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The effect of *Castor canadensis* on riparian zones of the Colorado River Basin

The North American beaver, *Castor canadensis*, is the largest rodent in the United States, and second largest in the world. Previous to European arrival in North America the beaver's range extended across the United States and into Canada with an estimated population size of 100-400 million individuals (Naiman et al. 1988). However, in the 17th and 18th centuries, beavers were hunted nearly to extinction. Their soft, water-proof pelts proved to be excellent material for the then-fashionable felt hat, and their castoreum, an excretion produced by adults for scent-marking territories, was prized by perfumers. Today, beaver populations are estimated to be between 10-15 million individuals, less than 10% of their historic population size (Naiman et al. 1988).

Beavers are widely considered to be important ecosystem engineers. Through dam building and associated river channel augmentation, beaver activity can have drastic effects on the landscape's topography and hydrology. In the arid west, the importance of beaver and their ability to manipulate hydrological systems is especially important because most of the biodiversity is concentrated in riparian zones. In the Grand Canyon in particular, beaver populations have been affected by the building of the Glen Canyon Dam, and beaver are currently under scrutiny for their potential role in the spread of the invasive plant tamarisk (*Tamarix spp.*), and the decline of cottonwood trees. In the arid west, beavers are incredibly important for maintenance of a healthy riparian system and can be useful for restoration of riparian zones (Pollock et al. 2014). However, translocation of beaver as a restoration tool for riparian ecosystems is controversial and poorly studied.

Beavers are ecosystem engineers

Beaver activity is considered a natural disturbance regime, which make beaver excellent ecosystem engineers. Beaver's main engineering act is perhaps the most familiar; dam building. Beaver build dams to provide protection from predators such as coyotes, wolves, mountain lions, and bears, and to provide easy access to food during the winter. Dams provide protection from predators by creating deep ponds. Beaver dams are generally accessed through underwater entrances, and deep water allows beaver to enter and exit their dams without alerting predators. A beaver dam has the unique ability to transform a terrestrial ecosystem to a wetland, and lotic ecosystems into lentic (Cunningham et al. 2006). Dams alter the rate at which water, solutes, and sediments travel downstream, which can have far reaching impacts on the river's ecology, hydrology, and chemistry (Andersen & Shafroth, 2009). Dam building can physically transform a landscape through the formation of beaver ponds and beaver terraces. When dams collapse or are destroyed a third habitat, beaver meadows, are formed.

A beaver pond is the body of water that often forms behind a dam, trapping slow moving water and fine-grained nutrient-rich sediment (Westbrook et al. 2011). Beaver dams have the ability to raise the water table through prolonged periods of standing water on the landscape, making ground water more accessible to riparian vegetation (Breck et al. 2003). Additionally, beaver ponds provide excellent nursery habitat for fish and frog species, and the associated increase in riparian vegetation has been shown to increase diversity of songbirds (Aznar & Desrochers 2008). Beaver ponds can alter patterns of sediment retention, rates of nutrient cycling, organic matter and nutrient deposition and retention, and change patterns of vegetation succession (Westbrook et al. 2011).

Beaver terraces are another important component of the engineering efforts of beaver. Terraces are formed through continual flooding and over-topping of beaver ponds. Depending on the height and intensity of the flood water, these terraces will have different amounts of sediment deposition and nutrient retention, leading to a diversity of riparian plants growing along the edges of beaver ponds. Almost as important as the building of beaver dams is their failure. When dams fail huge amounts of water and sediment are released downstream, and often beaver meadows can replace the beaver ponds through gradual infilling. Beaver meadows are quickly colonized by herbaceous plants and shrubs, increasing the overall heterogeneity of the plant community (Westbrook et al. 2011).

Beaver in the Colorado River Basin

In the arid western United States, anecdotal evidence suggests that beavers were once widespread, although permanent populations of beaver may have been concentrated at higher elevations, near relatively mesic headwaters (Weber, 1971). This is because stream systems in the arid west are generally snow fed and susceptible to loss of surface flows during the dry season. Today, many riparian habitats in the arid west have been lost or degraded as a result of land-use changes, and beaver populations have disappeared from many stream systems (Pollock et a. 2014). However, beaver still persist in some riparian zones, and efforts are underway to restore degraded riparian forests and create floods and base flows necessary for sustained riparian forest systems, and therefore beaver (Andersen & Shafroth, 2009).

In the Colorado River Basin, human dam-building has had mixed effects on beaver populations. Dams and their associated flow regulations have drastic effects on downstream river ecology. Generally, dam operations reduce flood pluses and flood events, and increase stream base flows. Flow regulation can negatively impact important woody riparian species including cottonwood trees (*Populus spp.*) and willow (*Salix spp.*) by altering processes required for reproduction and regeneration (Breck et al. 2001). Flow regulation can also alter sedimentation rates downstream of dams and can lead to fragmentation of the river corridor (Braatne et al. 2008). Beaver have been shown to respond relatively positively to human dam construction. In the Grand Canyon, beaver populations have increased downstream of the Glen Canyon Dam since it's construction in 1966, likely due to the increases in woody riparian vegetation (Hoffmeister, 1986). Notably, beaver in the Grand Canyon do not build dams, but instead dig burrows into the riverbank. This behavior is generally seen in beaver populations that reside in large rivers with existing deep water channels, where the building of a dam to create deep water habitat is unnecessary.

A 2001 study investigated the impact of human dams on beaver populations by comparing populations in two of the Colorado River's tributaries, the regulated Green River and the unregulated Yampa River (Breck et al. 2001). In the Green River beaver were found at higher densities and adult beaver had overall better body condition when compared to the Yampa populations. This difference was attributed to the improved quality of habitat on the Green River. Damming of the Green River maintained base flows all year round and decreased flooding events. These hydrologic changes allowed for greater availability of willow along the river edge, decreases in sandy flats and sand bars, and decreased formation of ice cover during the winter months (Breck et al. 2012). These changes likely decreased daily energy expenditure of Green River beavers, leading to better overall body condition. The formation of sandy flats, sandbars, and ice cover on the unregulated Yampa River result in beaver having to travel over land (or ice) to reach woody forage, resulting in higher overall energy expenditure (Breck et al. 2012).

Beaver's effect on riparian vegetation in Colorado River Basin

In the arid west and in the Colorado River basin in particular, cottonwood forests are a critical and often irreplaceable component of riparian ecosystems. Along with willow (*Salix sp.*), cottonwood and other *Populus* species form an important part of the beaver's diet. Cottonwood trees are highly dependent on shallow floodplain groundwater (< 4m) recharged by the adjacent stream, which makes them vulnerable to changes in river flow (Borman & Larson 2002). In addition, areas of moist sand, silt or gravel are necessary for cottonwood seedling establishment, which make cottonwood reproduction dependent on stream systems with sandbars and eddy-fan complexes (Borman & Larson 2002). Reduced cottonwood growth rates, canopy dieback, and tree death have all been attributed to changes in river hydrology, generally produced by human-constructed dams (Williams & Cooper 2005). It may come as no surprise that beaver have recently been implicated in the decline of cottonwoods and willows in the arid west, as beaver have both direct (herbivory) and indirect (hydrologic modifications) effects on cottonwood in riparian areas. There is some evidence that supports this claim. On the Green and Yampa Rivers cottonwood abundance and density was lower, and the probability of damage to any individual cottonwood tree was higher, in areas with beaver present (Breck et al. 2003). On the regulated Green River, controlled flooding increased the rate of beaver foraging on cottonwood by inundating patches of trees, allowing beaver easy access to woody forage (Breck et al. 2003). However, although a main component of beaver diet in the Colorado River basin is cottonwood, beaver herbivory likely plays only a minor role in limiting or regulating the cottonwood population (Andersen & Cooper 2000). In larger, flow-regulated rivers cottonwood recruitment could be spatially restricted, which could in turn lead to trees being more vulnerable to beaver herbivory (Breck et al. 2003). Overall, beaver likely do play a role in the declining cottonwood abundance in the Colorado River basin, but changes in flow regimes and human land use far outweigh those of the meager beaver.

Another pressing problem linked to riparian woody vegetation in the Colorado River basin is the spread of tamarisk (*Tamarix sp.*), a non-native shrub initially introduced to the area to control riverbank erosion. Tamarisk is now the dominant shrub on many river systems in the arid southwest. Tamarisk has higher salt tolerance, drought tolerance, resistance to water stress, and fire tolerance than native woody riparian tree species (Glenn & Nagler 2005). However, on rivers that still experience dynamic hydrological regimes it has been found that cottonwood and willow have the ability to establish despite the presence of tamarisk (Glenn & Nagler 2005).

Beaver have also been implicated in the spread of tamarisk along the Colorado River. The relationship between beaver and tamarisk is particularly interesting, because beaver rarely eat tamarisk (Kimball & Perry 2008). In fact, the high salt and tannin content in tamarisk is physiologically limiting to beaver, although beavers will use tamarisk in dam construction and occasionally eat small shoots and samplings (Kimball & Perry 2008). In the Grand Canyon, bank-dwelling beavers do not construct dams, yet studies have found that beaver presence can still influence tamarisk presence and abundance through preferential foraging (Mortenson et al. 2008). Beavers in the Grand Canyon preferentially forage on *Salix* species, and concern has been raised that the increasing beaver populations may lead to both tamarisk dominance and threaten the presence of *Salix gooddingii*, a rare willow species (Mortenson et al. 2008). There is some evidence that beaver presence may lead to increases in tamarisk. For example, along several rivers in eastern Montana, selective felling of cottonwood trees by beavers has led to growth and dominance of both tamarisk and Russian olive (*Elaeagnus angustifolia*), another invasive woody riparian species (Lesica & Miles, 2004). On the Colorado River, studies have shown that beaver presence and tamarisk cover do significantly overlap, but whether this overlap is due to beaver preferring habitats with high tamarisk cover or beaver contributing to tamarisk dominance through selective use of its native woody competitors is still up for debate (Mortenson et al. 2008). Although beaver may assist in the dominance of tamarisk though preferential herbivory of native species, changes in river hydrology play a much more critical role. In fact, because beaver do not eat tamarisk, its continued spread could cause declines in beaver populations, leading to far greater impacts to river systems through changes in hydrology, ecology, and geomorphology.

Beavers as a conservation tool

Due to the beaver's ecological impacts and associations with riparian vegetation and river hydrology, beavers are a high priority species for restoration and management programs in the Colorado River basin (Anderson & Shafroth 2010). The importance of riparian ecosystems in the arid west has long been recognized. Accounting for less than 2% of the total land area, riparian zones are hotspots of biodiversity in the western US (Poff et al. 2012). Riparian zones function as important nurseries for many native fish species, are critical sites for neotropical migratory birds, and help support many aquatic mammals, including the river otter (*Lontra canadensis*) (Gibson & Olden, 2014). In the arid west, 60% of all vertebrate species and 70% of all threatened and endangered species are riparian obligates (Poff et al. 2012). Riparian zones also act as buffers between upland areas and open water, and can help filter pollutants such as nutrients and sediments. Beavers ability to transform lotic landscapes into lentic landscapes, and drylands into riparian zones, has led some conservationists to use beaver introduction as a management tool. However, beaver activity can conflict with other ecological management goals, or even create significant economic damage (Anderson & Shafroth 2010). This stems from the fact that most of the research conducted on beaver takes place in temperate ecosystems; very little work has examined how and if beaver could act as riparian restorationists in the arid west

(Gibson & Olden 2014). In addition, beaver reintroduction would be returning beaver to areas that bear little resemblance to historic conditions, challenging conservationists to balance the contemporary uses of a riparian system with a more beaver-friendly environment.

Most of the ecosystem engineering ability attributed to beaver result from the construction of beaver dams. However, in the arid west, a relatively large proportion of beaver are bank-dwelling because much of the perennial water is concentrated in larger rivers. When beavers do construct dams in the arid west, floods and variable stream discharge generally cause large variability in dam longevity. For example, in a 17-year study on a small central Oregon stream, beaver dam density ranged from 9 to 103 dams present on 32km stretch of stream (Demmer & Beschta, 2008). This variability can be difficult to effectively manage, as it can result in constant shifts in river hydrology and ecology. In addition, dam construction can change the basic hydrology of a riparian system. Introduction of dam-building beavers can shift intermittent streams to perennial flows, and damming may reduce stream velocity and erosive power during peak flows (Gibson and Olden 2014). In many dryland ecosystems, riparian organisms are highly adapted and oftentimes dependent on high stream velocity during peak flows. For example, a study that compared two rivers of varying flow regimes in the southwestern US found that peak flows and high variability in flow rates sustained native fish species over non-native fish species between periodic flood events (Rinne & Miller 2006).

Although there are potential problems associated with beaver reintroduction in the arid west, there have been successes. Beavers are particularly good at reversing the effects of incised stream channels, a common problem for dryland streams. Channel incision is typically a result of land-use change and is especially common on heavily grazed landscapes. Channel incision is associated with rapid erosion, lowering of the water table, severed connectivity with the floodplain, and total loss of riparian vegetation (Gibson & Olden 2014). Beaver introduction can rapidly assist in the recovery of incised streams and can help create and maintain complex fluvial ecosystems (Pollock et al. 2014). Dams that are built across incised streams will gradually raise the water table, allowing for colonizing riparian vegetation. Eventually dams will infill the incised stream with sediment and reconnect the stream to its floodplain, assisting in long-term maintenance of the riparian ecosystem (Pollock et al. 2014).

Beaver re-introduction and translocation in the arid west, and the installation of instream structures that mimic the effects of beaver dams, has been used sporadically as a restoration technique for decades (Pollock et al. 2014). However, it has only been recently that the effectiveness of these projects has been examined. A 2017 review inventoried 97 beaver-related restoration projects in the western US over the past 10 years (Pilliod et al. 2018). The authors found that in the majority of cases, beavers were translocated without regard to genetics, disease, or potential conflict with nearby landowners. They found that few projects included long term monitoring of translocation success or consideration water rights, depending instead on ad-hoc agreements between participating land-owners (Pilliod et al. 2018). Restoration of riparian systems using beaver introduction has the potential to be a cheap, effective, and long-term solution to degraded riparian ecosystems. However, current beaver translocation projects are poorly monitored and information about successful or unsuccessful practices are rarely shared between agencies or landowners (Pilliod et al. 2018; Gibson & Olden 2014). Long-term monitoring of ecosystem responses is essential to understanding the long-term success of beaver reintroductions as a restoration strategy.

In the Grand Canyon and Colorado River Basin, little effort has been made to use the potential highly restorative power of beavers. In many of the Colorado River's tributaries, beavers are considered a nuisance species, as they build dams that block culverts or irrigation channels, leading landowners to trap and remove beaver from their property. Beavers are adept at responding to human land use change, and as such populations have drastically increased since the mid-1900s (Naiman et al. 1988). If humans can work together with beavers to harness their power as ecosystem engineers, the precious supply of water in the arid west can be more effectively shared between humans and the natural ecosystem.

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