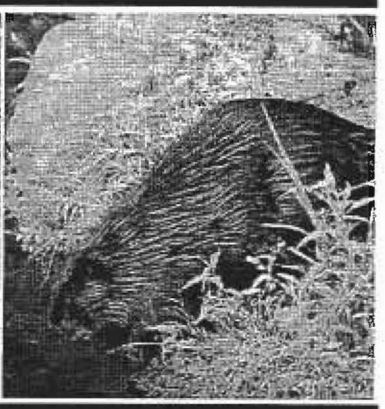
Wildlife & Riparian Areas



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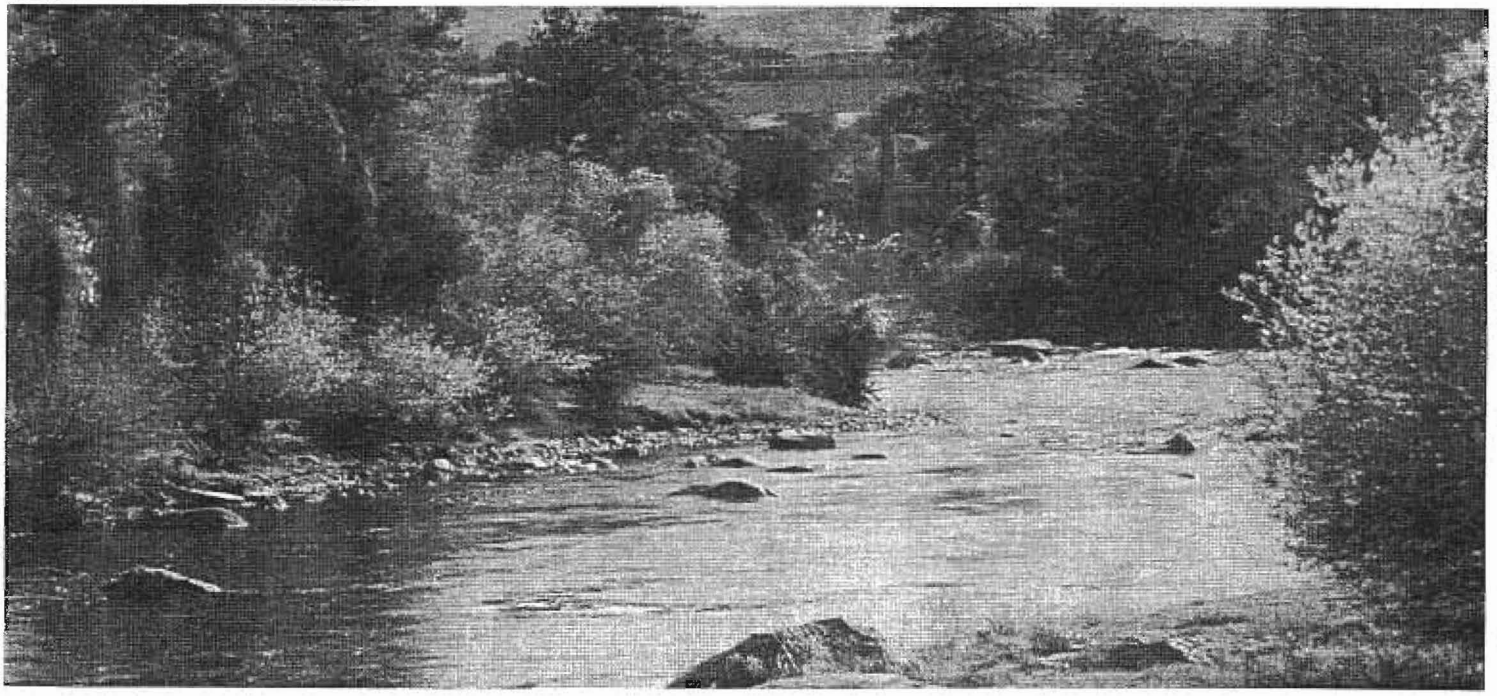

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WHY AREN'T THERE MORE BEAVER IN ROCKY MOUNTAIN NATIONAL PARK?[1]?

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ABSTRACT

Beaver populations have declined dramatically in Rocky Mountain National Park since 1940. Declines were initiated by trapping in 1941 – 1949. Blood tests of 39 livetrapped beaver indicated disease is not present in the population. Current beaver populations occur in areas with low willow use by elk. We compared use of woody stems in a winter food cache with nearby unused stems and found that beaver selected stems that had a lower percentage of leaders browsed by elk. We experimentally tested the effects of elk browsing on regrowth of simulated beaver-cut willow inside and outside 5 elk exclosures and found intense elk browsing produced plants of low vigor that were small, short, and hedged with a high percentage of dead stems. In contrast, regrowth of protected plants was large, tall, highly branched, and leafy with a low percentage of dead stems. We conclude that if beaver cut tall willow, and intense elk browsing suppresses regrowth, then the interaction of beaver and elk may function as a mechanism of declining riparian willow. Further, we speculate that intense elk browsing may decrease the suitability of willow as winter beaver food, increase willow mortality (directly or indirectly through loss of beaver), and increase elk carrying capacity by conversion of beaver-wetland to upland-meadow.

INTRODUCTION

Beaver (*Castor canadensis*) are a definitive example of both a keystone species and an ecosystem engineer (Baker and 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 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, thereby creating a new water table gradient. 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 (Baker et al. 1992). Thus, beaver can benefit the establishment and survival processes of willow and other phreatophytic species.

Willow (*Salix* spp) is important as food and construction material for beaver (Baker and Hill 2003). Willow leaves are high in protein content and are readily eaten during the summer. The bark of willow stems may be the only

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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 and Cade 1995). Beaver-cutting stimulates sprouting from below the cut. In a study of red willow (*S. 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). Where willows benefit beaver as food and construction material and beaver benefit willow establishment and survival processes, beaver and willow can be considered mutualists. Beaver-willow mutualisms can collapse in heavily browsed environments (Baker *in press*).

Here, we discuss factors that likely explain declines and limit populations of beaver in Rocky Mountain National Park (RMNP), Colorado.

STUDY AREA

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. Elk (*Cervus elaphus*) were reintroduced to RMNP in 1913!1914 after nearly being extirpated by the late 1800s. They had increased to 1200 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 elk control and their 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). 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 have both declined in heavily browsed environments within RMNP, but the underlying mechanisms have remained elusive.

LIMITING FACTORS ANALYSIS

From 9 August – 8 November, 1999, we conducted a survey of beaver activity and habitat factors that might be limiting their populations within the St. Vrain River, Big Thompson River, Cache la Poudre River, and Colorado River watersheds drainages in RMNP (Mitchell, D., J. Tjornehoj, and B. W. Baker. 1999. Beaver populations and possible limiting factors in Rocky Mountain National Park. Annual Report, U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526). Streams were surveyed by foot to locate current and past beaver activity, including lodges, bank dens, food caches, dams, trails, cuttings, stumps, scent mounds, scat, and sightings. Current activity was distinguished from past activity by fresh sign such as mud, cuttings and stumps, pungent scent mounds, active trails, broken ice, scat, and sightings. Recent aerial photographs (9 September 1999 at 1:3600 scale) and past surveys were used to help locate potential beaver habitat. Data were recorded for the following factors: (1) riparian shrub use (%) by ungulates, (2) canopy cover of riparian shrubs, (3) species composition of riparian shrubs, (4) river channel condition and suitability for beaver, and (5) river channel width (m). In this survey we used the number of active sites or colonies to estimate the population. Colonies were defined as separate areas that always contained a foraging area, and sometimes contained one or more active lodges, food caches with fresh cuttings, dams with fresh cuttings or recent activity, or scent mounds, slides, and beaver tracks. Multiple colonies along a stream reach typically were separated by at least 100 meters. In contrast to previous surveys, we did not multiply number of lodges by 6 and burrows by 2 to estimate populations, primarily because a single colony (family unit typically with 6 beaver) can have multiple lodges or dens.

Results indicated that most active beaver populations were located where ungulate use of riparian shrubs was least, and that beaver were largely absent from areas with heavy use by ungulates, especially elk.

HISTORICAL BEAVER POPULATION CONTROL

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 (Ducharme, H. C., D. C. S. Mitchell, B. W. Baker, T. R. Stanley, and H. R. Peinetti. 2000. Declining Beaver Populations in Rocky Mountain National Park.

2000 Annual Report. U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526). Radio tracking data (see below) from RMNP showed beaver colonies often used many more than 1 active lodge, which suggests historical estimates of beaver populations are likely very inflated. If Packard's pre-trapping estimates (1939 – 1940) of the beaver population are inflated, and data on the number of beaver removed by trapping are accurate, then it is likely that a larger percentage of the beaver population was killed by trapping than was realized at the time. The effect of this intensive trapping was likely greater than expected, as mortality is increased when an adult beaver is trapped from the colony or family unit (Baker and Hill 2003). Thus, the effect of trapping likely had a long-lasting impact on beaver populations. 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 and beaver populations even further.

BEAVER MORTALITY AND DISPERSAL

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 livetrapped using Hancock and box traps. 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. 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 low 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 mortality of 1 adult male beaver due to coyote (*Canis latrans*) predation and 1 adult female due to unknown causes. One adult male beaver dispersed about 10 km to a location within the town of Estes Park that was adjacent to RMNP. Radio tracking 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 telemetry. These data suggest that attempting to census beaver by multiplying counts of active dens and lodges by a constant to estimate populations would likely overestimate actual numbers.

INTERACTION OF BEAVER AND ELK HERBIVORY

Why have beaver populations failed to recover since trapping ceased in 1949? Beaver surveys and aerial photographs taken in 1999 revealed only one beaver colony in Moraine Park, which was located within a 30 m x 46 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 tbe 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 dominated much of the former beaver habitat in RMNP.

How did the formerly tall (>3 m) willow community become short (<1.5 m) and hedged? Elk can break tall willow stems to reach the tender tips of leaders. Although this behavior has been observed in RMNP, it usually results in broken stems that are >2 m tall and did 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 2 only 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 and 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 and 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 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. 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.

How can managers restore a beaver-willow mutualism given that browsing by elk has suppressed willow height and biomass enough to preclude beaver? Because willow utilization rates may remain high under a wide range of elk population levels, elk control via culling, hunting, or fertility reduction may not reduce competition with beaver unless elk numbers are severely reduced. Redistribution of elk in combination with population control may be necessary to reduce or eliminate elk use of willow. Fenced riparian pastures that protect willow from elk must be large enough to sustain a beaver colony, which is about 5 ha in RMNP (H. R. Peinetti, unpublished data). Predation risk also can reduce elk use of riparian areas. In Yellowstone National Park (YNP), USA, a 70-year absence of wolves (*Canis lupus*) as apex predators coincided with a period of poor cottonwood (*Populus angustifolia* and *P. trichocarpa*) recruitment, which suggests elk had lost their fear of browsing in riparian areas (Beschta 2003). After wolves were reintroduced to YNP, areas with higher predation risk (low visibility and/or presence of escape

barriers) had young cottonwood that was taller and less browsed by elk (Ripple and Beschta 2003). Recent observations in YNP suggest the release of willow is even stronger than cottonwood in wolf use areas, and corresponds to areas of new colonization by beaver (Smith, D. W. personal communication). We suggest the presence of ponds, dams, and canals built by beaver will further impede elk escape from wolves in riparian areas, as Ripple and Beschta (2003) suggested microtopography that restricts visibility or escape would increase predation risk to elk. Thus, the positive effect of wolves on release of willow from elk browsing likely overcompensates for wolf predation of beaver, and results in a net benefit to beaver. If willow is completely protected from elk browsing via high predation risk, fencing, or other methods, then the use of fire to remove existing stems may benefit subsequent beaver restoration as new willow shoots that arise from belowground would likely be more palatable and productive as beaver food than shoots released from the tips of severely hedged stems.

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