosa toad, *Bufo nelsoni* (Jones 2004).

Dalhousie Springs, South Australia

The Dalhousie Springs represent one of the largest and most intact desert spring ecosystems in the world. A

(a and c) Courtesy of EP Pister

Figure 2. *Matched photographs of two small springs in Ash Meadows National Wildlife Refuge, Nevada. (a) Indian Spring, November 1969 and (b) in March 2005. (c) Mexican Spring before fencing, November 1969, (d) after fencing, July 1980, and (e) in March 2005.*

70-km^2 area contains approximately 80 springs, of which 30 contained fish when first surveyed. The springs vary in size from a few square meters to 6100 m^2, and flow rate ranges from a tiny trickle to 138.5 L s^{-1}. The remoteness and harsh surroundings contributed to the springs' preservation, although some were impacted by homesteading and diversion of surface water for agriculture between the early 1900s and 1925, and again from 1933 to 1985 (Zeidler and Ponder 1989).

In 1985, the area was purchased by the South Australian Government to create Witjira National Park. Beginning in 1995, a major effort was initiated to remove feral livestock, fence the major springs, and control tourist traffic. By 2003, only a few donkeys and camels were present at outlying springs. Livestock had been absent from most of the area for many years, and both source pools and outflows were heavily overgrown, primarily with common reed, *Phragmites australis*. Open water was confined almost exclusively to the source pools and major outflows of the largest springs. Elsewhere, the emergent *Phragmites* were so dense that little light penetrated to the water, which was nearly anoxic due to the large quantities of dead and decomposing vegetation. Small springs had been most drastically altered by removal of feral livestock.

The Dalhousie spring system contains five genera and five species of native fishes (Glover 1989; Wager and Unmack 2000). When we thoroughly surveyed the springs in 1991, we confirmed all but one record of previous incomplete surveys made in the 1980s. There had been one extinction due to natural succession and drying of a small spring. The fish assemblages exhibited a near-perfect nested subset structure, with five species (perch, *Leiopotherapon unicolor*; hardyhead, *Craterocephalus dalhousiensis* or *Craterocephalus gloveri*; catfish, *Neosilurus gloveri*; gudgeon, *Mogurnda thermophila*; and goby, *Chlamydogobius gloveri*) in the largest springs, and only goby in the smallest springs (Kodric-Brown and Brown 1993).

We resurveyed the springs in 2003. We had reason to believe that their hydrology and fish faunas were highly dynamic, so we expected to record a modest and approximately equal number of both colonizations and extinctions. Contrary to expectations, however, extinctions far exceeded colonizations (Table 1). There were 18 extinctions and only two colonizations; hardyhead was the only taxon that did not suffer extinction of at least one local population. The majority of extinctions occurred in small springs (0.5–5 m^2). We attribute nearly all of these extinctions to the direct and indirect effects of the changes in vegetation due to exclusion of livestock. Often, there was no habitat suitable for particular fish species, and, in several cases, springs were completely dry, or the entire source pool and outflow were anoxic.

Interpretation

We hypothesize that the normal ecological structure and function of desert springs depends on continual, high levels of physical disturbance by large mammals. The springs historically experienced such disturbance, originally from native megafauna, then from aboriginal humans, and most recently from livestock. These mammals removed aquatic and riparian vegetation and maintained the open-water habitats required by native species. In the absence of such disturbance, springs have become overgrown by vegetation, hydrologic regimes have been altered, and populations of native fishes and other organisms have declined. Effects have been particularly severe in the smallest springs, which have become completely overgrown, resulting in reduced flows and extinctions of native species.

Indeed, both Ash Meadows and Dalhousie have experienced similar histories of large mammal activity, although the timing of events has been somewhat different. Both North America and Australia had mammalian megafauna, consisting of diverse species of grazers and browsers. The late Pleistocene mammal fauna of the desert surrounding Ash Meadows included mammoths, camels, llamas, horses, bison, mountain deer, giant mountain goats, and giant ground sloths (Kurtén and Anderson 1980; Faunmap 1996), as well as still extant mule deer and bighorn sheep. The arid center of Australia featured a late Pleistocene fauna of giant marsupials that included rhinoceros-sized *Diprotodon* as well as giant kangaroos and wombats (Murray 1991; Flannery 1994; Mulvaney and Kamminga 1999). There is every reason to believe that these species grazed and drank at the desert springs in both North America and Australia, and that they had major impacts on the vegetation and hydrology, just as large native mammals in Africa do today. The result would have been extensive trampling and removal of emergent vegetation.

The megafaunas of both North America and Australia disappeared toward the end of the Pleistocene, about 10 000 and 50 000 years ago, respectively. In both cases, the extinctions coincided with the colonization of the continents by aboriginal humans. Although the causes of the megafaunal extinctions are still debated, there is increasing evidence and agreement that human hunting played a major role (eg Martin and Klein 1984; Flannery 1994; Lyons *et al.* 2004; Martin 2005). Regardless, aboriginal humans replaced the megafauna as agents of disturbance. They camped, fished, hunted, and swam at the springs, and burned the emergent vegetation to reduce cover, provide access, and maintain open water (D Ahchee, pers comm).

On both continents, European settlers displaced aboriginal hunters and gatherers. Although homesteads were established at some springs and irrigation agriculture was attempted, the primary impact of European settlement came through the introduction of domestic livestock: horses, donkeys, cattle, and – in Australia – camels. In arid regions, springs were centers of large herbivore activity, because they provided reliable sources of forage and water for both tended herds and feral populations. Their impact on springs, as great as it was, may well have been weaker than that of the extinct megafauna, which included much larger species.

Desert springs on both continents therefore experienced an almost continuous history of major disturbance by large mammals. This disturbance removed a substantial portion of the emergent vegetation and maintained open-water habitats, but this has no longer been the case in the past few decades, since the springs have been set aside as nature reserves.

Management activities were implemented to protect these ecosystems and their unique biota by "restoring" spring habitat to presumed pre-European conditions. Management included fencing to exclude feral livestock and removal of exotic plant and animal species. On the one hand, managers at both Ash Meadows and Dalhousie point to the increases in vegetative cover and in abundances of certain plant species as evidence of "recovery from overgrazing" (S McKelvey and G Axford pers comm). On the other hand, managers at both reserves have found it necessary to institute major programs of vegetation removal in order to maintain habitat and species diversity. At both Ash Meadows and Dalhousie, these efforts have been inadequate to prevent overgrowth of vegetation, reduction of open-water habitat, and extinction of aquatic and riparian populations, especially in the smaller springs.

Implications

The situations described here for Ash Meadows and Dalhousie are not unique. Similar changes have occurred in many spring and riparian habitats throughout the arid regions of North America and Australia, and have probably occurred on other continents, as well. Examples in the US include Quitobaquito Spring in Organ Pipe Cactus National Monument and the Canelo Hills Cienega Reserve, both in southern Arizona. Efforts to conserve and restore these habitats have interrupted a long history of disturbance by large mammals, with concomitant increases in vegetation and decreases in some aquatic and riparian plant and animal species. Even though domestic and feral livestock are not

Table 1. Comparison of population extinctions of five fish species at Dalhousie Springs, South Australia

	Number of springs				
Species	*1990*	*2003*	*Loss*	*Gain*	*Net*
Goby	30	18	12	0	–12
Gudgeon	21	19	3	1	–2
Catfish	15	14	1	0	–1
Hardyhead	10	11	0	1	+1
Perch	7	5	2	0	–2
Total	83	67	18	2	–16

exact replacements for extinct megafauna, they and aboriginal humans have played important roles as agents of disturbance. Management practices which result in the almost complete elimination of disturbance are detrimental to the structure and function of aquatic and riparian ecosystems.

Recently, some managers have recognized this and have begun to implement programs of vegetation removal. Manual removal, as currently practiced in both Ash Meadows and Dalhousie, is extremely costly in terms of time, effort, and money. Consequently, it is impossible to treat all springs. We offer two comments on these activities. First, management efforts have often concentrated on large springs because of their higher levels of biodiversity and aesthetic appeal. As noted above, however, small springs have been most heavily impacted by lack of disturbance and have experienced the greatest habitat changes and the majority of extinctions. A goal of management should be to maintain landscape heterogeneity and metapopulation structure across systems of multiple springs. To do so will require increased attention to small and isolated springs.

Second, it seems ecologically desirable and practical to supplement manual vegetation removal with other management practices. The management of nature reserves in general, and aquatic and riparian reserves in particular, has been influenced by a naturalistic philosophy, subscribing to the idea that the pre-human state is natural and desirable, and that a goal of management should be to restore ecosystems to pre-human, and especially pre-European, conditions. Such a philosophy is obviously incompatible with one possible management strategy – reintroduction of exotic megaherbivores – even though this might offer the most ecologically effective and cost-effective alternative (Donlan *et al.* 2006). If this is unacceptable, other alternatives, such as controlled burns and large-scale mechanical disturbance, should be considered.

Desert springs provide a textbook example of situations in which it is not sufficient to set aside a reserve and let nature take its course. Nature reserves are islands in an environment that has been irrevocably altered by thousands of years of human activity. The challenge is to determine the "natural state" and to implement management practices that conserve these habitats and their biota.

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