Beaver (*Castor canadensis*) in heavily browsed environments[1]

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Abstract: Beaver (*Castor canadensis*) populations have declined or failed to recover in heavily browsed environments. I suggest that intense browsing by livestock or ungulates can disrupt beaver-willow (*Salix* spp.) mutualisms that likely evolved under relatively low herbivory in a more predator-rich environment, and that this interaction may explain beaver and willow declines. Field experiments in Rocky Mountain National Park, Colorado, USA, found the interaction of beaver and elk (*Cervus elaphus*) herbivory suppressed compensatory growth in willow. Intense elk browsing of simulated beaver-cut willow produced plants which were small and hedged with a high percentage of dead stems, whereas protected plants were large and highly branched with a low percentage of dead stems. Evaluation of a winter food cache showed beaver had selected woody stems with a lower percentage of leaders browsed by elk. A lack of willow stems suitable as winter beaver food may cause beaver populations to decline, creating a negative feedback mechanism for beaver and willow. In contrast, if browsing by livestock or ungulates can be controlled, and beaver can disperse from a nearby source population, then beaver may build dams in marginal habitat which will benefit willow and cause a positive riparian response that restores proper function to degraded habitat. In a shrub-steppe riparian ecosystem of northwestern Colorado, USA, rest from overgrazing of livestock released herbaceous vegetation initiating restoration of a beaver-willow community. Thus, competition from livestock or ungulates can cause beaver and willow to decline and can prevent their restoration in heavily browsed riparian environments, but beaver and willow populations can recover under proper grazing management.

Keywords: beaver, *Castor canadensis*, *Cervus elaphus*, competition, elk, facilitation, livestock, montane, mutualism, riparian restoration, *Salix,* shrub-steppe, tamarisk, *Tamarix ramosissima*, willow.

Introduction

Seton (1929) estimated the beaver (*Castor canadensis*) population in North America at 60-400 million before European settlement. Despite this legendary abundance most beaver populations were decimated by fur trappers during the 1700s and 1800s, primarily to support the European fashion for felt hats. Growing public concern over declines in beaver and other wildlife led to regulations that controlled harvest through seasons and methods of take, initiating a continent-wide recovery of beaver populations. To supplement natural recovery, beaver were live-trapped and successfully reintroduced into much of their former range during the mid-1900s, a remarkable achievement of early wildlife managers. Beaver now occupy much of their former range in North America and their population is estimated at 6-12 million (Naiman et al. 1988). However, beaver populations have not recovered or have failed to persist in many riparian areas that have become heavily browsed environments since European settlement. Livestock and ungulates congregate in riparian areas that provide water and productive vegetation and lack disturbance from large predators such as gray wolves (*Canis lupus*) (Belsky et al. 1999, Beschta 2003). Also, in 1968 the National Park Service initiated a natural regulation policy for parks in the United States, which restricted pop-

[1] Parts of this review paper were adapted or extracted from Baker & Hill (2003) and Baker et al. (in press).

ulation control and allowed wildlife to self-regulate. Since then elk (*Cervus elaphus*) populations in some parks have increased and large herds forage relatively undisturbed in open riparian meadows and remnant willow (*Salix* spp.) stands, areas that are popular tourist attractions because elk are easy to observe in the short vegetation. Willow is highly palatable and selected for by livestock and ungulates, especially after herbaceous vegetation becomes dormant during late summer (Kay 1994). The distribution and height of willow has dramatically decreased in these heavily browsed environments. However, willow and other woody riparian species may recover if browsing pressure is reduced. For example, cottonwood (*Populus* spp.) and willow increased in height following the introduction of gray wolves into Yellowstone National Park, USA, in 1995-1996 (Ripple & Beschta 2003). This suggests increased predation risk to elk in riparian areas and/or top-down population control may reduce competition for woody riparian vegetation and improve habitat for beaver.

Beaver are a definitive example of both a keystone species and an ecosystem engineer (Baker & Hill 2003). The dam-building, canal-building, and foraging activities of beaver have profound effects on ecosystem structure and function. Beaver dams slow current velocity, increase deposition and retention of sediment and organic matter in the pond, reduce turbidity downstream of the dam, increase the area of soil-water interface, elevate the water table, change the annual stream discharge rate by retaining precipitation runoff during high flows and slowly releasing it during low flows, alter stream gradients by creating a stair-step profile, and increase resistance to disturbance (Gurnell 1998, Naiman et al. 1988). Canals dug by beaver spread impounded water across a larger surface area, thus magnifying the effects of single dams. The foraging activity of beaver alters the species composition, density, growth form, and distribution of woody vegetation. Beaver dams raise the water table by creating a pond and an umbrella-shaped zone of influence that radiates out from the pond, creating a new water table gradient controlled by soil texture and other factors. The soil behind dams can act like a sponge, retaining water during wetter months and slowly releasing it during drier months. In areas of low or irregular precipitation, beaver dams may convert streams from intermittent flow to perennial flow. Changes in the amount, timing, or duration of available water can create a competitive advantage for many species of riparian-wetland plants such as willow, thus increasing their survival and dominance in the landscape. Higher water tables caused by beaver ponds generally kill upland vegetation and promote establishment and growth of wetland vegetation. Sediment deposited behind beaver dams creates an ideal moist soil substrate that can become exposed as water levels in the pond decrease due to dam washouts or other causes. Beaver cuttings also may be an important mechanism of plant establishment for willow (Cottrell 1995). Thus, beaver can benefit the establishment and survival processes of willow and many phreatophytic species.

Willow is important as food and construction material for beaver (Baker & Hill 2003). Willow leaves are high in protein content and are readily eaten during the summer. The bark of willow stems stored in a food cache accessible from under the ice may be the only source of winter food for beaver that live in climates where surface water freezes during winter; thus, the availability of suitable willow stems can limit beaver populations in cold climates (Baker & Cade 1995). Beaver-cutting stimulates vigorous sprouts from below the cut on the same stem or from nearby root suckers. In a study of red willow (*Salix lasiandra*) in Oregon, USA, trees that had a higher percentage of stems cut by beaver responded by producing a higher percentage of regrowth the following season (Kindschy 1985). Cutting by beaver can also stimulate plants to initiate growth earlier in the spring, further increasing stem production (Kindschy 1989). Thus, I suggest that where willow benefit beaver as food and construction material and beaver benefit willow establishment and survival processes, beaver and willow can be considered facultative mutualists.

In this paper I discuss how beaver-willow mutualisms can collapse in heavily browsed environments and how proper grazing practices can restore these mutualisms in degraded riparian ecosystems. As examples I use (1) a montane, beaver-willow community in Rocky Mountain National Park (RMNP), northcentral Colorado, USA, where elk are the dominant herbivore and (2) a shrub-steppe, beaver-willow community (Douglas Creek) on land managed by the Bureau of Land Management (BLM) in northwestern Colorado, USA, where livestock are the dominant herbivore.

Factors limiting beaver in a heavily browsed environment

Beaver were once abundant in RMNP but declined dramatically after 1940. Population estimates in Moraine Park, a riparian valley within RMNP, were 315 in 1939-1940, 102 in 1964, 12 in 1980, and 6 in 1999 (Baker et al., in press). Elk were reintroduced to RMNP in 1913-1914 after nearly being extirpated by the late 1800s. They had increased to 1,200 animals in 1940 when Packard (1947) first noted beaver and elk competition for willow. Control efforts reduced the elk population to 500 until 1968, when a policy of natural regulation precluded control and numbers had increased to 3,000 by the late 1990s (Singer et al. 1998, Lubow et al. 2002). Elk utilization of riparian willow (% leaders browsed) averaged 85% annually in 1968-1992 as the elk population increased to seven times its 1968 level (Zeigenfuss et al. 1999), evidence that willow was a highly preferred forage species. In a comparison of 1937/1946 and 1996 aerial photographs Peinetti et al. (2002) found tall willow (>3 m) cover declined by 54% in Moraine Park and 65% in Horseshoe Park, and that total willow cover declined by 20%. Short willow (<1.5 m) plants have dominated the area for several decades, likely a result of a change in individual plant stature rather than in willow species composition (Peinetti et al. 2001). Thus, beaver and willow populations both declined in heavily browsed environments within RMNP, but the underlying mechanisms have remained elusive.

Because factors other than competition with elk for willow might limit beaver populations, a radio-telemetry study was initiated to determine the importance of mortality, dispersal, or other life history factors in limiting the remaining beaver populations in RMNP. In fall 2001, 39 beaver were live-trapped using Hancock and box traps. The age distribution of beaver was 20 adults, 4 yearlings, and 15 juveniles. The relatively low number of yearlings suggested poor recruitment due to either dispersal outside RMNP or poor survival of juveniles, assuming no differential trapping success. Blood samples were drawn from each beaver via a blind-stick method through the dorsal surface of the tail. All samples tested negative for tularemia and plague, which effectively ruled-out disease as a mortality factor during at least the past five years. As an interesting side benefit, these blood samples were used to develop a 100% accurate genetic method of gender determination in beaver (Williams et al., in press). Beaver were radio-tagged at the capture site using tail-mounted transmitters (Rothmeyer et al. 2002) with activity/mortality switches to indicate movement, rest, or no movement for >6 hours (indicating possible mortality). Unfortunately, this radio attachment method proved to have poor retention time for most individuals, although it was easy to use and radios with intact whip antennas (those not chewed-off by beaver) had a good signal range (B.W. Baker, unpublished data). Radio tracking results showed 1 adult male mortality due to coyote (*Canis latrans*) predation, 1 adult female mortality due to unknown causes, and 1 dispersal of an adult male of about 10 km to a location within the town of Estes Park adjacent to RMNP. Results also showed that beaver used several different bank dens, bank lodges, or pond lodges, including many that would not have been discovered without the aid of radio telemetry; these data suggest that attempting to census beaver by counts of active dens and lodges would be highly problematic.

An investigation of trapping records in RMNP revealed that 218 beaver had been removed during 1941-1949, which suggests trapping was an important cause of initial population declines. A comparison of aerial photographs taken in 1947 and 1964 shows a dramatic reduction in the area inundated by beaver ponds and canals as beaver populations declined in the Moraine Park study site. Loss of beaver-engineered water sources likely caused loss of willow in some areas, which would reduce beaver habitat even further. But why did beaver populations fail to recover after trapping ceased in 1949? Beaver surveys and aerial photographs taken in 1999 revealed only one beaver colony in Moraine Park, and it was located within a 30x46 m study exclosure that had been erected to protect willow from elk browsing. The elk exclosure had become a beaver food plot. Willow plants protected from elk browsing had grown tall and vigorous, whereas most outside plants were short and hedged due to 30 years of intense use by elk. To determine if elk-browsing affected beaver winter food preferences, in November 2001, elk utilization rates (%) were compared on willow, river birch (*Betula fontinalis*) and alder (*Alnus tenuifolia*) stems used in a winter food cache to those stems available in the beaver colony territory, defined as the area containing recent beaver-cut stems. Results showed beaver had selected stems with a lower percentage of leaders browsed by elk, which suggests elk browsing reduced willow suitability to beaver (B.W. Baker, unpublished data). In addition, beaver had placed willow stems at the bottom of the cache and covered them with a cap of alder and birch stems, which suggests they placed the more preferred forage species (willow) at the bottom of the pond to ensure access when the pond surface was frozen in winter. Thus, beaver appear to prefer relatively tall, unbrowsed willow and to select against short, hedged willow, which dominates much of the former beaver habitat in RMNP.

How did the formerly tall (>3 m) willow community become short (<1.5 m) and hedged and how could beaver have influenced this change? Elk can and do break tall willow stems to reach the tender tips of leaders. Although this behaviour has been observed in RMNP, it usually results in broken stems that are >2 m tall and does not appear to be especially common. If beaver cut tall willow, and elk browsing strongly suppressed willow regrowth, then the interaction of beaver cutting and elk browsing could alter the structure and function of the willow community. This hypothesis was tested with a field experiment that compared willow regrowth 3 years after simulated beaver cutting on paired plants with and without intense elk browsing (85% utilization rate). Simulated beaver cutting with intense elk browsing produced willow regrowth that was small in biomass and diameter and short with far fewer but longer shoots and a high percentage of dead biomass (Baker et al., in press). In contrast, simulated beaver cutting without elk browsing produced willow regrowth that was large, tall, and leafy with many more but shorter shoots and a low percentage of dead biomass. Total stem biomass after 3 years of regrowth was 10 times greater on unbrowsed plants than on browsed plants. Unbrowsed plants recovered 84% of their pre-cut biomass after only two growing seasons, whereas browsed plants had recovered only 6%. Thus, the interaction of beaver cutting and elk browsing strongly suppressed compensatory growth in willow.

How does elk browsing differ from beaver cutting and how do these differences affect compensatory growth mechanisms? Elk and other large herbivores browse the tips of leaders, which removes mostly current annual growth (CAG). A large percentage of leaf and woody biomass remains intact, which contributes to the growth of new shoots via photosynthesis. Browsing frequency can be high because shoot regrowth rapidly becomes suitable as forage. Released apical dominance can activate dormant buds below the point of browsing, which increases branching and growth rates (Honkanen & Haukioja 1998). Repeated browsing of new shoots can create hedged plants that may maintain high forage productivity. However, browsing can reduce or eliminate sexual reproduction in willow by maintaining plants in a juvenile growth phase (Kay 1994). In contrast, beaver usually cut entire stems near ground level and at a relatively low frequency, as it takes several years for regrowth to become suitable as food or building material. Willow plants can rapidly recover mature stems so regrowth is more likely to reach sexual maturity and produce seed on plants where stems have been cut by beaver rather than browsed by elk. Regrowth of beaver-cut willow can be strongly suppressed by intense elk browsing, but willow can often tolerate herbivory by either species alone. The ability of willow to compensate for complete removal of aboveground biomass suggests they have a high level of nutrients stored in roots, which can be rapidly shunted from roots to shoots following herbivory (Strauss & Agrawal 1999). However, this mechanism likely reduces root reserves and places plants in a stressed state until new sprouts can recover stem and leaf tissue necessary for photosynthesis, which is a prerequisite of other compensatory growth mechanisms such as increased photosynthetic rate, leaf nitrogen, and growth rate. Also, when beaver cut tall stems they place regrowth under the canopy of surrounding herbaceous vegetation where further herbivory can prevent new stems from escaping competition for light and increasing their growth rates (Raven 1992). Thus, the interaction of beaver and elk herbivory can greatly reduce the effectiveness of compensatory growth mechanisms.

When beaver cut the stems of woody plants they function as an ecological driver by altering future plant-herbivore interactions and placing regrowth within easy reach of herbivores such as elk. When elk browse beaver-cut willow they can drive a tall willow community into an alternative state consisting of short, hedged plants that lack sexual reproduction and will eventually die of old age. If elk browsing decreases the suitability of willow as beaver food by reducing the biomass of twigs and bark on stems and their preference by beaver, then beaver populations will decline where willow limits populations. In these systems, willow that provides adequate biomass of twigs and bark is *necessary* for beaver as a winter food supply, but short or heavily-browsed willow (or no willow) is *sufficient* for elk, as they can subsist on herbaceous forage in areas lacking deep winter snow (Skovlin 1982). Thus, in riparian systems where elk are overabundant they will outcompete and exclude beaver. When beaver populations decline, then wetlands will lose key willow establishment and survival processes and beaver-engineered wetlands will collapse. Carrying capacity for elk can increase in these sites if areas dominated by beaver ponds and canals dry and succession forms a mosaic of mesic and xeric plant communities, a process equivalent to the agricultural practice of wetland drainage to increase livestock forage production. Alternatively, beaver may increase carrying capacity for elk (or livestock) in very dry environments where dams raise the water table and increase productivity enough to overcompensate for surface area lost to beaver ponds. Thus, when beaver cut willow, and intense elk browsing suppresses regrowth, then the interaction of beaver and elk herbivory will create a feedback mechanism that is negative for beaver and willow but positive, or negative, for elk depending on local conditions. Further research is necessary to determine the level of additional herbivory that beaver-willow communities can tolerate before a negative feedback mechanism will disrupt beaver-willow mutualisms that naturally occur in less competitive environments.

Beaver as a riparian restoration tool in shrub-steppe ecosystems

In the previous section I used a case study of intense elk browsing in RMNP to show how overgrazing by ungulates or livestock can interact with beaver cutting to suppress willow regrowth, which can cause the decline or prevent the recovery of beaver-willow communities. In this section I will present a riparian restoration hypothesis that suggests proper grazing management and beaver can initiate recovery of degraded riparian ecosystems.

Beaver were abundant in forested, shrub-steppe, and some hot desert habitats in the western United States until fur trapping had decimated most beaver populations by the late 1800s. From 1875-1892 shrub-steppe riparian areas experienced a period of low frequency but high intensity rainfall events, decreasing stream-side vegetation and increasing channel incision. Ranchers followed trappers in settlement of the west, and immense numbers of sheep and cattle were introduced during the late 1800s. Overgrazing further stripped streambanks of soil-binding vegetation which, lacking active, functional beaver dams, caused stream channels to respond with accelerated erosion and severe downcutting (see Elliott et al. 1999 for a discussion of possible mechanisms to explain observed channel incision). Willow populations declined and were often replaced with tamarisk (*Tamarix ramosissima*), an invasive, exotic riparian shrub. Restoration and revegetation of incised channels with willow or other native species can be expensive, labor-intensive, and often unsuccessful, so natural restoration can be an attractive alternative. The ability of beaver to store water, trap sediment, reduce channel erosion, and enhance establishment and production of willow and other phreatophytes can be used as a proactive management tool to restore degraded riparian habitat if proper grazing management is present.

Reintroduction of beaver into degraded riparian systems has shown promise as a restoration tool, even where willow or other suitable winter food may occur in remnant populations, usually in the upper stream reaches. In 1975, the BLM initiated restoration of the Douglas Creek watershed by resting the grazing allotment from cattle grazing for two years, developing water sources to attract cattle away from the riparian zone, and implementing a rest-rotation grazing system (Baker et al. 1992). The stream channel in the lower reaches of this watershed had incised nearly 20 m since 1882 when livestock were introduced. At the same time BLM prohibited trapping of a remnant beaver population that occurred at the uppermost reaches of the stream, where cattle had not eliminated willow. Improved livestock grazing management permitted the development of an adequate biomass of herbaceous aquatic and riparian vegetation for summer beaver food, which allowed beaver to disperse into marginal downstream habitat. Comparison of photographs taken before (1975) and after (1992) improved livestock and beaver management showed dramatic changes in riparian condition. The following hypothesis suggests a process of beaver-engineered riparian restoration in areas where proper grazing management can be implemented (figure 1).

Implementation of grazing practices that leave adequate herbaceous vegetation to support beaver during the summer and fall, and that permit willow or other winter food supplies to become established and grow to a size suitable for winter beaver food, must be in place before beaver benefits can be realized. Where beaver can disperse to marginal habitat they may subsist on herbaceous vegetation in summer and fall long enough to build dams, ponds, and canals that can initiate a riparian response, although beaver may occur as ‘sink populations’ if overwinter food is lacking. In some cases, aspen (*Populus tremuloides*), cottonwood, or willow can be provided at beaver reintroduction sites, or where beaver have initiated dam-building on their own, to encourage beaver to remain at the site and to provide them with stronger dam-building material (Apple et al. 1985). Overwinter beaver survival can also be enhanced where surface water freezes and thaws during winter, allowing increased foraging opportunity of herbaceous vegetation. Even relatively short-lived beaver dams can initiate a positive riparian response, which includes a higher water table, increased summer flows, increased silt deposition, and increased riparian width. This response can increase the establishment and survival of riparian woody vegetation suitable as winter beaver food. Adequate winter food stored in a cache can increase the survival and fecundity of beaver that live in climates where ponds or streams freeze in winter, creating a source population that can disperse to additional marginal habitat. Thus, beaver can create a positive feed-

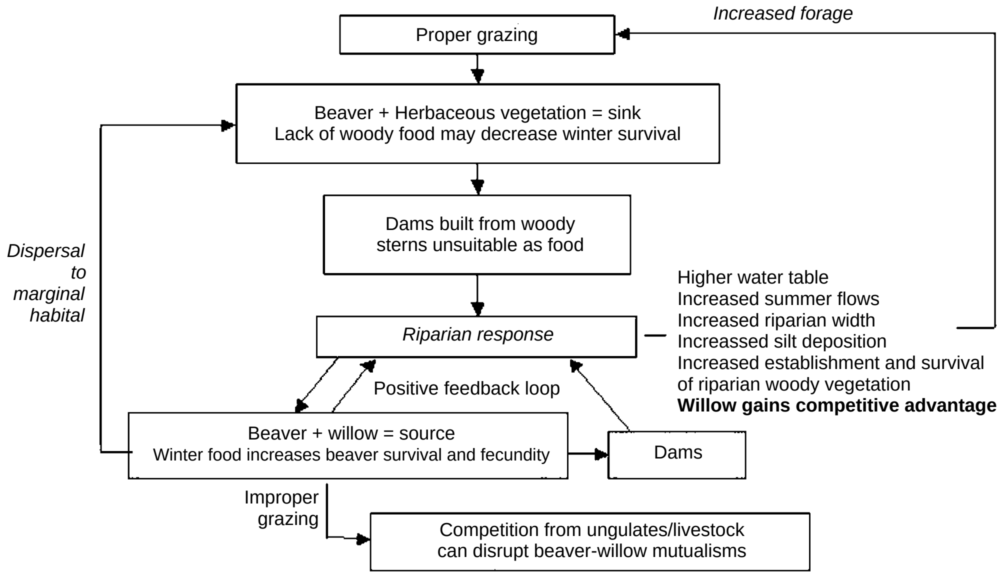

Figure 1. Beaver as a riparian restoration agent in shrub-steppe ecosystems. Modified from Baker & Hill (2003).

back mechanism by temporarily expanding into marginal habitat (naturally or by introduction), creating conditions for the establishment and survival of a winter food supply such as willow, and persisting long enough to raise young that can disperse to new marginal habitat. Increased livestock or ungulate forage in response to greater moisture availability is an additional benefit in many dry environments, which may increase carrying capacity under proper grazing management.

Beaver restoration in western riparian areas may also help control tamarisk, a facultative phreatophyte which tolerates drought and intermittent water tables much better than willow, an obligate phreatophyte. In northwestern Colorado, USA, beaver used tamarisk, big sagebrush (*Artemisia tridentata*), and black greasewood (*Sarcobatus vermiculatus*) as building material for a series of dams that appeared to increase the distribution and abundance of coyote willow (*Salix exigua*) relative to tamarisk (B.W. Baker, unpublished data). A similar response was observed on the Zuni Indian Reservation in New Mexico, USA, following the relocation of 23 beaver to 7 restoration sites (Albert & Trimble 2000). As beaver selectively cut vegetation and impound water behind dams, they alter conditions driving establishment and survival in riparian plant communities. Thus, beaver may create a competitive advantage for willow relative to tamarisk in some riparian systems, although specific mechanisms need further study at different spatial and temporal scales (B.W. Baker, unpublished data).

Conclusions

Where beaver benefit willow and willow benefit beaver, they can be considered mutualists. However, this mutualism can collapse in environments heavily browsed by ungulates or livestock. The interaction of beaver cutting and livestock or ungulate browsing can strongly suppress compensatory growth mechanisms that naturally occur in less competitive environments. More research is needed to determine the threshold of additional utilization that beaver-willow communities can tolerate before ecosystem collapse. Riparian ecosystems that have been overgrazed by livestock or ungulates can be restored if grazing practices are implemented that leave adequate herbaceous and woody vegetation for beaver and where beaver dams initiate a positive riparian response. Competition with other herbivores such as ungulates and livestock should be considered as an important limiting factor in the restoration and management of both species of beaver (*Castor canadensis* and *Castor fiber*).

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Samenvatting

Bevers (*Castor canadensis*) in sterk begraasde milieus

Beverpopulaties (*Castor canadensis*) zijn afgenomen of zijn niet hersteld in sterk begraasde milieus. Ik suggereer dat intensieve begrazing door landbouwhuisdieren of wilde hoefdieren de mutualistische relatie tussen bevers en wilgen (*Salix* spp.) kan verstoren, een relatie die zich waarschijnlijk ontwikkelde in meer predator-rijke milieus met relatief weinig herbivorie, en dat deze verstoorde relatie de afname van bevers en wilgen zou kunnen verklaren. Veldexperimenten in Rocky Mountain National Park, Colorado, VS, toonde aan dat de combinatie van begrazing door bevers en edelherten (*Cervus elaphus*) de hergroei in wilgen onderdrukt. Intensieve begrazing door edelhert van wilgen waar bevervraat was gesimuleerd, resulteerde in kleine, kort afgegraasde planten, met een hoog percentage aan dode stammen, terwijl beschermde planten groot en sterk vertakt waren, met een laag percentage aan dode stammen. De evaluatie van een door bevers aangelegde voedselopslag voor de winter liet zien dat bevers houtige stammen selecteren met een lager percentage door edelherten afgegraasde eindscheuten. Een gebrek aan geschikte wilgenstammen als wintervoedsel voor bevers kan de oorzaak zijn van een afname in beverpopulaties, wat vervolgens weer een negatief effect heeft op wilgen. In tegenstelling hiermee kunnen bevers dammen bouwen in marginaal habitat, mits begrazing door landbouwhuisdieren of wilde hoefdieren beperkt is, en dispersie van bevers mogelijk is vanuit nabijgelegen bronpopulaties. Dit komt de wilgen ten goede en leidt tot herstel van oevervegetaties in aangetaste (overbegraasde) habitats. In door struiken gedomineerde oevervegetaties in noordwest Colorado, VS, initieerde het stopzetten van overbegrazing door landbouwhuisdieren het herstel van een bever-wilgen gemeenschap. Concurrentie van landbouwhuisdieren of wilde hoefdieren kan dus betekenen dat bevers en wilgen afnemen, en kan voorkomen dat sterk begraasde oevervegetaties zich herstellen, maar bever- en wilgenpopulaties kunnen zich herstellen bij een gepast begrazingsbeheer.

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