

DECLINING BEAVER POPULATIONS IN ROCKY MOUNTAIN NATIONAL PARK

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This final report is a compilation of pertinent completed and submitted papers as of January 2005. It does not include 3 expected papers from Cherie Westbrook's Ph.D. dissertation. She is expected to complete these papers and her Ph.D. at Colorado State University (CSU) by September 1, 2005 under contract to CSU via David Cooper, her major advisor and co-investigator on the NRPP study. This report does not include 2 draft papers by Bruce Baker, Raul Peinetti, and Mike Coughenour that report results from an ecological modeling study of beaver, elk, and willow interactions funded primarily by the Park Oriented Biological Support program; we hope to have these papers completed by early summer 2005. Finally, a synthesis paper is planned after all the separate components of the research is completed and reported in individual papers. In addition, much information, including beaver surveys and historical reviews that are likely not publishable as scientific papers, have been fully documented in progress reports FY99 – FY 03 on file at ROMO. The objectives statement below summarizes these progress reports.

The objectives of this research are to evaluate declining beaver populations in Rocky Mountain National Park (ROMO) and beaver ecology in the Kawuneeche Valley, including the effects of dewatering by the Grand Ditch. In **FY99** we surveyed beaver populations and identified possible limiting factors throughout the park. In **FY00** we repeated beaver surveys on the east side and evaluated limiting factors and beaver historical declines, evaluated designs to understand effects of the Grand Ditch on the Colorado River via experimental water diversions and water table effects of existing beaver dams, collected data to evaluate elk browsing effects on regrowth of beaver-cut willow, and collected data to evaluate the use and availability of riparian shrubs by a beaver colony in Moraine Park. In **FY01** we initiated the radio telemetry portion of the study to evaluate beaver mortality, dispersal, and other population characteristics on the east side of the Park and continued ongoing research to understand how the Grand Ditch affects beaver ecology in the Kawuneeche Valley. In **FY02** we continued monitoring radioed beaver on the east side of the Park, interpreted data on the interaction of beaver and elk herbivory as a mechanism of declining willow, and continued the Grand Ditch study (including the addition of Ph.D. student Cherie Westbrook to the project). In **FY03** we completed monitoring radioed beaver on the east side of the Park, submitted a paper to Ecological Applications entitled 'Interaction of beaver and elk herbivory suppresses compensatory growth in willow', and continued the Grand Ditch study. In **FY04** we revised a paper accepted for publication by Ecological Applications, published and presented 2 papers in Proceedings of the Colorado Riparian Association, and submitted papers to the Wildlife Society Bulletin and Rangeland Ecology and Management. In addition, we collected new field data for the Kawuneeche Valley study (see ROMO Investigator's Annual Report), continued data analysis, and prepared a status report (CSU research proposal) to document remaining work proposed for this project (as of January 2005) as part of Cherie Westbrook's Ph.D. program at Colorado State University.

List of publications

- Baker, B. W., H. C. Ducharme, D. C. S. Mitchell, T. R. Stanley, and H. R. Peinetti. **2004.** Why aren't there more beaver in Rocky Mountain National Park? *Proceedings of the Annual Conference of the Colorado Riparian Association* 17:85-90.
- Baker, B. W., H. C. Ducharme, D. C. S. Mitchell, T. R. Stanley, and H. R. Peinetti. *In press.* Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecological Applications*
- Baker, B. W., H. R. Peinetti, and M. B. Coughenour. Resilience of willow stems after release from intense elk browsing. In Review. *Rangeland Ecology and Management*.
- Baker, B. W. Efficacy of tail-mounted transmitters for beaver. In Review. *Wildlife Society Bulletin*.
- Westbrook, C. J., D. J. Cooper, and B. W. Baker. Beaver as hydrological and ecological drivers of mountain valley functioning. Ph.D. Research Proposal (progress as of January 2005). Colorado State University, Fort Collins, Colorado.
- Westbrook, C. J., D. J. Cooper, and B. W. Baker. **2004.** Beaver vs. floods in controlling hydrological processes on floodplains. *Proceedings of the Annual Conference of the Colorado Riparian Association* 17:91-93.

Why aren't there more beaver in Rocky Mountain National Park¹?

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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

¹ Parts of this paper were adapted or extracted from Baker and Hill (2003), Baker (*in press*), and Baker et al. (*in press*).

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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 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 enclosure that had been erected to protect willow from elk browsing. The elk enclosure 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 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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RH: Herbivore interaction suppresses willow • Baker et al.

Interaction of beaver and elk herbivory suppresses standing crop in willow

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1 *Abstract.* Populations of beaver and willow have not thrived in riparian environments that are heavily
2 browsed by livestock or ungulates, such as elk. The interaction of beaver and elk herbivory may be an
3 important mechanism underlying beaver and willow declines in this competitive environment. We
4 conducted a field experiment that compared the standing crop of willow 3 years after simulated
5 beaver cutting on paired plants with and without intense elk browsing (~85% utilization rate).
6 Simulated beaver cutting with intense elk browsing produced willow that was small (biomass and
7 diameter) and short with far fewer but longer shoots and a high percentage of dead biomass. In
8 contrast, simulated beaver cutting without elk browsing produced willow that was large, tall, and
9 leafy with many more but shorter shoots (highly branched) and a low percentage of dead biomass.

1 Total stem biomass after 3 years was 10 times greater on unbrowsed plants than on browsed plants.
2 Unbrowsed plants recovered 84% of their pre-cut biomass after only 2 growing seasons, whereas
3 browsed plants recovered only 6%. Thus, the interaction of beaver cutting and elk browsing strongly
4 suppressed the standing crop of willow. We predict a lack of willow suitable as winter food for
5 beaver can cause beaver populations to decline, creating a feedback mechanism that reduces beaver
6 and willow populations. Thus, intense herbivory by ungulates or livestock can disrupt beaver-willow
7 mutualisms that naturally occur in less competitive environments.

8 *Key words: beaver, Castor canadensis, compensatory growth, elk, herbivory, livestock,*
9 *plant-herbivore interaction, Rocky Mountain National Park (USA), Salix monticola, standing crop,*
10 *ungulate, willow.*

11 INTRODUCTION

12 Compensatory growth, defined as the positive response of plants to injury, helps plants
13 tolerate damage from abiotic and biotic causes, such as fire, wind, commercial harvest, and
14 herbivores ranging in size from insects to large mammals (McNaughton 1983). Plant response to
15 herbivory varies in form and magnitude depending on how plants are grazed or browsed (Belsky
16 1986, Milchunas and Lauenroth 1993, Brookshire et al. 2002). Large mammals often repeatedly
17 browse shoot tissue from the tops of woody plants, a model system widely used to develop and test
18 theory about mechanisms of compensatory growth. In response to mammalian herbivory, woody
19 plants can shunt carbon stores from roots to shoots; increase leaf N, photosynthetic rate and growth
20 rate; and increase branching in response to released apical dominance (Hobbs 1996, Strauss and
21 Agrawal 1999).

22 Beaver (*Castor canadensis*) are central place foragers that cut and remove entire stems at or
23 near the ground surface. They often cut all stems from preferred shrubs growing near their winter
24 food caches, dams, and lodges, but become more selective as foraging distances increase (Baker and

1 Hill 2003). In response to beaver cutting, red willow (*Salix lasiandra*) increased stem production in
2 proportion to the number of stems cut per plant, with a stem elongation rate of 3.3 cm/day on cut
3 plants compared with 0.4 cm/day on uncut controls (Kindschy 1985, 1989). Beaver cutting of
4 sprouting woody species is most analogous to coppicing, an ancient forestry practice that involves
5 cutting trees down close to the ground to induce production of basal sprouts, which are allowed to
6 grow until suitable for harvest; woodlands systematically coppiced in this manner can remain
7 productive for centuries (Hardesty and Box 1988, Del Tredici 2001). Traditional logging, fire, wind,
8 and floodwater also can remove entire stems from plants, thus they share some characteristics and
9 effects with beaver cutting (Spiller and Agrawal 2003).

10 Historically, a beaver-willow community dominated many riparian landscapes in North
11 America. Seton (1929) estimated beaver numbered 60!400 million before European settlement.
12 Beaver modify their environment by cutting willow for food and construction material, by building
13 dams that raise the water table, and by building ponds that trap sediment and increase N availability
14 to willow (Naiman et al. 1988). These modifications benefit willow by creating bare moist soil for
15 seed germination, by increasing late-season moisture regimes for seedling survival, and by increasing
16 stem turnover rate (asexual reproduction). The sprouting ability of willow, and the ability of beaver to
17 shift their foraging upstream or downstream if needed as willow recovers, suggests that beaver and
18 willow can persist indefinitely within the same stream reach (Hall 1960). Because beaver facilitate
19 willow establishment and survival processes, and willow is important as food and construction
20 material for beaver (Baker and Hill 2003), we suggest beaver and willow are mutualists.

21 Despite their legendary abundance, fur trappers decimated most beaver populations during the
22 1700's and 1800's to support the European fashion for felt hats (Baker and Hill 2003). Although
23 beaver reintroduction helped recover populations throughout much of their former range, beaver-
24 willow communities have declined or failed to recover in riparian environments that have become

1 heavily browsed by livestock or ungulates since European settlement. Large herbivores congregate in
2 these areas because they lack disturbance from large predators and provide water and productive
3 vegetation (Belsky et al. 1999). These additional herbivores directly compete with beaver for willow,
4 which is highly palatable and selected for by livestock and ungulates, such as elk (*Cervus elaphus*).
5 We suggest this new level of competition is unnatural to beaver-willow mutualisms, which likely
6 evolved under relatively low herbivory in a more predator-rich environment. Thus, the interaction of
7 beaver and elk herbivory may be an important mechanism underlying beaver and willow declines in
8 this new competitive environment, and represents a model system where intense disturbance can alter
9 plant-herbivore interactions and ecosystem processes.

10 Here, we present experimental evidence that intense browsing by elk can suppress the
11 standing crop of simulated beaver-cut willow. This suppression can drive declines or prevent
12 restoration of beaver-willow communities in heavily browsed environments.

13 METHODS

14 *Study Area*

15 We chose a beaver-willow community in Rocky Mountain National Park (RMNP), Colorado
16 that was heavily browsed by elk as our model plant-herbivore system. Study sites were in Moraine
17 Park (elevation 2500 m) and Horseshoe Park (elevation 2600 m), which were broad flat alluvial
18 valleys dominated by willow (*S. monticola*, *S. geyeriana*, *S. planifolia*) and alder (*Alnus tenuifolia*)
19 with a herbaceous understory of *Carex* and grass that averaged ~ 30 cm in height during late summer.
20 Beaver were once abundant in the study area but declined dramatically after 1940; for example,
21 population estimates in Moraine Park were 315 in 1939!1940, 102 in 1964, 12 in 1980, and 6 in
22 1999. Elk were reintroduced to RMNP in 1913!1914 after nearly being extirpated by the late 1800s.
23 They had increased to ~ 1,200 animals in 1940 when Packard (1947) first noted beaver and elk
24 competition for willow. Control efforts reduced the elk population to 500 until 1968 when a policy of

1 natural regulation altered management and elk increased to ~ 3000 by the late 1990s (Singer et al.
2 1998). Elk utilization of riparian willow (% leaders browsed) averaged ~85% annually in 1968!1992
3 (Fig. 11; Zeigenfuss et al. 1999) as the elk population increased to 6 times its 1968 level (Table 1;
4 Lubow et al. 2002), evidence that willow utilization rates were both very high and independent of elk
5 population levels for many years. In a comparison of 1937/1946 and 1996 aerial photographs,
6 Peinetti et al. (2002) found tall willow (>3 m) cover declined by 54% in Moraine Park and 65% in
7 Horseshoe Park. Short willow plants (< 1.5 m) have dominated the study area for several decades,
8 likely a result of a change in individual plant stature rather than in willow species composition. Thus,
9 beaver and willow populations have both declined in heavily browsed environments within RMNP.

10 Experimental Design

11 We experimentally tested the effects of elk browsing on willow (*S. monticola*, a tall shrub) 3
12 years after simulated beaver cutting. Morphology, biomass, N, and percent recovery were compared
13 for 712 stems on plants paired inside (unbrowsed) and outside (browsed) 5 elk exclosures (treatment
14 replicate) in RMNP (exclosure numbers 3&7 in Moraine and Horseshoe Parks). Elk exclosures were
15 30 m × 46 m in size and erected in August!November 1994 by randomly locating adjacent paired
16 willow sites in elk winter range and randomly selecting 1 site for exclosure treatment and the other as
17 a paired control left available to elk (Peinetti et al. 2001, Zeigenfuss et al. 2002). In May 1997, one
18 plant was randomly selected from “the most frequent size type (canopy volume and height)” inside
19 and outside the 5 exclosures (10 plants in total) and cages were placed around outside plants to
20 protect them from elk browsing during the 1997 growing season (Peinetti et al. 2001:335). In
21 September 1997, all stems (age 7!10 years) from paired treatment and control plants were cut and
22 removed at the ground level, effectively simulating beaver cutting as the initial condition for this
23 study. Neither 1997 shoot biomass nor total aboveground woody biomass differed for browsed and
24 unbrowsed treatments, which showed, respectively, that browsed plants had likely recovered biomass

1 removed by elk during the previous winter (Peinetti et al. 2001) and that paired plants likely began
2 this study with a similar initial condition. Paired treatment and control plants also were likely in
3 similar hydrologic environments, as they were < 20 m apart and were similar in distance from
4 streams. In addition, previous studies in the same areas found the water table was high enough to be
5 accessible to mature willow (Alstad et al. 1999) and that depth to water table had no effect on willow
6 response to elk browsing (Zeigenfuss et al. 2002). After 3 years we again removed all stems (August
7 29&September 7, 2000) from the 10 paired plants to compare treatment effects. Biomass removed by
8 elk (the offtake component of compensatory growth) was not estimated as we were interested in the
9 *consequences* of elk browsing to beaver. Thus, we compared the standing crop of simulated beaver-
10 cut willow plants that remained after 3 years of growth in browsed and protected environments.

11 Sampling and Analysis Procedures

12 Whole stems were aged, measured (basal stem diameter and height from cut end to tip of
13 tallest leader), and cut into segments. Segments were sorted into age cohorts (1998, 1999, or 2000),
14 browsed or unbrowsed, and live or dead. Age cohort was determined from the presence of nodes,
15 sympodial branching patterns, leaf presence, and condition of bark (Alliende and Harper 1989,
16 Peinetti et al. 2001); stems and stem segments could be from 1 of only 3 possible years, which
17 simplified age cohort classification. Estimates of segment length were obtained from a size-based,
18 stratified random sample of 6 stems from each of the 10 plants. To include radial growth in the proper
19 year we adjusted biomass values for 1998 and 1999 by the proportion of annual radial growth, which
20 we developed from width measurements of growth rings on a random sample of 15 stem segments
21 from each age cohort. For example, 1998 stem segments had annual radial growth from 1998, 1999,
22 and 2000. To ensure statistical independence, we randomly selected 5 different stem segments from
23 this sample and measured ring widths for each of the 3 years via an integrated system consisting of a
24 movable viewing platform, stereoscope, and Measure 2JX software. Stem segments and leaves from

1 all 712 stems were oven-dried at 65° C until dry and then weighed to compute biomass. Biomass
2 recovery (%) was estimated by comparing aboveground biomass before and after simulated beaver-
3 cutting ($100 \times \text{Biomass}_{2000}/\text{Biomass}_{1997}$) for the same 10 plants. However, because Peinetti et al.
4 (2001) had temporarily fenced control plants to preclude elk browsing during the 1997 growing
5 season, we subtracted biomass of current annual growth (CAG) from both data sets before computing
6 biomass recovery. Percent N was estimated from 0.1-g samples of dried, ground stem segments and
7 leaves via a LECO CHN analyzer. All statistical tests were constructed using paired *t*-tests. Data were
8 examined for normality using normal probability plots and the Shapiro-Wilk statistic (Shapiro and
9 Wilk 1965), and were \log_e transformed where necessary.

10 RESULTS

11 *Browsing effects on stem morphology*

12 Simulated beaver-cut willow plants located outside exclosures were heavily browsed by elk
13 during the study, as utilization rates (% leaders clipped) were $86.4 \pm 4.8\%$ ($0 \pm \text{SE}$) for extant year
14 1998 stems and $92.6 \pm 4.1\%$ for extant year 1999 stems. These data are consistent with previous
15 studies in RMNP that showed elk utilization of willow averaged ~85% annually during 1968!1992
16 (Zeigenfuss et al. 1999). We found the utilization rate of extant year 2000 stems was $64.6 \pm 5.9\%$ in
17 early fall 2000, which indicates substantial summer browsing had occurred before elk concentrated
18 on winter ranges.

19 Mean number of stems/plant for all 3 years combined did not significantly differ for
20 unbrowsed and browsed plants; however, the age distribution of stems suggested a strong treatment
21 effect (Table 1a). Year 1998 stems composed 98% of unbrowsed plants, but only 58% of browsed
22 plants. Thus, plants protected from elk responded with vigorous sprouting in the first year and added
23 new growth to existing stems in successive years. In contrast, browsed stems likely responded to
24 released apical dominance either by sprouting a new basal stem from the collar (regeneration tissue

1 located between roots and stems just below the soil surface, Del Tredici 2001), which increased stem
2 turnover rate, or by lateral branching of dormant buds located directly below the point of browsing.

3 Mean stem height was 4 times greater on unbrowsed plants than on browsed plants (Table
4 1b). Maximum stem height of browsed plants was only 31.7 cm, and variation among stems was low.
5 Because the height of surrounding herbaceous vegetation in late summer was also ~ 30 cm, these
6 results suggest elk were attracted to willow stems after they had emerged from the herbaceous
7 canopy.

8 Mean stem diameter was greater on stems protected from elk browsing (Table 1c). Stem
9 diameter increased with age for both browsed and unbrowsed plants (Table 1c), however, browsed
10 plants did not increase height as they aged (Table 1b). After 3 years unbrowsed stems were tall and
11 relatively thin, whereas browsed stems had developed a short and stout form (diameter relative to
12 height was greater).

13 Mean number of segments/stem, or branching, was nearly 7 times greater on unbrowsed stems
14 (25.0) than on browsed stems (3.7) after 3 years (year 2000, Table 1d), perhaps because browsing by
15 elk had reduced the number of growing points on plants (Danell and Bergstrom 1989).

16 Mean segment length was greater on unbrowsed plants for year 1998 and year 1999 stem
17 segments, but greater on browsed plants for CAG (year 2000, Table 1e). Differences were most
18 dramatic in the first year after cutting (1998) when unbrowsed stem segments were an average of
19 64.2 cm in length and browsed stems were an average of 8.5 cm in length. This may indicate either
20 that elk browsing arrested vertical growth by removing the shoot tip during the first growing season
21 or that elk browsing after the growing season removed a substantial portion of CAG. In contrast,
22 segment length of CAG shoots was nearly 3 times greater on browsed (15.2 cm) than on unbrowsed
23 plants (5.5 cm), a very significant difference considering that on browsed plants elk had already
24 removed some length from 65% of the shoots during the summer before measurement. This pattern

1 of fewer but longer shoots on browsed plants is consistent with studies of moose (*Alces alces*)
2 browsing on birch (*Betula*) in Sweden and may suggest plants had allocated more photosynthates to
3 fewer shoot segments in response to herbivory (Danell and Bergstrom 1989).

4 Browsing effects on stem biomass

5 Mean total biomass (1998!2000) was ~10 times greater on unbrowsed plants than on browsed
6 plants (Table 1f). Treatment differences were consistent for all years with the greatest contrast
7 between unbrowsed and browsed plants in the first year (1998), when biomass averaged 251.0 g on
8 unbrowsed plants but only 14.2 g on browsed plants. Leaf biomass also was ~ 10 times greater on
9 unbrowsed plants than on browsed plants, which was consistent with differences in stem height and
10 other morphometrics. Percent of total biomass composed of dead tissue (not separable by age cohort)
11 was 4 times greater ($P = 0.031$) on browsed plants ($16.1 \pm 4.1\%$) than on unbrowsed plants ($4.1 \pm$
12 0.9%). This suggests elk browsing may increase the mortality of stems or shoots, either as a direct
13 result of browsing, or as plants shift growth away from browsed shoots (which then die back) to new
14 basal stems arising from the collar (Table 1a) or to elongate unbrowsed leaders (Table 1e).

15 *Browsing effects on N*

16 Percent N was greatest in leaves and decreased with age of stem segment for both browsed
17 and unbrowsed stems (Table 1g). Percent N in older stem segments (1998 and 1999) was higher on
18 browsed than on unbrowsed plants, which is consistent with the general pattern that browsing
19 increases N in aboveground plant biomass (Hobbs 1996). Percent N in CAG did not differ for either
20 woody material or leaves, which suggests plants may have already translocated N away from active
21 growing tissues for winter storage in roots and older portions of aboveground plant tissues. This
22 explanation is consistent with observed phenological evidence, as leaf color had already turned from
23 green to yellow/brown when plants were cut.

Browsing effects on stem recovery

In a comparison of standing crop before and after simulated beaver cutting, we found unbrowsed plants recovered 148.4% of their pre-cut number of stems after 1 year (1998), whereas browsed plants recovered only 78.5% of stems after 1 year but had recovered 132.9% of stems after 3 years (1998 – 2000), and at that point did not significantly differ from unbrowsed plants (Table 2a). In contrast, elk browsing had a large and sustained effect on recovery of stem biomass. After 2 years (1998 – 1999) unbrowsed plants had recovered 84% of their pre-cut biomass and browsed plants had recovered only 6% (Table 2b). Thus, recovery of standing crop biomass was rapid and vigorous following simulated beaver cutting, but was strongly suppressed by intense elk browsing.

DISCUSSION

Intense elk browsing for 3 years following simulated beaver cutting resulted in willow standing crop that was small, short, and relatively unbranched with a high percentage of dead biomass and longer but far fewer shoots. In contrast, simulated beaver cutting in the absence of elk browsing resulted in plants that were large, tall, highly branched, and leafy with a low percentage of dead biomass and shorter but many more shoots. Aboveground biomass was 10 times greater on unbrowsed plants than on browsed plants. Unbrowsed plants had recovered 84% of their pre-cut standing crop biomass after only 2 years, whereas browsed plants had recovered only 6%. Thus, the interaction of beaver cutting and intense elk browsing strongly suppressed the height and biomass of willow standing crop, which was much more substantial in the absence of elk browsing.

Elk herbivory effects on N content of simulated beaver-cut willow

Herbivory can increase plant N via increased demand by browsed stems and increased availability in the soil due to urine and feces deposition (Hobbs 1996). We found percent N of 1- and 2-year-old stem segments was higher on plants browsed by elk than on unbrowsed plants, but percent N of leaf and woody CAG did not differ. Previous studies in RMNP found higher leaf N on elk-

1 browsed willow in June, but these effects had diminished by September (Alstad et al. 1999, Peinetti
2 et al. 2001). In studies of moose browsing on birch in Sweden, the leaves of moderately browsed
3 plants contained more N than did slightly browsed plants in July, but differences had diminished by
4 October (Danell et al. 1985). Thus, our results confirm browsing increases stem N, but effects
5 diminish as plants enter senescence in late summer. Hobbs (1996:701) listed 6 studies that suggested
6 either “increased allocation of nitrogen to leaves” or “increased uptake of nutrients by roots” as
7 mechanisms that contribute to compensatory growth following plant defoliation. Our findings suggest
8 the interaction of beaver cutting and intense elk browsing can negate the positive effects of increased
9 N on standing crop, as we found browsed plants were much smaller than unbrowsed plants even
10 though they had a higher N content.

11 *Herbivore effects on standing crop and mechanisms of compensatory growth*

12 *Elk.* Compensatory growth mechanisms may be influenced by how woody plants are
13 browsed. Large herbivores browse the tips of leaders, which removes mostly CAG. A large
14 percentage of leaf and woody biomass remains intact, which contributes to the growth of new shoots
15 via photosynthesis. Browsing frequency can be high because shoot regrowth rapidly becomes suitable
16 as forage. Released apical dominance can activate dormant buds below the point of browsing or
17 increase the number and size of lateral shoots, which increases branching and growth rates
18 (Honkanen and Haukioja 1998). When new shoots are within reach of elk then repeated browsing
19 may create hedged plants, which often can maintain high forage productivity. However, browsing can
20 reduce or eliminate sexual reproduction in willow, maintain plants in a vegetative or juvenile growth
21 phase, and reduce plant fitness (Kay 1994). Summer elk browsing is especially detrimental to beaver
22 because summer growth may provide a high percentage of beaver food on stems procured in the fall
23 for a winter food cache (Baker and Cade 1995) and because summer browsing can be more
24 detrimental to compensatory growth mechanisms than dormant season use (Danell et al. 1994).

1 *Beaver.*! Beaver typically cut entire stems near ground level rather than the tips of leaders.

2 Frequency of beaver cutting is relatively low compared to ungulate browsing because it takes several
3 years for regrowth to become large enough to justify the cost of procuring a stem in terms of
4 predation risk, energy expended, and transport to a safe eating site, winter food cache, dam, or lodge
5 (Baker and Hill 2003). In addition, beaver may avoid juvenile sprouts because they can contain
6 higher concentrations of phenolic glycosides or other defensive chemicals (Basey et al. 1990).
7 Willow can rapidly recover stems cut by beaver (Kindschy 1985, 1989). In our study, willow
8 regained 151% of stems and 84% of biomass in only 2 years following complete removal of all stems
9 (Table 2). Because the frequency of herbivory is usually low and plants can rapidly recover lost
10 biomass and height, beaver-cut plants are more likely to reach sexual maturity and produce seed than
11 are plants browsed by elk.

12 *Beaver and elk interaction.*! The combined effects of beaver cutting and intense elk browsing
13 strongly suppressed the standing crop of willow in our study. After 3 years browsed plants had
14 averaged only 12% of CAG woody biomass, 9% of leaf biomass, and 10% of total biomass relative to
15 paired unbrowsed control plants (Table 1), and after 2 years had recovered only 6% of their pre-cut
16 biomass (Table 2b). In a previous study, these same plants equally recovered from elk herbivory as
17 CAG, leaf biomass, and woody biomass were similar for browsed and unbrowsed treatments under
18 similar elk densities but in the absence of beaver cutting (Peinetti et al. 2001). In an African browsed
19 environment, where the large herbivore density was 10 animals/km² and greater kudu (*Tragelaphus*
20 *stresiceros*) was the dominant species, the deciduous tree *Combretum apiculatum* showed exact
21 compensation to clipping (simulated browsing) but strong undercompensation to cutting (stem
22 removal to simulate fire or stem breakage, which also simulated beaver) (Bergstrom et al. 2000). In
23 this experiment, trees were either clipped via a 55% one-time reduction in number of annual shoot
24 tips < 6 mm in diameter, or cut at 0.5 m above ground, and then compared to unclipped/uncut

1 controls after all 3 treatments were subjected to large herbivore browsing for 8 months. The biomass
2 of clipped trees was similar to controls but biomass of cut trees was only 15% of controls, evidence
3 that browsing strongly suppressed cut trees. This analogous system suggests our results may have
4 some general application, as we found the combined effects of beaver cutting and intense elk
5 browsing strongly suppressed the standing crop of willow that was evident when either herbivore
6 operated independently.

7 What mechanisms explain how willow can tolerate either complete infrequent cutting by
8 beaver, or partial frequent browsing by ungulates, but not both? The ability of willow to vigorously
9 sprout following complete removal of aboveground biomass suggests they have a high level of
10 nutrients stored in roots, which can be rapidly shunted from roots to shoots following herbivory
11 (Strauss and Agrawal 1999). However, this mechanism likely reduces root reserves and places plants
12 in a stressed state until new sprouts can recover stem and leaf tissue necessary for photosynthesis,
13 which is a prerequisite of other compensatory growth mechanisms such as increased photosynthetic
14 rate, leaf N, and growth rate. Also, when beaver cut tall stems they can place regrowth under the
15 canopy of surrounding herbaceous vegetation where further herbivory can prevent new stems from
16 escaping competition for light and increasing their growth rates (Raven 1992). In our study all 3 age
17 cohorts of browsed willow averaged < 30 cm in height and plants continued to sprout new stems each
18 growing season, which suggests browsed plants were unable to gain a competitive advantage for light
19 above the herbaceous canopy. Alternatively, if some stems or shoots on a plant escape beaver or elk
20 herbivory, then the plant may compensate for partial stem or shoot loss via a more complete suite of
21 mechanisms than is available under more intense herbivory. Thus, individual shoots, stems, plants,
22 and populations will likely exhibit a range of morphologies that reflect their particular browsing
23 history and the compensatory growth mechanisms available in response to herbivory.

24 Beaver alter future plant-herbivore interactions when they cut the stems of woody plants.

1 Breaking apical dominance can improve plant quality for herbivores as it increases the number of
2 vigorously growing shoots, which are rich in nutrients and sugars and poor in proteinaceous material
3 (Honkanen and Haukioja 1998). Intense disturbance to plants by beaver, other herbivores, coppicing,
4 fire, or floodwater can enhance plant susceptibility to herbivory via induced neotany, increased leaf
5 size but reduced toughness, and reduced levels of defense (Spiller and Agrawal 2003). Elk and
6 grasshoppers were attracted to arroyo willow (*S. lasiolepis*) that had vigorously sprouted following a
7 fire, likely because regrowth was more succulent and nutritious (Stein et al. 1992).

8 When beaver cut tall woody plants they increase stem turnover rate and place regrowth within
9 easy reach of herbivores. Although large herbivores can break stems and make existing food or
10 regrowth available to themselves and other species (Bergstrom 1992), beaver cutting can greatly
11 enhance the process of shrub height reduction in browsed environments with effects that can cascade
12 to a new suite of herbivores. In Africa, megaherbivores (elephants, *Loxodonta africana*) break and
13 trample woody vegetation as they browse, which places regrowth within easy reach of
14 mesoherbivores and creates a trophic cascade of altered plant-herbivore interactions and competition
15 among herbivores (Fritz et al. 2002). Thus, beaver herbivory represents a model system where intense
16 disturbance alters future plant-herbivore interactions.

17 Interaction of beaver and large herbivores as an ecological driver

18 Given our experimental evidence, we offer a series of predictions about the interaction of
19 beaver cutting and intense elk browsing as the cause of declining beaver-willow ecosystems. We
20 suggest that beaver and willow are mutualists, and this mutualism collapses in heavily browsed
21 environments where asymmetrical competition favors elk over beaver. We refer to elk and willow for
22 simplicity, but suspect these mechanisms apply equally well to other large ungulates or livestock, to
23 other woody plant species that are benefited by beaver, and to other systems where anthropogenic or
24 natural disturbance mimics the effects of beaver cutting.

1 First, we predict that when beaver cut willow in a heavily browsed environment they can
2 drive a tall willow community into an alternative state consisting of short, hedged plants that are
3 vegetatively productive but less likely to mature and produce seed. Lacking sexual reproduction, this
4 state will persist only until plants die of old age or other causes, which may take many decades.
5 Second, we predict that elk browsing decreases the suitability of willow as beaver food by reducing
6 the biomass of twigs and bark on stems and their preference by beaver, leading to beaver declines
7 where willow limits populations. In these systems, willow that provides adequate biomass of twigs
8 and bark is *necessary* for beaver as a winter food supply, but short or heavily-browsed willow (or no
9 willow) is *sufficient* for elk, as elk can subsist on herbaceous forage in areas lacking deep winter
10 snow (Skovlin 1982). Thus, in riparian systems where elk are overabundant they will outcompete and
11 exclude beaver. Third, we predict when beaver populations decline then wetlands will lose key
12 willow establishment and survival processes provided by beaver dams and canals, such as increased
13 sediment deposition and soil moisture and higher water tables spread across larger areas. Loss of
14 these functions will decrease the distribution and abundance of willow and contribute to the eventual
15 collapse of beaver-engineered wetlands, with effects cascading throughout the ecosystem. Fourth, we
16 predict the carrying capacity for elk is altered by the presence or absence of beaver. Where beaver
17 dams and canals create landscapes dominated by open water, then beaver declines will likely increase
18 elk carrying capacity in a process equivalent to the agricultural practice of wetland drainage to
19 increase livestock forage production. Alternatively, beaver may increase carrying capacity for elk in
20 dry environments where dams raise the water table and increase productivity enough to
21 overcompensate for surface area lost to beaver ponds. Thus, we predict that when beaver cut tall
22 willow, and intense elk browsing suppresses the height and biomass of willow available to beaver,
23 then the interaction of beaver and elk herbivory will create a feedback mechanism that decreases
24 beaver and willow but either increases or decreases elk depending on local conditions.

RESEARCH AND MANAGEMENT IMPLICATIONS

1
2 Further research is necessary to determine the level of additional herbivory that beaver-willow
3 communities can tolerate before willow becomes unsuitable to beaver. As a guide to recognize trends
4 we suggest that a beaver-willow community is likely *stable* if ungulate or livestock utilization of
5 willow is absent or limited to the perimeter of the community and interior stems are mostly full-
6 height, *declining* if herbivory has penetrated the interior of the community and suppressed regrowth
7 of beaver-cut stems, and *recovering* if interior or perimeter plants show evidence of previous hedging
8 but include many unbrowsed leaders.

9 Trapping, disease, and other limiting factors may cause beaver populations to decline, in
10 addition to competition with other herbivores. If beaver decline, then the distribution and abundance
11 of willow may decline in areas formerly influenced by beaver. Where beaver and willow have both
12 declined, how can we determine cause and effect? It may be important to consider that suitable
13 willow may be necessary for beaver, but beaver are sufficient for willow, as willow can establish and
14 persist without beaver; thus, the location and success of willow establishment and survival processes
15 relative to beaver activity and browsing pressure by other herbivores may provide clues to decipher
16 cause and effect on the landscape.

17 How can managers restore a beaver-willow mutualism given that browsing by elk (or other
18 herbivores) has suppressed willow height and biomass enough to preclude beaver? Because willow
19 utilization rates may remain high under a wide range of elk population levels, elk control via culling,
20 hunting, or fertility reduction may not reduce competition with beaver unless elk numbers are
21 severely reduced. Redistribution of elk in combination with population control may be necessary to
22 reduce or eliminate elk use of willow. Fencing can protect willow from elk, but riparian pastures
23 must be large enough to sustain a beaver colony. Herding or hazing livestock away from riparian
24 willow has been effective on western rangelands (Baker, B.W. personal observation), and may have

1 application for wild ungulates. Predation risk also can reduce elk use of riparian areas. In
2 Yellowstone National Park (YNP), USA, a 70-year absence of wolves (*Canis lupus*) as apex
3 predators coincided with a period of poor cottonwood (*Populus angustifolia* and *P. trichocarpa*)
4 recruitment, which suggests elk had lost their fear of browsing in riparian areas (Beschta 2003). After
5 wolves were reintroduced to YNP, areas with higher predation risk (low visibility and/or presence of
6 escape barriers) had young cottonwood that was taller and less browsed by elk (Ripple and Beschta
7 2003). Recent observations in YNP suggest the release of willow is even stronger than cottonwood in
8 wolf use areas, and corresponds to areas of new colonization by beaver (Smith, D. W. personal
9 communication). We suggest the presence of ponds, dams, and canals built by beaver will further
10 impede elk escape from wolves in riparian areas, as Ripple and Beschta (2003) suggested
11 microtopography that restricts visibility or escape would increase predation risk to elk. Thus, the
12 positive effects of wolves on release of willow from elk browsing likely overcompensates for wolf
13 predation of beaver, and results in a net benefit to beaver. If willow is completely protected from elk
14 browsing via high predation risk, fencing, or other methods, then the use of fire to remove existing
15 stems may benefit subsequent beaver restoration as new willow shoots that arise from belowground
16 would likely be more palatable and productive as beaver food than shoots released from the tips of
17 severely hedged stems.

18 We conclude the interaction of beaver cutting and intense elk browsing can strongly suppress
19 the standing crop of willow, especially willow height and biomass. We predict a lack of willow stems
20 that are suitable as winter food for beaver will cause beaver populations to decline, creating a
21 feedback mechanism that reduces beaver and willow populations and either increases or decreases elk
22 populations depending on local conditions. Thus, intense herbivory by ungulates or livestock can
23 disrupt beaver-willow mutualisms that naturally occur in less competitive environments.

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TABLE 1. Effects of elk browsing on willow (*Salix monticola*) standing crop 3 years after simulated beaver cutting (fall 1997) inside (unbrowsed) and outside (browsed) elk exclosures ($n = 5$) in Rocky Mountain National Park, Colorado, USA. Year 2000 represents current annual growth (CAG).

Willow plants were sampled August 29&September 7, 2000. Differences are computed as unbrowsed minus browsed.

Year	Unbrowsed $0 \pm SE$	Browsed $0 \pm SE$	Difference $0 \pm SE$	p
a. Stems/plant (no)				
1998	69.4 ± 21.1	41.2 ± 15.4	27.6 ± 23.6	0.306
1999	1.7 ± 0.3	15.2 ± 4.5	16.3 ± 7.2	0.152
2000	0.0	14.0 ± 6.2	NA	NA
1998–2000	70.4 ± 21.3	71.0 ± 21.2	0.6 ± 30.8	0.985
b. Stem height (cm)				
1998	111.2 ± 9.7	26.9 ± 2.5	84.3 ± 9.2	<0.001
1999	67.9 ± 9.1	25.0 ± 2.4	41.3 ± 9.0	0.044
2000	NA	28.8 ± 3.7	NA	NA
1998–2000	110.5 ± 9.7	26.8 ± 2.6	83.7 ± 9.2	<0.001
c. Stem diameter (mm)				
1998	8.1 ± 0.7	5.6 ± 0.4	2.5 ± 0.7	0.022
1999	4.4 ± 0.6	3.9 ± 0.3	0.5 ± 0.3	0.187
2000	NA	3.2 ± 0.2	NA	NA
1998–2000	8.0 ± 0.7	4.7 ± 0.4	3.3 ± 0.6	0.005

d. Segments/stem (no)				
1998	1.0 ± 0.0	1.0 ± 0.0	0.0 ± 0.0	0.712
1999	3.6 ± 0.4	1.9 ± 0.1	1.7 ± 0.4	0.023
2000	25.0 ± 2.6	3.7 ± 0.5	21.3 ± 2.3	0.003
e. Segment length (cm)				
1998	64.2 ± 4.9	8.5 ± 1.5	54.5 ± 6.2	<0.001
1999	20.2 ± 1.8	9.0 ± 2.1	11.2 ± 3.0	0.021
2000	5.5 ± 0.8	15.2 ± 3.5	&9.8 ± 4.0	0.071
f. Biomass (g)				
1998	251.0 ± 122.7	14.2 ± 4.1	236.0 ± 123.6	0.007
1999	414.9 ± 219.7	34.3 ± 8.7	380.6 ± 221.4	0.013
2000 woody	659.2 ± 402.9	80.5 ± 24.0	578.6 ± 412.9	0.098
2000 leaves	351.4 ± 172.4	31.5 ± 12.0	319.7 ± 176.5	0.023
1998–2000	1717.8 ± 907.2	173.4 ± 48.6	1544.4 ± 924.9	0.029
g. N (%)				
1998	0.47 ± 0.09	0.65 ± 0.07	&0.18 ± 0.07	0.076
1999	0.60 ± 0.04	0.77 ± 0.04	&0.17 ± 0.03	0.009
2000 woody	0.87 ± 0.09	0.85 ± 0.06	0.02 ± 0.11	0.877
2000 leaves	1.80 ± 0.11	1.97 ± 0.13	&0.16 ± 0.21	0.475

Notes. Year indicates origination year for entries “a – c” and growth year for entries “d – g”. NA = not available (no stems present). Biomass and N values for 2000 woody exclude leaves; biomass values for 1998–2000 includes leaves.

TABLE 2. Effects of elk browsing on recovery (%) of willow (*Salix monticola*) stems (no/plant) and biomass (g) 3 years after simulated beaver cutting (fall 1997) inside (unbrowsed) and outside (browsed) elk exclosures ($n = 5$) in Rocky Mountain National Park, Colorado, USA. Willow plants were sampled August 29&September 7, 2000. Recovery (%) is computed as $100 \times \text{fall 2000}/\text{fall 1997}$. Differences are computed as unbrowsed minus browsed.

Year	Unbrowsed $0 \pm \text{SE}$	Browsed $0 \pm \text{SE}$	Difference $0 \pm \text{SE}$	<i>p</i>
a. Stem recovery (%)				
1998	148.4 ± 25.5	78.5 ± 21.4	69.9 ± 24.1	0.044
1998&1999	151.0 ± 26.3	106.7 ± 26.1	44.3 ± 29.1	0.203
1998&2000	151.0 ± 26.3	132.9 ± 25.9	18.2 ± 35.9	0.640
b. Biomass recovery (%)				
1998	63 ± 20	3 ± 1	59 ± 19	0.038
1998&1999	84 ± 28	6 ± 1	77 ± 27	0.046
1998&2000	93 ± 32	NA	NA	NA

Notes: Year indicates origination year for entry “a” and growth year for entry “b”. NA = not available, see *Methods*.

Resilience of willow stems after release from intense elk browsing

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Abstract

The resilience of willow (*Salix monticola*, *S. geyeriana*, *S. planifolia*) stems released from intense elk (*Cervus elaphus*) browsing in Rocky Mountain National Park, Colorado, USA, was quantified in 1998 with a retrospective study that compared biomass, number, and length of segments on willow stems located inside (protected) and outside (browsed) elk exclosures. Segment biomass increased each year after protection by about 3 – 12 g year⁻¹ on browsed stems and 10 – 27 g year⁻¹ on protected stems. The number of segments on stems was similar for browsed and protected stems in the first 2 years after exclusion but differed in the next 3 years, when they increased exponentially on protected stems. Nearly 80% of segments on browsed stems were < 5 cm in length in 1994 – 1997, which caused stems to develop a short-hedged morphology. Protected stems had more long segments and fewer short segments than browsed stems for the first 3 years, but then increased their number of short segments as stems became tall and bushy. Thus, evidence suggests short-hedged willow stems are highly resilient and can rapidly recover height and vigor after protection from intense elk browsing.

Introduction

Ecological resilience can be defined as the speed at which a system returns to a former pristine state after it has been perturbed and displaced into a degraded state (Suding et al. 2004). Stability of a new state in the absence of continued manipulation is evidence the system has moved to an alternative stable state (Beisner et al. 2003). Intense herbivory has created an alternative stable state if cessation of herbivory alone fails to restore pristine plant conditions (Laycock 1991). Thus, strong resilience of degraded plants after release from intense herbivory can indicate the absence of an alternative

stable state and a positive direction toward restoration of pristine conditions.

Willow (*Salix*) communities dominated many riparian ecosystems before European settlement of North America. Many of these communities developed degraded conditions after intense herbivory by livestock and/or native ungulates, which can congregate near water and heavily browse willows (Belsky et al. 1999, Brookshire et al. 2002). The elimination of large predators has reduced predation risk in some riparian areas, which historically prevented intense browsing of willows by large herbivores (Laundre et al. 2001, Ripple and Beschta 2004). Thus, intense browsing can dramatically reduce the extent of willow communities and suppress the height of remaining stems.

Why are tall willow stems important to riparian ecosystems? Tall willows provide shade to streams and critical habitat for a diverse array of terrestrial and aquatic species, as well as energy dissipation and sediment retention during floods (Case and Kauffman 1997, Belsky et al. 1999). Tall willows can be necessary to beaver (*Castor canadensis*) as winter food and used for construction material in dams and lodges, which can greatly benefit wetland ecosystem processes (Baker and Hill 2003). Willows can sprout new stems in proportion to the number cut by beaver (Kindschy 1985, 1989) and benefit from beaver ponds that raise the water table and improve establishment and survival processes; thus, beaver and willows are mutualists. This mutualism can be disrupted in heavily browsed environments when beaver cut tall willow stems and place regrowth within easy reach of herbivores (Baker 2003). The interaction of beaver and elk (*Cervus elaphus*) herbivory greatly reduced the height and standing crop of willow regrowth in Rocky Mountain National Park (RMNP), Colorado, USA (Baker et al. *in press*). Tall willow communities and beaver populations have both declined dramatically in RMNP where

intense elk browsing has created short-hedged willow stems that are unsuitable to beaver (Peinetti et al. 2002, Baker et al. 2004). Are short-hedged willow stems resilient to cessation of elk browsing or are they in an alternative stable state that requires more than release from elk to recover tall willow stems?

Here, we show how protection from elk browsing affected the morphology of severely hedged willow stems in RMNP. Specifically, we tested the null hypotheses that there were no differences within each of 5 segment years in the biomass, number, and length of stem segments sampled from the tallest stems within the tallest plant strata for 3 willow species (*S. monticola*, *S. geeyeriana*, and *S. planifolia*) located inside (protected) and outside (browsed) 4 elk exclosures.

Methods

Study Area

Study sites were in Horseshoe Park (elevation 2600 m), RMNP, a broad flat alluvial valley dominated by willows (*S. monticola*, *S. geeyeriana*, and *S. planifolia*), birches (*Betula* spp.), grasses, and sedges. Formerly abundant, most beaver populations declined after about 1940. Declines were likely initiated by trapping but recovery has likely been precluded by reduction in willow height and biomass due to intense elk browsing (Baker et al. *in press*). Elk were reintroduced to RMNP in 1913–1914 after nearly being extirpated by the late 1800s. Control efforts maintained the elk population at 500 until 1968, when a policy of natural regulation altered management and elk increased to ~ 3000 by the late 1990s (Singer et al. 1998). Elk utilization of riparian willows (% leaders browsed) averaged ~85% annually in 1968–1992 (Zeigenfuss et al. 1999) as the elk population increased to 6 times its 1968 level (Lubow et al. 2002). Elk were primary

browser of willows; mule deer (*Odocoileus virginianus*) use was very light and moose (*Alces alces*) were absent. The height of mature stems of *S. monticola*, *S. geyeriana*, and *S. planifolia* was 2 – 4 m in nearby areas of RMNP that received much less elk use. Tall willow cover (>2.0 m) declined by 65% in Horseshoe Park in the past 50 years and short-hedged willows (< 1.5 m) have dominated the study sites for several decades (Peinetti et al. 2002).

Experimental Design

We measured stem response on *Salix monticola*, *S. geyeriana*, and *S. planifolia* plants 4 years after cessation of intense elk browsing with a retrospective design. Biomass, number, and length of stem segments were compared for willows stems (woody located inside (protected) and outside (browsed) 4 elk exclosures (treatment replicates; RMNP exclosures 3, 4, 5, and 6). Elk exclosures (3-m-tall net wire) were constructed in August – November 1994 after randomly locating adjacent paired 30 m × 46 m plots in a short-hedged willow community located in elk winter range and randomly selecting 1 plot for exclosure treatment and the other plot as a paired control left available to elk (Peinetti et al. 2001, Zeigenfuss et al. 2002, Baker et al. *in press*). Previous studies of these plots found a shallow water table that was equally accessible to mature willow plants (Alstad et al. 1999), depth to water table had no effect on plant response to elk browsing (Zeigenfuss et al. 2002), and soil texture and N availability were similar inside and outside elk exclosures 3 years after elk exclusion (Menezes et al. 2001). These multiple lines of evidence support the assumption that plants within paired plots grew in similar environments, although factors other than elk browsing likely influenced the morphology of specific stems.

Sampling procedures were constrained to include only taller willow stems in the target population because RMNP managers were interested in recovery of tall stems as a prerequisite for restoration of the historical beaver-willow community. To exclude shorter stems we arbitrarily determined the tallest size stratum in each of the 8 plots by measuring the height of the tallest willow in the plot (any of the 3 species) and multiplying this upper bound by 0.75 to determine the lower bound of the stratum. For each of the 3 willow species in the 8 plots we selected the plant that was nearest a random point and constrained by the strata bounds. On each plant we selected either the tallest stem or the stem that was nearest the random point, if there appeared to be > 1 stem that was tallest.

Stem Measures and Statistical Analysis

The literature is controversial and inconsistent regarding plant morphology. We follow Dahl (1995) for all terms except *segment*, which we define below. Shrubs like willow typically have multiple *stems* that are distinct at ground level. *Shoot* is a collective term for the stem and leaves, or any young growing branch or twig. Shoots typically consist of repeated structural units called phytomers or metamers, which contain leaf nodes, internodes, and leaves. Shoots can be further defined as *short shoots* and *long shoots* and the tips of shoots are called *leaders*, as we explain in Discussion. It is the leaders that are typically browsed by large herbivores. Willows exhibit a sympodial branching pattern with distinct bands around the entire stem that readily separate linear growth years (Alliende and Harper 1989). We defined the stem material between these bands as *segments* or *segment years*.

At the end of the 1998 growing season (late August), selected stems were cut and

removed at ground level, their total length was measured, leaves and dead portions were removed, and the stem was cut and sorted into segment years (range 1983 – 1998). Stems were processed by beginning at leaders and working toward the base of stems to locate and cut bands and place the resulting segments into segment years or age cohorts; the number of cohorts was confirmed by counting the number of annual rings at the base of stems (Peinetti et al. 2001, Baker et al. *in press*). In this retrospective design we were unable to measure stem material lost to shoot shedding (loss of short shoots as stems age) or herbivory and we did not estimate annual radial growth as a component of segment biomass. Segment length was measured and segments were placed into 1 of 3 arbitrary classes (0 – 5 cm, 5 – 15 cm, and >15 cm) to compare proportional segment length among treatments and years. All stem segments were oven-dried at 65° C and weighed to compute biomass.

Segment biomass data were transformed to the log (biomass + 1) scale to stabilize variances and analyzed separately for each segment year as split-plot ANCOVA's in SAS (proc mixed; class block treatment species; model biomassafter = treatment | species biomassbefore / ddfm = satterth solution; random block treatment*block; /smeans treat / pdiff cl;). Exclosures and paired adjacent plots were treated as whole plots (blocks) and species were treated as sub-plots, with a total of 23 degrees of freedom in the error terms (Satterthwaite method). The variable “biomassbefore” was a covariate to account for differences in initial condition and was the sum of biomass values for segment years before the exclosures were constructed (segment years ≤ 1994); the variable “biomassafter” was the biomass of a particular segment year after the exclosures were constructed. Segment number data were transformed and analyzed with the same

procedures, with number of segments before the exclosures were constructed (segment years \leq 1993) as the covariate. Segment length data were converted to proportions to symmetrically relate differences among treatments and years; proportions were transformed to the arcsine ($\sqrt{\text{proportion}}$) scale to normalize data. Transformed proportion data were analyzed same procedures, with the proportion of segments in each length class as the covariate (segment years \leq 1993). Each length class and segment year combination ($n = 15$) was analyzed with a separate ANOVA. Repeated measures analyses were not used for response variables because variance changed greatly across time and because explicit comparisons across time were of no interest.

Results

Segment biomass

Test results for treatment \times species interactions for segment biomass by year were $P = 0.813$ for 1994, $P = 0.158$ for 1995, $P = 0.463$ for 1996, $P = 0.218$ for 1997, and $P = 0.832$ for 1998. Thus, segment biomass results are reported for combined species because we found no evidence that treatment effect depended on willow species.

Willow stems inside exclosures rapidly increased segment biomass following release from intense elk browsing (Fig. 1a). Biomass of protected stems increased by 20 – 30 g/year for the first 3 years (1994 – 1996) then by 10 – 20 g/year for the next 2 years (1997 – 1998). In contrast, biomass of browsed stems increased by only 5 – 10 g/year in 1994 – 1997, likely because elk removed current annual growth during winter browsing. Segment biomass inside and outside exclosures did not differ in 1998, likely because we had removed stems for analysis *before* elk had returned to winter ranges. Taken together these results suggest browsed stems at least partially compensated for

biomass removed during the previous winter, but that a large amount of new growth was subsequently removed by elk during winter browsing. Most browsing occurred in November – April when elk densities in Horseshoe Park were 30 – 64 elk km⁻², although some browsing could occur in any month (Singer et al. 2002).

Segment number

Test results for treatment × species interactions for segment number by year were $P = 0.524$ for 1994, $P = 0.868$ for 1995, $P = 0.587$ for 1996, $P = 0.935$ for 1997, and $P = 0.823$ for 1998. Thus, segment number results are reported for combined species because we found no evidence that treatment effect depended on willow species.

The number of stem segments on browsed and protected stems were relatively similar for the first 2 years after protection from elk (1994, 1995), but then differed greatly in later years (1996 – 1998; Fig. 1b). Differences were greatest in 1997 and 1998, when protected stems developed a tremendous pulse of new segments.

Segment length and stem length

Treatment × species interactions for segment length by class by year were not significantly different ($P > 0.050$) for 14 of 15 ANOVA's (3 length classes × 5 years). We did find a significant species effect ($P < 0.001$) for year 1998, length class > 15 cm, however, the effect was due to variation in magnitude among species rather than variation in direction (browsed length was > protected length in all species). Thus, segment length results are reported for combined species because we found little evidence that treatment effect depended on willow species.

How did segment length differ on browsed and protected stems? In 1994 – 1997, nearly 80% of segments on browsed stems were < 5 cm in length, with relatively few

segments > 15 cm in length (Fig. 2 a – d). There was a greater number of longer segments, especially segments > 15 cm in length, and fewer shorter segments on protected stems than on browsed stems in 1994 – 1996, but in 1997 these differences had disappeared (Fig. 2d). For segment year 1998, browsed stems had a higher proportion of segments >15 cm in length than protected stems (Fig. 2e), likely because we removed stems before winter elk browsing reduced leader length and because there were fewer stems < 15 cm in length in 1998 than in previous years. Over 80% of segments on protected stems were < 5 cm in length in 1998 (Fig. 2e), whereas short segments comprised only about 10 % of segments in the first 2 years after protection (Fig. 2a and 2b). The mean height of entire stems before they were cut into segments was 2.2 m (SD = 0.2) for protected stems and 1.3 m (SD = 0.3) for browsed stems. These patterns suggest that stems responded to protection from elk browsing by growing much taller and increasing the production of short segments on tall stems as plants matured and became highly branched or bushy. Patterns for browsed stems showed proportional lengths were similar among years, however, length patterns were difficult to interpret on browsed stems because both elk browsing and plant growth affected segment length.

Discussion

Retrospective measurements of stem segments made 4 years after cessation of winter elk browsing showed severely hedged willow stems (*S. monticola*, *S. geyeriana*, and *S. planifolia*) produced longer stem segments that resulted in taller stems, which produced many more, but shorter segments as stems aged. These morphological changes greatly increased segment biomass of protected willows relative to stems that remained available to elk, especially during the first 3 years after protection. In contrast, stems that

remained outside elk exclosures accumulated a relatively small number of segments and segment biomass as winter browsing by elk removed current annual growth and maintained willow stems in a suppressed short-hedged (< 1.5 m tall) morphological state. Thus, we found strong evidence that hedged willow stems were not in an alternative stable state but rather were highly resilient after release from intense elk browsing (treatment effect), despite the small sample size ($n = 4$) of this experiment. However, evidence for population estimates and estimates indicating lack of treatment effects due to willow species were weak because our design lacked replication at the within-plot scale.

Effects of Browsing on Willow Stem Morphology

How does browsing by elk or other large herbivores affect the morphology of willow stems? Browsing removes tissue from the tops of stems (leaders) and plants can respond by shunting carbon stores from roots to shoots (new growth), increasing leaf N, photosynthetic rate, and growth rate, diameter near the bite, and branching (Danell et al. 1994, Hobbs 1996, Honkanen and Haukioja 1998, Strauss and Agrawal 1999). Willows can largely compensate for biomass lost to winter browsing by increasing productivity of browse-damaged stems (Wolff 1978, Hjalten 1999, Peinetti et al. 2001).

The stems of willows and many other plants contain both long and short shoots (Del Tredici 2001;), which affects stem morphology and response to browsing (in this paper the term shoot includes only new growth whereas the term segment includes any age cohort separated by nodes on stems). Short shoots lack lateral branches and are more prevalent on older stems that exhibit fourth or fifth order branching. The presence of numerous short shoots at the tips of mature, unbrowsed stems gives stems a full and soft

appearance. Browsing frequency can be high on willows because regrowth rapidly becomes suitable as elk forage, although sexual reproduction can be eliminated and fitness can be reduced (Kay 1994). Thus, repeated browsing can create productive but short-hedged plants with all stems in reach of elk.

Release of Willow Stems from Elk Browsing

What mechanisms likely explain the patterns we observed when severely hedged willow stems were released from elk browsing? We found that protected stems had many more long segments (> 15 cm) and many fewer short segments (< 5 cm) than did browsed stems in 1994 and 1995 (Fig. 2), which suggests stems initially responded to cessation of browsing by elongating existing shoots. This pattern reversed in 1997 and 1998 when $> 80\%$ of segments were < 5 cm in length, which is consistent with the expected pattern of fewer long shoots and more short shoots on stems that exhibited fourth and fifth order branching. These segments were small enough (< 3 mm in diameter) to be entirely consumed by beaver (Baker and Cade 1995), which suggests released stems were suitable as beaver food after 4 years of protection from elk. Browsed stems were largely comprised of short segments in all years, although 1998 had relatively more segments > 15 cm in length because we removed stems before winter elk browsing could remove current annual growth. We suggest caution in relating our segment length data to shoot morphology patterns as we did not attempt to distinguish between long and short shoots on stems; thus, our short stem segments may have been either morphologically short shoots or long shoots that had been browsed shorter by elk.

Restoration and Management Implications

Evidence from this study suggests that willows are highly resilient to cessation of

browsing and managers can restore tall willow stems simply by protecting short-hedged stems from further herbivory. In an Oregon study, removal of livestock with and without removal of wild ungulate browsing resulted in dramatic regrowth of existing willows in both cases, but continued ungulate browsing significantly suppressed recovery of willow height, crown area, crown volume, biomass, and sexual reproduction (Case and Kauffman 1997). The strong resilience of willow stems after release from intense herbivory suggests that some degraded riparian ecosystems have not reached alternative stable states (Beisner et al. 2003). Other degraded sites that have lost critical willow establishment and survival processes do not respond well to release from browsing, such as in areas of Moraine Park, RMNP, where loss of beaver dams caused a drop in the water table and the subsequent death of willow plants (Gage 2003, B. W. Baker unpublished data).

How can land managers recover tall willow communities and beaver-willow mutualisms in heavily browsed environments? Redistribution of herbivores in combination with reduced stocking rates or population control may be necessary to reduce willow use, which can remain high under a wide range of herbivore densities (Belsky et al. 1999, Zeigenfuss et al. 1999). Exclosure fencing or riparian pastures to protect willows from large herbivores must be large enough to meet management objectives. In RMNP, ecological modeling suggests elk exclosures along streams must be at least 5 ha in size to sustain a beaver colony comprised of 6 individuals (H. R. Peinetti unpublished data). In Moraine Park, RMNP, beaver colonized a series of 4 small elk exclosures (30 × 46 m) 5 years after their construction and clear-cut tall willows from a single exclosure in each of 4 successive years, but could not be sustained by the

exclosures alone (Baker, B. W. personal observation). Herding livestock to protect riparian willows has been effective on western rangelands, and may have application for native ungulates in park settings. 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* spp.) recruitment, which suggests elk had lost their fear of browsing in riparian areas (Beschta 2003). After wolf reintroductions, areas with higher predation risk, such as those with low visibility or presence of escape barriers, had young cottonwood that were taller and less browsed by elk (Ripple and Beschta 2003). Thus, recovery of tall willow in heavily browsed environments may require some difficult and controversial decisions.

In conclusion, we found willow stems were strongly resilient to release from intense elk browsing. Protected stems (inside elk exclosures) rapidly increased in biomass and length for several years and then increased number of short segments stems aged, morphological changes which resulted in tall and vigorous stems after 4 years. Hedged stems that remained available to elk were productive but gained little biomass and height each year as winter browsing removed current annual growth. We suggest future research investigate the response of entire plants to release from browsing, including stem turnover rate relative to segment elongation rate.

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Figure Captions

Fig. 1. Comparisons (mean and SE) of segment biomass (a) and segment number (b) on willow stems (*S. monticola*, *S. geeyeriana*, *S. planifolia*) located outside (browsed) and inside (protected) elk exclosures ($n = 4$) in Rocky Mountain National Park, Colorado, USA. Exclosures were constructed in fall 1994 and stems were sampled in late August 1998, thus year 1998 represents segments that had not been browsed by elk during the 1998/1999 winter season. Probability values based on transformed data (see Methods).

Fig. 2. Comparisons of the proportion of segments in 3 length classes on willow stems (*S. monticola*, *S. geeyeriana*, *S. planifolia*) located outside (browsed) and inside (protected) elk exclosures ($n = 4$) in Rocky Mountain National Park, Colorado, USA. Exclosures were constructed in fall 1994 and stems were sampled in late August 1998, thus year 1998 represents segments that had not been browsed by elk during the 1998/1999 winter season. Probability values based on transformed data (see Methods).

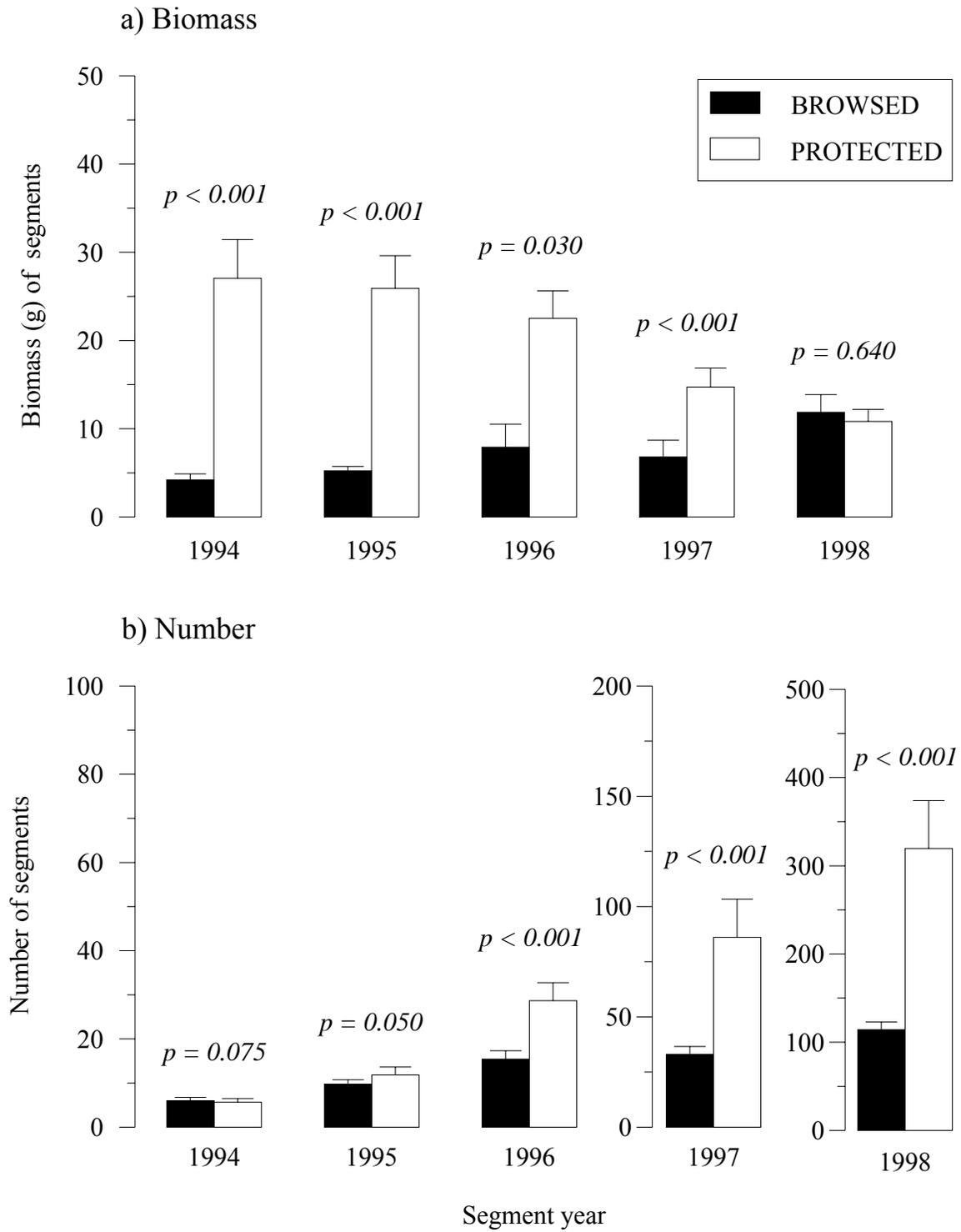


Figure 1.

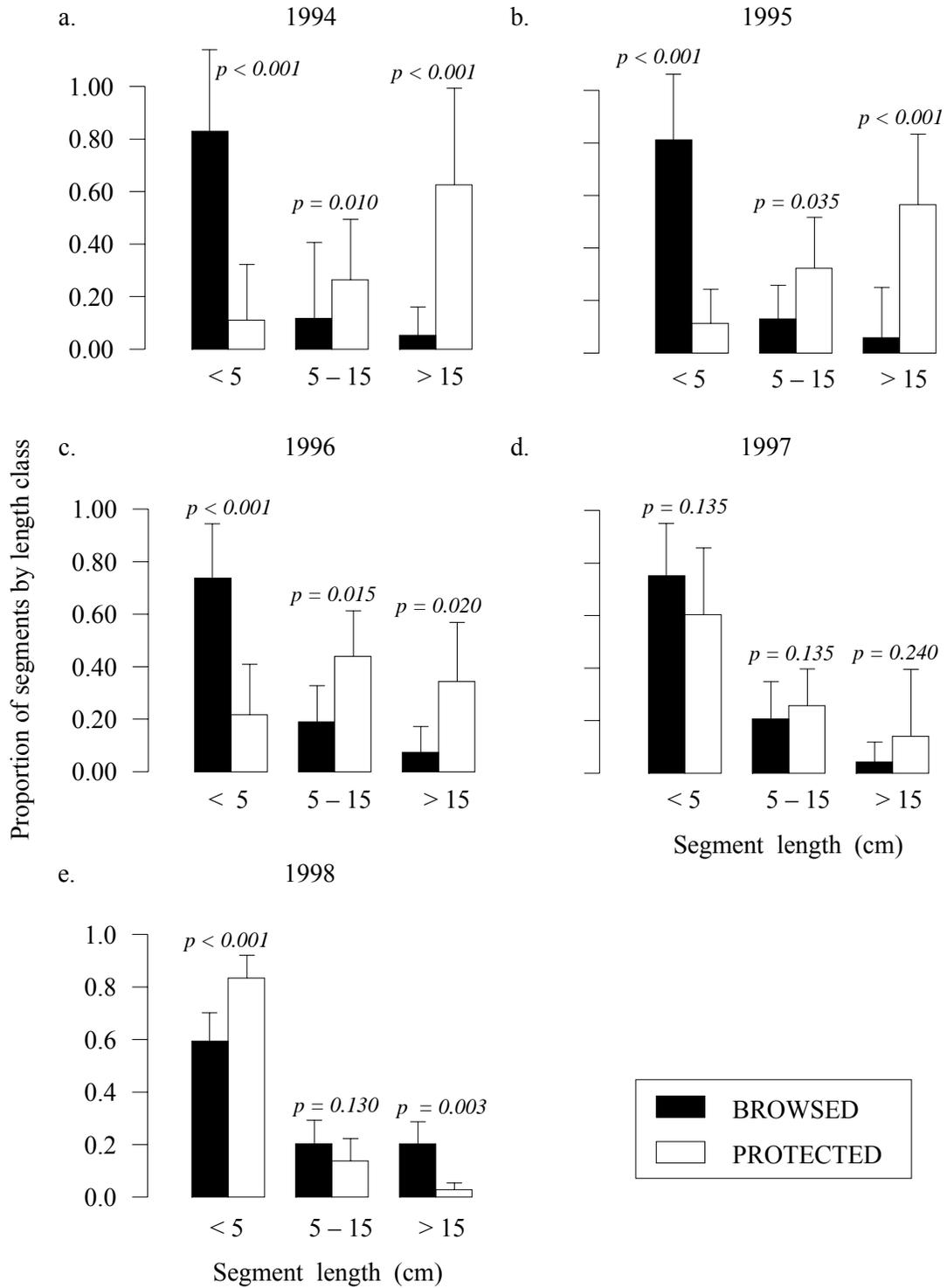


Figure 2.

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Efficacy of tail-mounted transmitters for beaver

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Key words: beaver, *Castor canadensis*, radio transmitter, radiotelemetry, Rocky Mountain National Park, telemetry, transmitter

Beaver (*Castor canadensis*) are semi-aquatic mammals that usually spend daylight hours inside lodges or bank dens and may be confined under the ice in ponds during winter, characteristics which make radiotelemetry very useful for life history studies (Baker and Hill 2003). Neck collars are not suitable because beaver have fusiform bodies with thick necks that cause collars to easily fall off. Intraperitoneal implantation of transmitters (implants) has been the method of choice since first used for beaver in the 1980s, but they also have problems. Implants require surgery via a dorsal (Davis et al. 1984), ventral-lateral (Wheatley 1997), or ventral-midline (Ranheim et al. 2004) incision. Surgery can increase mortality rates and cause logistical and ethical concerns. The signal range of implants is less than external transmitters because the body attenuates the signal and because the coiled antennas used for implants are less efficient than external whip

antennas. Thus, external transmitters may be more desirable than implants, if a successful attachment method can be found.

Beaver have large, flat tails composed of dense adipose tissue, a central tailbone, and tough, scaly skin. Tails vary greatly in size among and within individuals, depending on their age and condition. Collars placed around the base of tails are problematic because they can slip off narrow tails or tails that decrease in size following attachment (Bruce W. Baker unpublished data). Rothmeyer et al. (2002) developed a new tail-mounted radio transmitter for beaver using a modified livestock ear tag that was attached via a hole drilled through the tail. Comparisons among implants, tail collars, and modified ear-tag transmitters showed that modified ear-tag transmitters had the greatest efficacy in their study of translocated beaver in Wyoming. But they also found the average retention time of modified ear-tag transmitters (hereafter tail-mounted transmitters) was only 104 days (range 5 – 503 days). Because these transmitters were recovered from upland sites, they suggested translocated beaver that lacked established ponds and lodges may have had higher predation rates and greater opportunity for transmitters to be torn from the tail (McKinstry and Anderson 2002, Rothmeyer et al. 2002). Thus, transmitter retention time should be longer in studies of resident beaver.

Here, I evaluate the efficacy of tail-mounted transmitters in a life history study of resident beaver at Rocky Mountain National Park (RMNP), Colorado.

Study Area

Beaver populations in RMNP declined dramatically in the 1940s and have failed to recover since then. A beaver life history study was initiated in August 2001 to help explain these patterns, in addition to concurrent beaver habitat studies (Baker et al. *In*

press). Willow (*Salix monticola*, *S. geyeriana*, *S. planifolia*) dominated most of the active beaver sites, which included Wild Basin, Boulder Brook, Hollowell Park, Big Thompson River, and Endo Valley. Beaver were largely absent from Moraine Park, Horseshoe Park, and Beaver Meadows where intense elk (*Castor canadensis*) browsing had severely hedged willow plants. The exception was a single beaver colony that persisted in Moraine Park within and near several elk exclosures. Most beaver territories included several lodges, bank dens, dams, and ponds. Ponds and most stream sections were covered with ice during November – March. The terrain was very mountainous with steep ridges that separated east-west trending valleys.

Methods

Thirty-four beaver were trapped in Hancock and box (1 kit, 1 adult) traps from streams on the east slope of the continental divide, which likely represented 80 – 90% of the east slope population in RMNP. Transmitters were attached to the tail using the methods provided by Rothmeyer et al. (2002), with some modifications. Instead of using a capture pole to restrain beaver, beaver were placed inside burlap sacks before removal from Hancock traps by working a sack through the gap at the back of the trap. Sacked beaver were removed from the trap, weighed, and the tail was exposed while someone gently kneeled over the beaver to prevent movement. A second person used a large caliper to locate a spot on the tail that (1) equaled the 10 mm depth of the transmitter attachment post or was the thickest spot available on thin tails and (2) was the greatest distance from the edge of the tail, nearest to the base of the tail, and not within 3 cm of the midline to avoid the tail bone and blood vessels. A 5 mm diameter hole was drilled through the tail with a sterilized bit and anesthetic/analgesic was applied to the post and

hole to prevent infection and ease pain during healing. Injected analgesic was not used before drilling because the adipose tissue of the tail was too dense to absorb liquid. A Passive Integrated Transponder (PIT) tag was placed under the skin on the back about 2 cm anterior to the dorsal surface of the tail base. A foam spacer was glued to some transmitters when the available tail area was too thin to fill the transmitter post depth. Blood samples were drawn via a blind stick method on the dorsal surface of the tail 1 – 2 cm posterior to the hairline and 3 – 5 mm lateral to the midline. Blood was lab-tested and found negative for tularemia (*Francisella tularensis*) and plague (*Yersinia pestis*), and was used to develop a new genetic method of gender determination for beaver (Williams et al. *In press*). Beaver gender was determined in the field via anal gland secretion (Schulte et al. 1995) and palpation for the baculum, and later confirmed or corrected (in 4 cases) in the lab via the new genetic method (19 male, 15 female). Body mass was used to separate the 34 captured beaver into 2 age classes for this analysis; body mass was 3.2 – 5.2 kg for 12 kits (< 1 year) and 8.6 – 22.3 kg for 22 adults (> 1 year). Kits also had much smaller tails than adults. All beaver were processed and released at capture sites, which took 30 – 60 minutes/individual.

Transmitters were made by Advanced Telemetry Systems (ATS, Isanti, Minnesota) and were 2 different sizes (Fig 1). Large transmitters (Model M3530) were similar to those used by Rothmeyer et al. (2002) and had pulse rate of 40 pulses/minute (ppm), a weight of 36.5 g with the attachment post, and an expected battery life of 558 days. Large transmitters had a mortality switch (pulse rate 80 ppm) that engaged after 6 hours without movement and an activity switch (pulse rate varied with activity level) that engaged when transmitters were moving. A smaller transmitter (Model M3520) was

designed by ATS after a large transmitter tore from the tail of a 3.2-kg kit only 2 days after attachment. Small transmitters were attached only to kits and had a pulse rate of 40 ppm, a weight 18.8 g with attachment post, an expected battery life of 349 days, a 12-hour duty cycle, a 6-hour mortality switch, and no activity switch. The dimensions (thickness \times width \times length) were $6 \times 7 \times 7$ mm for small transmitters and $6 \times 11 \times 18$ mm for large transmitters; their attachment systems were identical.

During 13 August – 20 November 2001, transmitters were attached to 34 first-captured beaver and 7 recaptured beaver after transmitters had torn loose in Hancock traps or the hole in the tail had enlarged and the transmitter was moved to a new spot on the tail. Observers used 3- or 4-element hand-held Yagi antennas to locate signals, usually once or twice weekly, from 13 August 2001 to 6 August 2003; date, time, signal location, and signal type (inactive, active, or mortality) were recorded. If a mortality signal was received, then observers attempted to recover the radio and determine the outcome. No attempt was made to recover radios that were deep inside active beaver lodges because digging into active lodges would cause beaver to temporarily or permanently abandon lodges and increase their risk of predation, which could affect beaver mortality and dispersal data. If active lodges became inactive, and transmitter signals came from the edge of lodges, then transmitters were recovered with minimal disturbance to lodges. Thus, the cause of mortality signals located inside most beaver lodges could not be confirmed as either detached transmitters or dead beaver. Transmitter retention time was calculated by taking the difference between the attachment date and the midpoint between (1) the last date an active or an inactive signal was detected and (2) the first date a definite mortality signal was detected.

Results

Tail-mounted transmitters were very easy to attach to beaver at the capture site using the methods provided by Rothmeyer et al. (2002) and some modifications. Most beaver were docile while in the burlap sack and did not react to the drill or transmitter attachment except to try to move forward in the sack. A few beaver struggled to escape. One adult male that appeared healthy in the trap died unexpectedly during processing and 1 adult female that appeared distressed in the trap died shortly after release from rapid processing, but necropsies were inconclusive regarding cause of death. A fixed-length attachment post relative to highly variable tail dimensions resulted in attachments that were sometimes close to the edge of tail or were loose on thin tails. The foam backing that was used to create a tighter fit on some thin tails was either worn away or water-logged and compressed on recovered transmitters, which suggests it was an ineffective modification.

The 41 transmitter attachments had the following outcomes. One transmitter was found after 119 days at an upland site where tracks and drag marks in the snow indicated coyote (*Canis latrans*) predation on the adult beaver. One transmitter was found after 332 days still attached to an adult beaver inside a bank den, which had died of unknown causes. One transmitter failed after 94 days when the signal clicked and then quit and 1 transmitter failed after 499 days when the signal weakened and then quit. One large transmitter was removed by observers after 5 days on a kit and replaced with a small transmitter and 1 transmitter was moved to a new location on the tail after 32 days because the attachment hole in the tail had become enlarged. Four of 20 beaver that were recaptured in Hancock traps after 1, 33, 49, and 55 days had transmitters that became

detached during capture; all transmitters were reattached to a different location on the tail. One transmitter switched to mortality mode after 130 days, but power line interference with the signal precluded recovery and outcome confirmation. Nine transmitters switched to mortality mode after 9, 15, 41, 76, 86, 200, 224, 239, and 278 days, but recovery and outcome confirmation were precluded because signals came from inside active beaver lodges. Twenty-one transmitters that switched to mortality mode were confirmed as detached from the tail without evidence of beaver mortality, either when transmitters were recovered (20 cases) or the beaver was recaptured without its transmitter (1 case).

Nineteen of 21 transmitters became detached before they reached their expected battery life (Fig. 1). Retention time averaged 96 days and 41 days for 4 small and 4 large transmitters, respectively, on 8 kits, and 276 days for 13 large transmitters on adults. None of the 4 large transmitters on kits were retained > 60 days. Two small transmitters were retained on kits for 159 days, which was still less than half of their expected battery life of 349 days. Two of 13 large transmitters on adults were retained and still functional about 2 months longer than their expected battery life of 558 days; in contrast, 2 others were retained only 6 and 16 days.

Recovered transmitters were found inside bank dens, at the edge of beaver lodges, in stream channels, on beaver dams, or in food caches. Where transmitters were recovered in beaver lodges and bank dens, they were usually found near or within a tangled mass of beaver-cut sticks that often lined the entrances. Transmitters were often found by probing burrows with a hand or a stick to attempt to move the transmitter and switch the signal from mortality mode (80 ppm) to active or inactive mode. Small

transmitters lacked activity switches and were much more difficult to recover because after they were moved once further movement did not change the signal. Large transmitters had activity switches that increased pulse rate each time they were moved, which made them much easier to find within confined underground burrows and lodges.

The condition of recovered transmitters varied greatly and sometimes revealed how they became detached (Fig. 2). Entire antennas were missing and likely chewed-off on 11 of 18 detached transmitters (Fig. 2 A – K; 2 recovered transmitters missing) and antennas were intact on 7 others (Fig. 2 L – R). The post and button attachment system was intact on 11 of 18 detached transmitters (Fig. 2 A, F – N, Q – R), which indicates they likely became detached when the hole in the tail enlarged or the tail tore from the attachment hole to the edge. The button portion of the post, which prevented the post from pulling through the attachment hole, was partly or completely missing on 3 detached transmitters (Fig. 2 D, E, P). The transmitter base plate was broken on 1 detached transmitter (Fig. 2O) and chewed-off on 1 detached transmitter (Fig. 2C). The 2 transmitters that remained attached until the beaver's death both had missing antennas (Fig. 2 A – B); the attachment system was intact but the epoxy had been broken by biting, likely by a coyote, on 1 transmitter (Fig. 2A; coyote predation) and the attachment button was partly broken on 1 transmitter (Fig. 2B; unknown cause of death).

Signal detection distance varied due to location of the beaver, topography, and presence or absence of the transmitter antenna. Most radiotracking occurred during daylight hours when beaver were in burrows or lodges, which usually attenuated signals and reduced range to 100 – 200 m. Signal range was also reduced by about one-half when antennas were chewed-off by beaver. Maximum signal range was 1 km when observers

on the ground were elevated by topography (< 200 m), transmitters were outside of burrows, and transmitter antennas were intact. Although the terrain was very mountainous most beaver stayed within relatively small territories in separate valleys, which facilitated radiotracking.

In spite of the problems encountered with tail-mounted transmitters, the use of telemetry yielded knowledge that was not evident from previous field studies. For example, biologists in RMNP have historically estimated beaver population size by multiplying the number of active lodges by 6 individuals. Radiotracking data from this study suggested this method likely overestimated population size, as telemetry confirmed active lodges contained 1– 6 individuals and multiple active lodges or bank dens were often used by the same individual (B. W. Baker unpublished data).

Discussion

Tail-mounted transmitters on beaver were easy to attach and the signal range was good with intact antennas, but antennas were missing and likely chewed-off by beaver on 13 of 20 recovered transmitters. Transmitters had much shorter than expected retention time, which was less than expected battery life in 19 of 21 cases and less than 60 days in 8 of 21 cases (Fig. 1). The outcome was uncertain for 9 transmitters that emitted mortality signals from locations that prevented transmitter recovery, such as active beaver lodges.

Rothmeyer et al. (2002:427) found retention time averaged 104 days for 44 beaver in Wyoming and suggested that “low retention times and high variance were due to the high mortality of translocated beavers (36%).” Beaver in their study weighed 2.7 kg – 25.8 kg, which was similar to the 3.2 – 22.3 kg weight of kits and adults in this

study. Retention time for the combined kit and adult data ($n = 217$) in this study averaged 197 days, about twice as long as their Wyoming study. Radiotracking data in this study showed most beaver were residents that had small territories of < 2 ha and used multiple lodges and bank dens. The only exception was an adult male beaver that dispersed about 7 km downstream of its capture site, which may not have been found without the stronger signal strength of tail-mounted transmitters. Recovery of detached transmitters showed that established lodges and bank dens contained a large number of protruding sticks and roots within confined spaces, which provided ample opportunities for transmitters to catch and tear free of the tail. Data from this study supports the assumption of Rothmeyer et al. (2002) that transmitters found detached in upland sites are likely predation events and transmitters found detached in wetland sites likely represent tear-outs from live beaver.

The inability to recover some transmitters that emitted mortality signals from inside active lodges was frustrating. A major objective of the study was to determine the rate and cause of beaver mortality. A transmitter in mortality mode with an unknown cause was a failure to meet this objective, which occurred in 9 cases when signals came from inside active beaver lodges. In addition, the high incidence of false mortality signals led observers to suspect that all mortality signals from dens and lodges were the result of detached transmitters. This assumption was incorrect in 1 case when mortality signals from a bank den eventually led observers to find a dead beaver within the formerly active bank den. Observers also had other difficulties interpreting mortality signals. Sometimes observers recorded a series of inactive or active signals from beaver insides lodges for several weeks, then 1 or more mortality signals on successive visits, then back to inactive

or active signals. In some cases it appeared that mortality switches were triggered by beaver that had not moved for > 6 hours, and in other cases it appeared detached transmitters on mortality mode were bumped by beaver moving inside lodges that caused transmitters to reset back to inactive or active mode. In some cases beaver appeared to move inside lodges as observers approached, which triggered a change in signal. Unfortunately, these assumptions were impossible to confirm. Beaver in this study had been implanted with PIT tags, but it was not possible to identify the tag on a live beaver or use other cues to positively identify beaver observed after transmitters had detached. However, in a Massachusetts study observers visually confirmed active beaver with similar tail-mounted transmitters in mortality mode (Kiana Koenen personal communication). The use of implants for beaver would largely solve the problem of false mortality signals if they included a thermistor to detect loss in body temperature when animals die (Chris Kochanny personal communication).

What modifications might improve transmitter retention and function? Rothmeyer et al. (2002) suggested several ideas based in part on preliminary results from this study, including a bolt inside a hollow sleeve to reduce enlargement of the attachment hole. The condition of recovered transmitters in this study suggests some additional ideas. A steel tube to encase the antenna wire near the transmitter, or thicker antenna wire, might prevent beaver from chewing off the entire antenna, as they did with 11 transmitters in this study. A bolt, washer, and nut would permit transmitter attachment to thicker portions of the tail and a tighter fit, which might reduce transmitter loss due to broken plastic posts and to tear-outs. This attachment method was successful for 2 Eurasian beaver (*Castor fiber*) in Norway (Sharpe and Rosell 2003). A 2003 version of the Model

M3530 transmitter used an adjustable depth attachment post with promising results in Massachusetts (Chris Kochanny, ATS, personnel communication). In 2004, the National Wildlife Research Center (USDA/APHIS/WS) was testing several different transmitter designs via captive and non-captive beaver (Wendy Arjo personnel communication). Thus, others continue to search for more effective tail-mounted transmitters for beaver.

In conclusion, tail-mounted transmitters for beaver had some success in this beaver life history study but are not recommended for long-term monitoring without significant modifications to the original design. Hopefully, the efficacy of tail-mounted transmitters will improve as successive versions are developed because the flat tail of a beaver is a very convenient place to attach a transmitter.

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Figure Legend

Figure 1. Retention times for 21 tail-mounted transmitters confirmed as detached from the tails of beaver without evidence of mortality. Expected battery life was 349 days for small transmitters and 558 days for large transmitters. Most large transmitters were retained longer than most small transmitters, but no small transmitters were placed on adult beaver.

Figure 2. The condition of 18 recovered transmitters varied greatly and sometimes revealed how they became detached from the tails of beaver. Transmitter's A – B were retained until death by predation (A) or unknown causes (B) and transmitter's C – R detached from the tails of beaver without evidence of mortality. Transmitter's K, Q, and R were small-sized models placed only on kits and the others were large-sized models placed on adults and some kits. Transmitter's D, E, and P were inverted to show the broken attachment button. Transmitter R was inverted to show the compressed and torn foam backing (just above the address label) used as a spacer on thin beaver tails.

Beaver as Hydrological and Ecological Drivers of Mountain Valley Functioning

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Research Goals

The goal of this research is to explore the interactions of beaver with floodplains. We focus on beavers as hydrological and ecological drivers of floodplain functioning in mountain valleys by intensively studying beaver dams in the headwaters of the main river in southwestern North America, the Colorado River. There are three objectives in this research, and each is described below.

1. The first research objective is to compare and contrast the influence of beaver versus floods on floodplain hydrological processes over several years for a broad section of the upper Colorado River valley.

Floodplains are ecosystems distinct from rivers and uplands [Mertes, 1997; Naiman and Decamps, 1997; Thoms, 2003], and are often considered seasonal or permanent wetlands because of regular flooding and water tables that are frequently close to the soil surface [Hill, 2000; Kroes and Brinson, 2004]. Complex interactions among groundwater, river water, direct precipitation, and tributary inflow from adjacent hillslopes govern floodplain water table dynamics [Winter, 1995; Moorhead, 2001; Burt et al., 2002a]. Any soil above the water table is likely to stay near saturation because of low topographic relief and the upward extension of the capillary fringe [Gillham, 1984; Burt, 1995]. Groundwater levels often decrease over the summer months due to the combined effects of evapotranspiration by riparian vegetation, reduced inputs from adjacent hillslopes, and lower river stage. In many montane areas, groundwater levels may not recover until the following spring because snowmelt dominates streamflow and is also provides recharge for hillslope aquifers. Knowledge of floodplain water table dynamics is essential as the hydrological environment controls habitat diversity [Naiman et al., 2000], biocomplexity [Ward, 1998; Boulton et al., 1998; Amoros and Bornette, 2002; Wright et al., 2003], and biogeochemical transformations [Triska et al., 1993; Brunke and Gonser, 1997; Hedin et al., 1998; Takatert et al., 1999].

The mode of floodplain inundation and recharge of alluvial aquifers is critical for scientists to understand in managing river corridors and watersheds. The flood-pulse concept describes the movement of water from the river to the floodplain [Junk, 1989]. The concept has been expanded recently to consider the antecedent floodplain conditions [Mertes, 1997], and needs to be further modified for arid regions where overbank flows occur only in large flow years. River water can be transferred from the channel to the floodplain through increased infiltration into underlying alluvial aquifers, depending on the relative positions of the stream stage and groundwater tables, and/or by overbank flooding [Winter, 1995; Mertes, 1997; Chen and Chen, 2003]. Alluvial rivers such as those found in Rocky Mountain watersheds are commonly losing streams, and soil water and groundwater recharge in the riparian areas may depend primarily on overbank flood events [Stanford and Ward, 1988]. However, recent work has focused on the

role of riparian zone in attenuation of flood waves [Whiting and Pomeranets, 1997] rather than water table dynamics [Vekerdy and Meijerink, 1998; Burt et al., 2002a,b].

In addition to floods, beaver (*Castor canadensis* Kuhl) can also control floodplain hydrological processes in many river systems. Beaver-induced alterations to drainage networks are not unusual or localized. Populations were greatest in the early 19th century [60-400 million: Seton, 1929], extirpated from many watersheds before 1900, and are rapidly increasing today. Their historic range in North America is estimated at 15 million km² in nearly all streams, ranging from the arctic tundra to northern Mexico [Naiman et al., 1988]. Beaver dams can alter stream stage and therefore control the exchange of water between stream channels and riparian wetlands [Woo and Waddington, 1990; Lowry and Beschta, 1994; Zav'yalov and Zueva, 1998]. In headwater systems where hillslopes abut the channel the main hydrological response to beaver dams will be the formation of an upstream pond that causes elevated groundwater levels within the pond's vicinity [Naiman et al., 1988]. However, this conceptual model may under-predict the hydrological effects of beaver in systems where floodplains are wide but rivers are small enough to be impounded. In such systems beaver often build canals and dams on the floodplain to further spread and redirect water so they can access new foraging areas [Baker and Hill, 2003]. Because beaver populations are currently increasing over much of their former range due to harvesting regulations and re-introduction programs [Naiman et al., 1988; Baker and Hill, 2003], it is essential to understand their potential effects on rivers and floodplains.

Overbank flooding and beaver damming are two key hydrological processes that can regulate floodplain water table dynamics, however their effects have not been directly compared. The objective of this paper is to compare the influence of flooding vs. beaver effects over several years on mountain valley hydrological processes. We hypothesize that:

- 1a. Water levels downstream of beaver dams will be higher than the stream surface. 1b. Beaver, by building cross-channel dams, will inundate terraces while overbank flood events will inundate the floodplain.*

2. The second research objective is to determine how beaver contribute to mountain valley fluvial landform development.

Beaver are thought to be historically critical to the formation and functioning of mountain valleys [Cottrell, 1995]. Ruedemann and Schoonmaker [1938] hypothesized that since the last glaciation layer upon layer of sediment-filled beaver ponds caused valley floors to aggrade creating horizontal plains. The resulting landforms allowed water to spread widely establishing extensive wetlands and willow thickets. Recently, Meentemyer and Butler [1999] and Bigler et al. [2001] provided empirical evidence that these processes occurred in Glacier National Park, Montana. However, these studies were conducted on small streams where dams stayed intact for decades to centuries. In stream environments with high energy it is more likely that cross-channel dams would breach during spring peak flows, resulting in sediment collected behind dams being carried downstream by flood waters. The importance of beaver in creating landforms in such systems may lie in the ability of in-channel beaver dams to divert water from streams onto mountain valley floors, particularly during low flows. The resulting vertical accretion of sediment on the floodplain, as stream water follows new flowpaths, could create landforms on the valley floor.

As stream water is advected across the floodplain, nutrients are transported with the sediment through transient sorption [Triska, et al., 1994]. The flooded conditions on the valley floor create favourable conditions for anoxic biogeochemical transformations [Naiman et al., 1988, 1994; Triska et al., 2000]. Songster-Alpin and Klotz [1995] showed that flooding can promote higher microbial activity in these areas as deposition of fine-grained sediments create more surface area per sediment mass for microbial colonization. Drying of soils after beaver dams are breached and floodplain water levels decline may result in sequestration of bio-available nitrogen and phosphorus that may be released on re-wetting [Schotz et al., 2002].

As floodwaters recede, sediments deposited on the floodplain can quickly become firmly bound together by the roots of grasses [Ives, 1942]. Plants from the family *Salicaceae* (*Salix* spp. and *Populus* spp.)

are also believed to be key players in the colonization and stabilization of riparian landforms [Gurnell *et al.*, 2001]. (NOTE: we are still finalizing ideas for this section).

The development and maintenance of mountain valleys is a complex product of hydraulic and sediment transfer processes coupled with vegetation colonization and growth [Gurnell, 1995] that can be regulated in part by beaver activities. The transport of sediment and its associated nutrients from rivers to riparian zones have been emphasized in the geomorphological literature during floods [Pinay *et al.*, 1995; Steiger and Gurnell, 2002]. However, no studies have investigated the ability of beaver to control sediment and nutrient diversion onto the floodplain [Gurnell, 1998]. Further, there have been no studies investigating the ability of beaver to create landforms capable of supporting willow establishment on the floodplain in high energy stream environments. It is hypothesized that:

2a. In-channel beaver dams cause vertical accretion of sediment on the floodplain and terraces.

2b. Sequestration of nutrients will increase with the quantity of deposited sediment, and also with an increase in the percentage of silt plus clay. 2c. Release of inorganic forms of N and P in the sediments will occur the first year following the beaver dam failure and drying out of the sediment. 2d. Colonization of the site by plants from the family Salicaceae will depend both on sediment presence and the hydrological condition.

3. The third research objective is to determine the flowpath biogeochemistry of stream water advected across the floodplain due to in-channel beaver dams.

NOTE: Our ideas for this research objective are still developing, thus this paragraph provides only an indication of the likely direction for research.

The most general biogeochemical model that explains nutrient dynamics in river systems is the nutrient spiraling concept, which couples nutrient uptake and hydrological transport. Spiraling length is the downstream distance a molecule or particle travels before it is removed from the water column by some physical or biological process [Fisher *et al.*, 2004]. Stream water is subject to biogeochemical transformations as it is transported out of the channel, across the floodplain, and eventually back to the channel. I am interested in whether beaver activities cause nutrients to be essentially lost from the stream to the terrestrial floodplain environment in these broad mountain valleys.

The hypotheses are:

3a. Solute (DIN, DON and DOC) concentrations will decrease as stream water is advected across the floodplain. 3b. Nitrogen will be more limiting to the algal community on than phosphorus in the upper Colorado River above the beaver dam following peak flow and in late summer.

Study Site

The primary research site is a 1 km long reach of the headwaters of the Colorado River in Rocky Mountain National Park, Colorado, USA (40°22'N and 105°51'W). The site is a broad, low-gradient (0.01%), subalpine, alluvial valley at 2720 m elevation (Figure 1). The area of the upper portion of the watershed is 138 km² with elevations ranging from 2667 to 3944 m. The west-facing Front Range consists of Precambrian metamorphic rocks. The east-facing Never Summer Range is comprised of granitic magmas covered by an extensive lateral moraine deposited during the Pleistocene glaciation, and has several alluvial fans (Braddock and Cole 1990). Mineral soils in the valley are 0.9 m thick on average, and are mainly silt loam and loamy sand. Hydraulic conductivities range from 1×10^{-4} cm/s to 3×10^{-6} cm/s, determined using both falling and rising head tests (Fetter 2001). Peat deposits 0.3 to >1.5 m thick are

present along the valley margins, and have hydraulic conductivities of 2 to 4×10^{-4} cm/s. Soils are underlain by 3 to 4 m of gravelly alluvium, which has a hydraulic conductivity of approximately 2×10^{-3} cm/s.

Precipitation varies greatly over the elevation gradient of this watershed. Runoff in the valley is derived primarily from snowmelt above treeline, with periodic summer thunderstorms occurring between late July and the end of August. Mean annual precipitation at the Phantom Valley SNOTEL station (CO05J04S, 2750 m) is 640 mm with 42 % falling as snow, and is 885 mm with 84 % falling as snow at the Lake Irene SNOTEL site (CO05J10S, 3260 m). Mean annual potential evapotranspiration for the floor of the valley is 432 mm, calculated using the Thornthwaite equation for the period 1949-2002 (Dunne and Leopold 1978). The long-term mean December and July air temperatures at the Phantom Valley SNOTEL site are -9.6 and 12.4 °C, respectively. Vegetation in the valley is a mix of riparian shrublands dominated by *Salix monticola*, *S. geyeriana*, and *Betula fontinalis*, dry meadows dominated by *Deschampsia cespitosa* and *Calamagrostis canadensis*, and peat-accumulating wetlands dominated by *Salix planifolia* and *Carex aquatilis*.

The Colorado River is a third-order stream within the study reach, ranging in width from 8 to 15 m. The hydrograph is typical of a snowmelt dominated river, having a distinct seasonal flow regime and marked daily fluctuations in flow during the melt period. Mean annual discharge for the period 1954-2001 was 1.8 m³/s, and mean annual peak flow was 16.1 m³/s.

Beaver Dams

There are two beaver dams under intensive study in the upper Colorado River valley as part of this research (Figure 1). The dams have been named “Hilda” and “Floyd” so that we could easily refer to each.

“Hilda” (Figure 2), an L-shaped dam spanning the 10 m wide Colorado River, was constructed in early August 1997 by a beaver family. It remained intact until it was breached by high streamflow on 29 May 2003. The total dam length was 65 m, ranging in height from 0.7 to 1.7 m, and consisting of willow and alder stems, mud, and river rocks. It diverted 70 % of the river volume onto the floodplain within a week of its completion (Woods 2000), allowing the beaver to create a network of dams and canals on the floodplain. These dams varied greatly in size, from 0.1 m tall by 0.3 m wide to 0.5 m tall and 100 m wide.

“Floyd” (Figure 3) is a linear dam spanning the 6 m wide Colorado River, and was constructed in late August 2003 by a beaver family. It is presently intact. The total length of the dam is 8 m, and it has a maximum height of 0.8 m, consisting primarily of alder stems with some willow stems, mud, and river rocks. Similar to “Hilda”, it diverted water out onto the floodplain before it was completed, which allowed the beaver to create a network of dams and canals on the floodplain. These dams varied greatly in size, and are up to 100 m long.

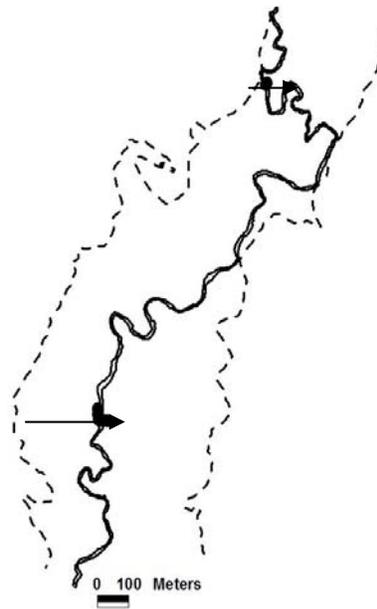


Figure 1: Location of the Hilda (lower arrow) and Floyd (upper arrow) beaver dams in the upper Colorado River Valley. The dotted line delimits the valley floor and the solid line is the Colorado River.



Figure 2: Hilda beaver dam before and after its breach. The arrow indicates the location of the same tree in each photograph.



Figure 3: Floyd beaver dam in September 2004.

Methods

I. Beaver vs. floods in controlling hydrological processes of mountain valleys

Streamflow and climate data

Stream discharge is continuously recorded by the U.S. Geological Survey (gauge #09010500) 4.5 km downstream of the study site (2667 m). A flood frequency curve of the annual peak discharge data for 1954 to 2003 was constructed, and a Log Pearson Type III distribution was found to best represent the data. The watershed is affected by diversion of water from 13 high-elevation tributaries out of the basin, resulting in essence in a contributing area that varies in size by up to 30%. While some of the flood peaks in the historical record were affected by the diversion and others were not, the flood frequency curve was developed using the recorded discharge data, regardless of whether water diversion impacted the annual peak. The 2003 flood was the second largest on record, making extrapolation of the rating curve tenuous, and thus the recurrence interval estimate uncertain.

Rainfall was measured within the study reach using a tipping bucket rain gauge (Onset Computer Corporation), located at a height of 1 m. Air temperature and relative humidity were monitored in 15 min intervals with HOBO data loggers (Onset Computer Corporation) between late May and October both study years.

Flooding

The extents of overbank flooding by the 2003 peak streamflow and as a result of the in-channel beaver dam (2002) were hand sketched on low-altitude (1:4000) aerial photographs that were printed at a scale of 1:700. Photographs and the location of flood debris and fresh sediment were used to assist in delineation of overbank flooding in 2003.

Groundwater Levels

Approximately 200 shallow wells, situated in transects across the valley (Figure 4) were installed to measure groundwater levels. Wells were constructed of 3.2 cm diameter, fully slotted PVC pipe, capped at the bottom, and installed with a hand auger to the base of the soil column. As there were locations in the valley where the water table dropped into the underlying gravelly alluvium during the summer, five wells were installed approximately 1 m below the soil column. These wells were comprised of a 3.2 cm diameter steel drive point (0.9 m screen) connected to a threaded and slotted 3.2 cm diameter PVC pipe. The drive points were installed using a post pounder or sledge hammer as the study site lies within a National Park and power tools are not permitted. The UTM coordinates and heights of the wells were surveyed using a Trimble 4800 survey-grade GPS. Depth to the water table was measured weekly at each well with an electronic tape between May and September of 2002 and 2003.

Contour plots of water table elevations for several dates during the study, including maximum depth to the water table, were derived by kriging point observations in Surfer (Golden Software Ltd.) using a

Gaussian model. The volume of saturated soil in the valley was calculated from the spatially interpolated position of the water table above the gravel layer for each sampling date. These values were converted to percentages by dividing the volume of saturated soil by the total volume of soil in the valley.

Hydrographs of hydraulic head versus time for individual wells were also used to evaluate the response of the unconfined floodplain groundwater system to beaver activity. Agglomerative cluster analysis of well data, calculated with Euclidean distance and average linkage grouping methods, was used as an unbiased and efficient tool to objectively identify wells with similar patterns of water level measurements over time [Cooper *et al.*, 1998]. Data for June and July (eight weeks) were used in this analysis as it represents the period when the water table drawdown was greatest. Cluster analysis was performed on data standardized to the ground surface, using the computer program PC-ORD, separately for each year. The clustering groups were plotted as a layer in ARCVIEW, and the mean hydrograph for each group was computed. Wells were examined to determine whether those located within the vicinity of the beaver dam changed groupings after the dam was breached, and wells that changed groups were considered to have a hydrograph influenced by the beaver dam. A total of 72 wells were used for this analysis due to missing data or water tables remaining below the bottom of the well for extended periods of time. Missing data were linearly interpolated if there were values for the sampling dates prior and following the missing date; otherwise the wells were excluded from the analysis.

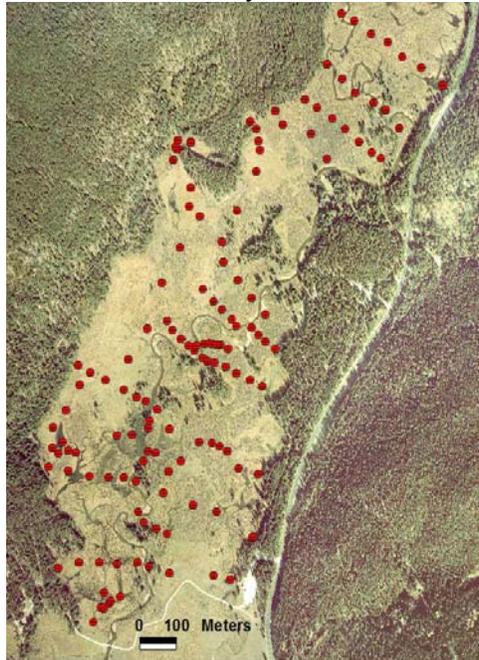


Figure 4: Groundwater well network in a section of the upper Colorado River valley.

II. Mountain valley formation

An area (180 m X 240 m) known to be hydrologically influenced by the Hilda dam was gridded into 10 m x 10 m cells in July 2003. A 1 m x 1 m plot was randomly located in each cell using a military-grade GPS (obtained from the USGS), yielding a total of 432 plots (Figure 5). Each plot was further subdivided into 4 quadrants, and sediment thickness was sampled at the visually highest and lowest elevation in each quadrant during August 2003. Mean sediment thickness was determined for the high and low spots in each plot, and a two sample *t*-test was run on all 432 plots to determine if accumulation of sediment was dependent on elevation. As this test was non-significant, all eight sediment thickness replicates were averaged to obtain one value for the plot. One composite sample was obtained for further physical and chemical analysis. Particle size on a subsample from each plot was determined via the hydrometer method. A few grams of dried (at 60°C for 5 days) and ground subsamples from each plot were analyzed for total carbon (all of which was organic) and total nitrogen on a LECO. The same subsamples were analyzed for total phosphorus and potassium by conducting nitric-perchloric digests and subsequently analyzing them by inductively coupled plasma (ICP).

The ion exchange resin bag technique [Binkley, 1984] was used to assess the bio-availability of N and P the second growing season (2004) following the breach of the Hilda beaver dam. Resin bags were prepared by sealing 14 mL of anion resins and 14 mL of cation resins in separate pouches of a nylon stocking. One bag was buried at 5 cm depth in the center of each plot from 8 June through 23 August 2004. Bags were desorbed in 100 mL 2 M KCl and shaken mechanically for 1 h. The KCl extracts were filtered through Whatman #42 filters and subsequently frozen. They will be analyzed for $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, and $\text{PO}_4^{3-}\text{-N}$ colourimetrically on an Alpkem.

Foliar cover for each plant species were estimated for each plot using six percent cover classes (<1, 1-5, 6-25, 26-50, 51-75, and 75-100 percent) in August 2004. The number of *Salix* spp. and *Populus tremuloides* (aspen) seedlings present in each plot were recorded.

Since the plots were arranged in a regular grid, spatial interpolation via kriging will be used to determine the total amount of sediment deposited on the floodplain. Further, kriging will also be used to model the spatial variation in sediment accumulation, nutrient sequestration, nutrient release, and the number of plant species. Correlations among soil nutrient availability and sediment texture will be explored using regression analysis. Similarly, correlations among sediment texture, thickness, number of plant species, and seedling establishment will be explored using regression analyses.

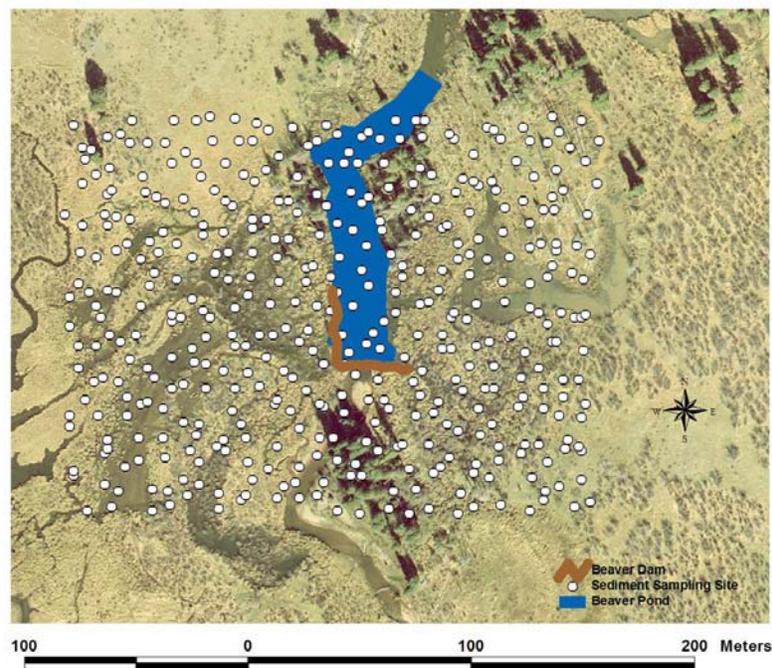


Figure 5: Layout of the sampling design for sedimentation in an area affected by the Hilda beaver dam.

III. Flowpath biogeochemistry

The extents of flooding as a result of the in-channel beaver dam (Floyd) were hand sketched in June 2004 on low-altitude (1:4000) aerial photographs that were printed at a scale of 1:700. Twenty four sampling locations were established using a hand-held GPS along the floodplain flowpath and in the Colorado River (Figure 6). Surface water samples were obtained in 100 mL, thrice-rinsed polyethylene containers on six occasions between June and August 2004 at all sampling locations. Samples were refrigerated, filtered through Whatman GF/C filters within 24 hours of sampling, and subsequently frozen.

The samples were analyzed for $\text{NH}_4^+\text{-N}$ and NO_3^-N content colourimetrically on an Alpkem, and will be analyzed for DON and DOC content on a Shimadzu TOC-V and TNM-1.

To determine whether the effects of beaver dams on the biogeochemistry of stream water advected across floodplains are ubiquitous in the central Rocky Mountains, an additional five to seven sites in mountain valleys will be similarly sampled in spring/summer 2005. The extent of flooding will be mapped on aerial photographs and water quality will be assessed three times following stream peak flows. These sites have yet to be chosen. In addition, a nutrient limitation experiment will be performed on Colorado River water to determine whether N or P is limiting. A nutrient-diffusing bioassay for faster flowing rivers will be used [Scrimgeour and Chambers, 1997]. Ten replicates of each nutrient-enriched treatment (N, P, and N+P amended) and unamended controls will be randomly dispersed throughout a 150 m riffle reach of the Colorado River above the Floyd beaver dam. The nutrient diffusing substrata will be attached to the river bottom for about 25 days following peak flow and then sampled for epilithic chlorophyll *a* as per Scrimgeour and Chambers [1997]. The effects of nutrient treatment on epilithic chlorophyll *a* will be tested with a single factor analysis of variance.

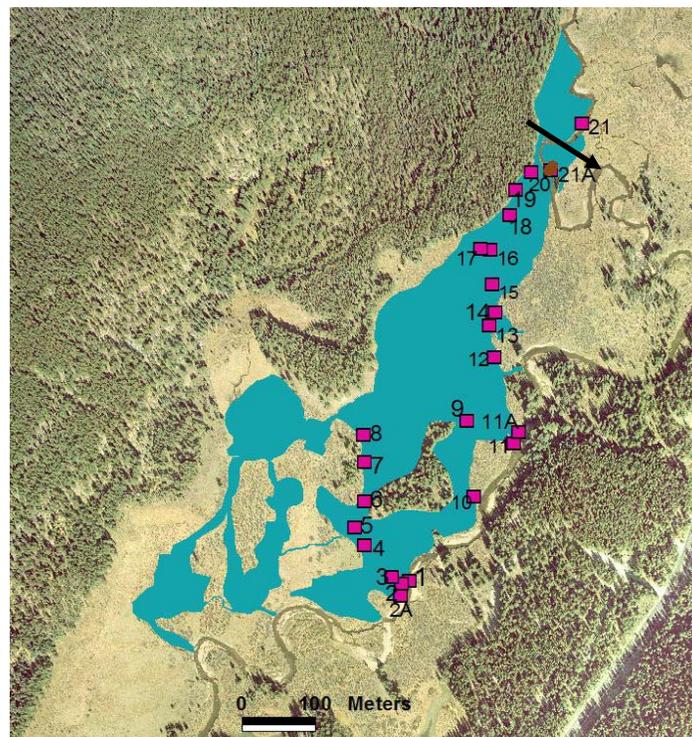


Figure 6: Extent of flooded area (shaded) and flowpath biogeochemistry sampling locations due to the Floyd beaver dam. The dam is indicated by the arrow.

Work Completed to Date

I. Beaver vs. floods in controlling hydrological processes of mountain valleys

- Obtained weekly measurements of groundwater levels for late May through September/October 2002, 2003, 2004 in the ~200 floodplain wells
- Mapped the areas flooded by beaver activities in 2002 and 2004
- Mapped the area flooded by the overbank flood event in 2003
- Surveyed location of (almost) all wells and important beaver features

- Measured hydraulic conductivities for nearly every well and all piezometers
- Data analysis 90% complete (still need to perform spatial statistical modeling to compute the volume of water stored in the floodplain for each week in the summers of 2002 and 2003)
- First draft of introduction and methods completed (paper format)

II. Mountain valley formation

- Sediment thickness sampling completed in 2003
- One composite sample for sediment texture and nutrient (N, P, K, C) content obtained in 2003
- One resin bag buried at each site during 2004 growing season (~45% recovery)
- Survey of vegetation species percent cover and seedling (willow and aspen only) count completed (2004)
- Lab analyses of chemistry and texture completed
- GIS layers of depth, texture, chemistry created
- Vegetation 30% identified
- Resin bags extracted (ready for dissolved N and P analysis)

III. Flowpath biogeochemistry

- Mapped area inundated or saturated because of Floyd beaver dam in 2004
- Located 24 sampling locations (2004) along the new flowpath
- Sampled water chemistry on 6 occasions (approximately biweekly) between June and August 2004
- Analyzed 2004 samples for NH_4^+ -N, NO_3^- -N, pH, TN (calculated DON), DOC

IV. Course work

Course Number	Name	Course Number	Name
BZ 530	Ecological plant morphology	EY 592	Interdisciplinary seminar in ecology
CE 531	Groundwater hydrology	EY 693	Research seminar
ER 416	Land use hydrology	L CC 200F (audit)	Second year French I
ER 417	Watershed measurements	L CC 201F (audit)	Second year French II
ER 552	Isotope hydrogeology (advanced topics in hydrogeology)	NR 512	Spatial statistical modeling in natural resources
ER 567	Sedimentary geochemistry	NR 575	Systems ecology
ER 616	Hillslope hydrology and runoff processes	NR 684	Supervised college teaching
EY 505	Foundations of ecology	WR 714	Water quality for wildland managers
EY 571	Forest ecology (advanced topics in ecology)		
EY 581	Ecosystem ecology		

Schedule of Work to be Completed

	2005											
	J	F	M	A	M	J	J	A	S	O	N	D
Project												
Location of other beaver sites in southern Rocky Mountains												
Map flooding by beaver												
Sampling & analysis of flowpath biogeochemistry												
Analysis of resin bag extracts												
Complete hydrology paper												
Analysis of sedimentation data												
Complete sedimentation dynamics paper												
Analysis of flowpath biogeochemistry data												
Complete flowpath biogeochemistry paper												
Complete thesis												
Thesis to committee												
Other												
Candidacy Exam												
Teaching: WR416 – Land Use Hydrology												
Final Presentation and defense												

BEAVER VS. FLOODS IN CONTROLLING HYDROLOGICAL PROCESSES ON FLOODPLAINS

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INTRODUCTION

Water table dynamics in montane riparian wetlands are controlled by complex interactions among groundwater, river water, and lateral inflow from adjacent hillslopes (Moorhead 2001; Burt et al. 2002). Streams may be the primary water source for riparian wetlands, and peak flows are generally regarded as the main hydrologic mechanism for sustaining high water tables. However, beaver dams may also alter stream stage and the exchange of water between stream channels and riparian wetlands (Woo and Waddington 1990; Lowry and Beschta 1994). This study tests the hypothesis that beaver, by building cross-channel dams, can maintain higher groundwater levels than low recurrence-interval floods, and produce distinct spatial and temporal patterns of flooding. Data were collected in 2002, which was a dry year when beaver dams spanned the Colorado River, and in 2003, when an estimated 17-year flood washed out all of the beaver dams.

METHODS

The study was conducted along a 1 km long reach of the Upper Colorado River (40°22'N and 105°51'W), Colorado, USA. The reach is in a broad, low-gradient, subalpine, alluvial valley at 2700 m elevation. Mineral soils are 0.9 m thick on average, and are mainly silt loam and loamy sand. Soils are underlain by 3 to 4 m of gravelly alluvium with a hydraulic conductivity of approximately $2 \times 10^{-3} \text{ cm s}^{-1}$.

Streamflow data are recorded on a U.S. Geological Survey gauge (#09010500), 3 km downstream of the study site. A flood frequency curve of the stream peak discharge data for 1954 to 2003 was constructed, and a Log Pearson Type III distribution was found to best represent the data. Water levels are monitored weekly between May and September in 200 shallow wells, situated in transects across the valley. Wells affected by the beaver dam were identified using agglomerative cluster analysis, calculated with Euclidean distance and average linkage grouping methods. The extents of overbank flooding by the 2003 peak streamflow, and as a result of the in-channel beaver dam (2002) were hand sketched on low-altitude (1:4000) aerial photographs that were printed at a scale of 1:700.

RESULTS

The 2002 water year had the lowest peak discharge on record ($5.2 \text{ m}^3 \text{ s}^{-1}$), and a 2 m tall by 65 m long beaver dam present throughout the year. Water flowed from the beaver pond to the western side of the valley, inundating 8.7 ha adjacent to and downstream of the dam in 2002 (Figure 1a). Ground water levels in the area adjacent to the beaver dam were stable and remained within 0.30 m of the ground surface all summer (Figure 2). The beaver dam caused elevated water levels in the middle of the valley floor both east and west of the river during mid and late summer (Figure 3).

In 2003, the snowmelt peak flow was $25 \text{ m}^3 \text{ s}^{-1}$ and this had an estimated recurrence-interval of 17 years. The beaver dam was breached on 29 May 2003, just prior to peak runoff, and was absent for the remainder of the year. Water moved down-valley with floodwaters inundating 4.9 ha of the study reach when the beaver dam was absent (Figure 1b). Water levels in the areas previously influenced by the beaver dam declined after peak runoff in 2003 (Figures 2 and 3) by as much as 1 m at some sites.

CONCLUSIONS

The results confirm the critical role of beaver in maintaining high water tables in riparian wetlands. Others have

shown that beaver pond water behind their dams, resulting in an elevation of the local water table (Neff 1957; Lowry and Beschta 1994). However, our results demonstrate that the hydrologic influence of beaver dams can encompass a much larger area than just the upstream pond, and may extend considerable distances both laterally and downstream. The area that can be inundated or saturated is controlled by the height of the ponded water and the topography of the valley bottom. In comparison, the area inundated by the high flow in the absence of the beaver dam appeared to be limited to a narrow zone immediately adjacent to the channel because of channel incision. The water table shows a distinct draw-down during the summer in the absence of beaver dams, suggesting that low recurrence-interval floods cannot maintain high water tables throughout the summer when vegetation water demands are high and streamflows are low. In conclusion, the control of beaver over groundwater levels overrides other key factors such as annual peak flows, which have previously been regarded as the main hydrologic mechanism for sustaining high water tables in riparian wetlands.

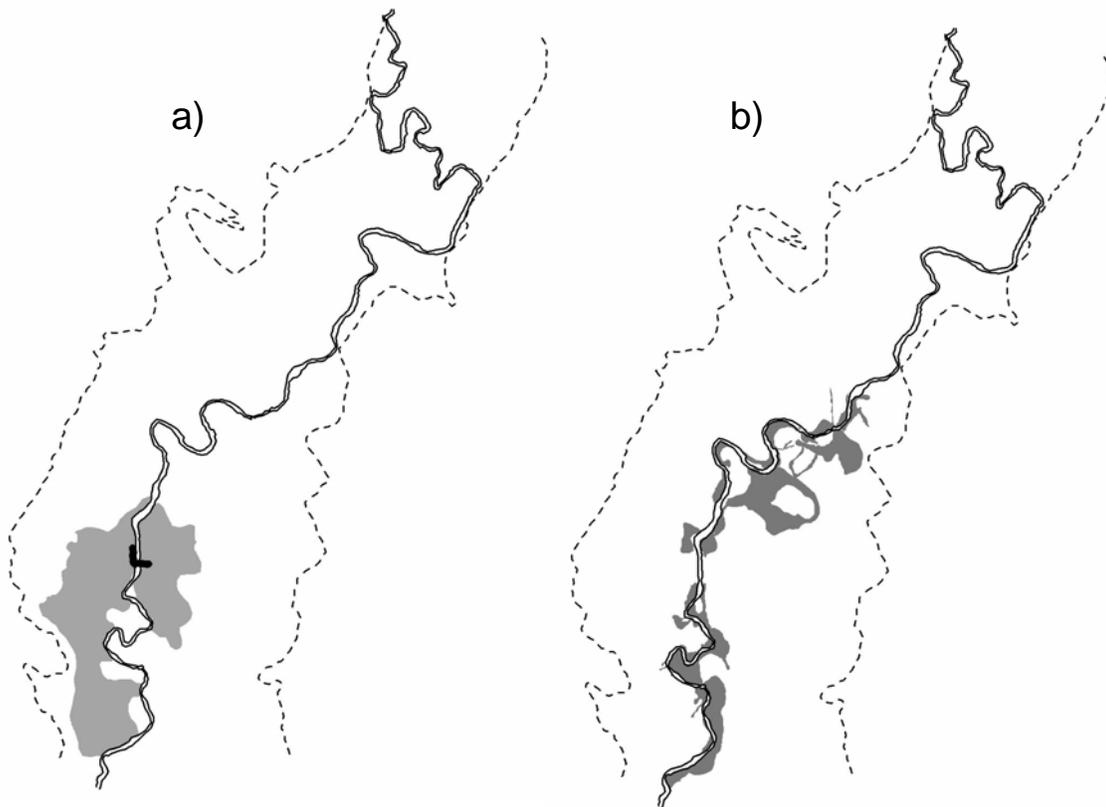


Figure 1: Flooding (shaded) due to one L-shaped beaver dam (a), and due to the 2003 peak stream flow (b). Dotted line delineates the valley bottom, the solid line is the Colorado River, and map scale is 1:6400.

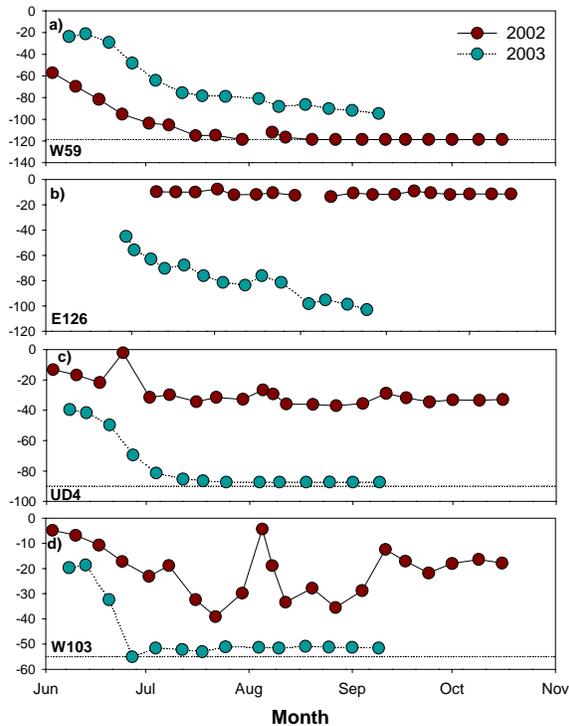


Figure 2: Well hydrographs for 2002 and 2003 at sites (a) unaffected by the beaver dam, (b) adjacent to the beaver pond, (c) 50 m downstream of the dam, and (d) 92 m downstream of the dam. The dotted line represents the bottom of the well.

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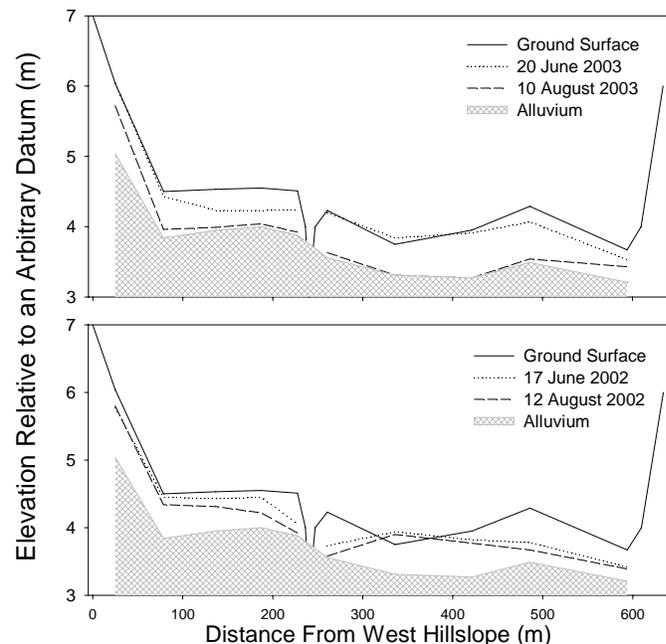


Figure 3: Groundwater levels along a valley-wide transect when beaver were absent (top panel) when a beaver dam was present 100 m upstream (bottom panel).