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DISSERTATION

THE EFFECTS OF FLOW REGULATION ON THE POPULATION BIOLOGY AND ECOLOGY OF BEAVERS IN NORTHWESTERN COLORADO

Submitted by

Stewart Breck

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctorate of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2001

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY STEWART BRECK ENTITLED THE EFFECTS OF FLOW REGULATION ON THE POPULATION BIOLOGY AND ECOLOGY OF BEAVERS IN NORTHWESTERN COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Committee on Graduate Work

Adviser

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ABSTRACT OF DISSERTATION

THE EFFECTS OF FLOW REGUALTION ON THE POPULATION BIOLOGY AND ECOLOGY OF BEAVERS IN NORTHWESTERN COLORADO

There are approximately 75,000 dams on the streams and rivers of the United States, with nearly all the large rivers having been severely altered. The downstream effect of a dam often includes the elimination of the flood pulse, which plays an important role in the creation and maintenance of riparian ecosystems, some of the most ecologically valuable ecosystems particularly in the western U.S. Such large-scale manipulations of a key disturbance are responsible for numerous ecological changes. My research assessed the effects of flow regulation on beaver (*Castor canadensis*) populations and on the interaction between beavers and two important plant species, sandbar willow (*Salix exigua)* and Fremont cottonwood (*Populus deltoides* spp. wislizenii). I gathered comparative data on two 6th-order alluvial rivers, the free-flowing Yampa River and flow-regulated Green River in Northwest Colorado from 1997-2000. In these systems beavers are bank dwelling and cottonwood and willow are the dominant native woody species.

I assessed the effects of flow regulation on the demography of beavers by comparing the density, survival, home range and body size of bank-dwelling beavers. Flow regulation on the Green River has altered fluvial geomorphic processes, influencing availability of willow and cottonwood that has, in turn, influenced the demography of beavers. Beaver density was higher on the Green River (0.5-0.6 colonies/km of river) than the Yampa River (0.35 colonies/km of river). Adult and sub-adult beavers were in better condition on the Green River as indicated by their larger body mass and tail size. Evidence suggested mortality due to predation was higher for adult beavers on the Yampa River. There was no detectable difference in home range size though there were areas on the Yampa River that no beavers used. I attribute the improved habitat quality on the Green River to a greater availability of willow. I suggest that the sandy flats and bars that form during base flows on the Yampa River increase the energy expended to attain food and increase the predation risk and thus lower the availability of woody forage.

I quantified the abundance and density of sandbar willow and the amount of willow taken by beavers on alluvial sections of the flow-regulated Green River and free-flowing Yampa Rivers in northwest Colorado. I used beaver exclosures to determine differences in growth rate of willow between rivers. On the Green River, willow has shifted its distribution from a primarily bank-oriented to a primarily island-oriented species. The total area of willow was similar on each river, though on the Green River patches were smaller, more numerous, contained a lower density of stems, and stems grew faster. Beavers selected stems that were larger in diameter and closer to the river and cut twice as much willow on the Green River as on the Yampa River. This resulted in an 8-fold difference in the percent of stems removed on the Green River because of the lower density of willow stems. The difference in rate of herbivory between rivers can be attributed to a higher availability of stems, a higher density of beavers, and less young cottonwood (an alternative food source) on the Green River. Flow regulation increased the availability of willow by altering its distribution so that patches were adjacent to water year around and had a greater amount of willow perimeter interfacing with water on the Green River than on the Yampa River. This provides safer foraging and involves less energy expenditure.

I studied the impact of beaver herbivory on young cottonwood tree survival by measuring the abundance and density of cottonwood on a 10-km stretch of the Green River and a 7.5-km stretch of the Yampa River. I followed the fates of individually marked young saplings in 3 patches of cottonwood on the Yampa and 2 on the Green River. I measured the diameter and distance from water of each monitored tree. From May 1998 through November 1999 two natural floods occurred on the Yampa River and one controlled flood was released on the Green River, which allowed us to determine the effect of flooding on beaver herbivory. Flow regulation has caused a decrease in number of cottonwood patches per km of river, area of patches per km, and average stem density within cottonwood patches on the Green River. The number of stems cut per beaver was 3 times lower on the Green River than on the Yampa River but cottonwood survival was still lower on the Green River because of the lower abundance of cottonwood there. Factors that influenced beaver herbivory included the abundance of cottonwood, the distance of cottonwood patches from the river and controlled flooding. Controlled flooding appeared to increase the rate of foraging on the Green River only during the flood in 1999 which was of greater magnitude and duration than the flood in 1998. I suggest regulation has magnified beaver's impact on cottonwood through interrelated effects on plant spatial distribution and cottonwood abundance.

I demonstrated how interaction strength of beavers varies spatially depending on environmental context. I first qualitatively compared interaction strength of beavers in smaller streams where they are able to build dams, with beavers in larger rivers where they are bank dwelling and unable to build dams. Second, I quantified interaction strength of beavers on two comparable 6th-order rivers, the Green and Yampa in northwest Colorado, for two community traits (cottonwood survival and percent of willow removed). Interaction strength of beavers was context dependent, decreasing considerably from small ordered streams (2nd-4th) to large ordered rivers (5th-7th), primarily because they are unable to build dams in larger-ordered rivers. Beaver interaction strength also varied within comparable 6th-order rivers, being much greater on the flow-regulated Green River than the free-flowing Yampa River. I attribute variation in interaction strength to the amount and variability of hydrologic energy associated with the flow regime. Small ordered streams contain less energy enabling beavers to build dams, which increases their interaction strength, though variation in flows can reduce interaction strength by temporarily destroying dams. On the Yampa River variation in hydrologic energy lowered interaction strength of beavers by maintaining a high abundance of cottonwood trees and increasing the expenditure of energy and risk of predation for beavers. On the Green River variability in hydrologic energy has been eliminated through flow regulation, which has stabilized the system and allowed beavers to have greater interaction strength. Classifying beavers as keystone species is justified on 2nd-4th ordered rivers but not on larger ordered rivers.

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This document contains words, numbers, graphs and tables that provide new knowledge about beavers and their ecology. Like a glacier drifting at sea, this knowledge is only the tip of a larger entity that provides the foundation for the information. Simply recognizing the tip of the glacier, without acknowledging its support is unjust and denies the critical process that leads to reliable knowledge. My dissertation is supported by thoughts and ideas focused-refined-refocused, days and nights cloaked in the intriguing seasons of northwestern Colorado, hard labor and tedious data collection, wonderful hours exploring the river and riparian ecosystem, and much time synthesizing, writing and editing. Only a small portion of this effort was mine and to that end I would like to acknowledge and offer my sincere thanks to individuals who helped me generate this knowledge and achieve this personal milestone.

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CHAPTER 1

INTRODUCTION

Communities and ecosystems are influenced by a variety of factors both abiotic and biotic. For example, riparian ecosystems are often structured by flood events and the actions of plants and animals (Fenner et al. 1985, Naiman and Decamps 1997, Scott et al. 1997). It is generally believed that of these two forces, flooding is the more important for influencing structural and functional aspects of riparian ecosystems. Consequently, there has been a wealth of research regarding the influence of flooding on riparian ecosystems, but a general paucity of research on the influence of biotic factors. If we are to fully understand the structure and function of riparian systems it will be necessary to understand the influence of both abiotic and biotic components, particularly considering that on many rivers flooding no longer occurs due to the construction and operation of dams. For flood-controlled systems, biotic factors may play a more dominant role in structuring the ecosystem and certainly will have a different role due to the alterations caused by flow regulation. Understanding how biological agents have reacted to flow-regulation and in turn have changed their role in structuring the ecosystem may be important for management and restoration efforts.

The need to understand the processes that form and maintain riparian ecosystems is underlain by the importance of these systems ecologically. Less than 2% of the United States is comprised of riparian habitat, yet more vertebrate species use these areas during some phase of their life cycle than any other habitat type (Sedgwick and Knopf 1987, Douglas et al. 1992, Naiman et al. 1993, Popotnik and Giuliano 2000). In the arid western United States, riparian ecosystems are especially important because of their lush vegetation and high productivity in an otherwise desert-like landscape.

Arguably the venerable riparian species along large western rivers are cottonwood trees (*Populus spp.*). Their structural and functional attributes provide unique cover and forage for wildlife, help transport and cycle nutrients, and provide aesthetic relief for humans in systems often devoid of other native trees. Flow modification due in part to the operation of large dams has helped cause a drastic decline in cottonwood recruitment along many rivers (Fenner et al. 1985 Snyder and Gary C. Miller 1991, Howe and Knopf 1991, Rood and Mahoney 1995, Busch and Smith 1995, Braatne et al. 1996, Cooper et al. 1999). The reasons for the decline involve both biotic and abiotic processes that are influenced by flow regulation and vary based on the geomorphic setting and ecological factors that influence the growth and survival of cottonwood (Braatne et al. 1996, Scott et al. 1996). Although it is generally accepted that abiotic factors play an important role in the recruitment process, little is known about biotic influences that affect this tree (Andersen and Cooper 2000).

Herbivory is a biotic factor that can play an important role in the structure and functioning of many ecosystems (Gessaman and MacMahon 1984, Huntly 1991, Hobbs 1996, Naiman and Rogers 1997). In riparian ecosystems vertebrate herbivores, including livestock (Green and Kauffman 1995, Popotnik and Giuliano 2000), native ungulates (Singer et al. 1998, Opperman and Merenlender 2000), and beavers (McGinley and Whitham 1985, Kindschy 1985, Johnston and Naiman 1990) can impact riparian habitat through their foraging activities. These impacts can lead to changes in the plant community composition and vegetation structure, which can impact the native fauna (Andersen and Nelson 1999, Popotnik and Giuliano 2000). Given the importance of herbivory in riparian ecosystems, it is surprising that few studies have investigated how flow regulation may alter the dynamics between an herbivore and plant populations and communities.

Andersen and Cooper (2000) addressed this issue by studying the impact of mammalian herbivores on Fremont cottonwood on the free-flowing Yampa River and partially flow regulated Green River in Northwest Colorado. One of their findings indicated that a small mammal (*Microtus montanus*) reduced seedling and sapling survivorship on the Green River because flow regulation allowed Microtus populations to escape mortality normally accompanying the annual spring floods. Our work was similar to Andersen and Cooper (2000), but focused strictly on beaver populations and herbivory. I asked if flow regulation was correlated with a detectable demographic response in beaver populations and if there was evidence that it enhanced beaver herbivory on willow or cottonwood trees.

Flow Regulation and the High Desert Riparian Ecosystem

The Colorado River basin, which includes the Green and Yampa Rivers, was historically subject to annual flooding. Today, this system is an example of one of the most regulated river systems in the world, due to the construction and operation of numerous dams. While much of the Green River is regulated by controlled releases from Flaming Gorge Dam, the Yampa River is the last major tributary that remains relatively unregulated (i.e., no dams).

Flow regulation on the Green River has eliminated the spring flood pulse, reduced in-stream sediment loads, and increased base flow. These changes have had profound effects on the channel morphology. Most notable are the transformation elimination of the higher portions of the former floodplain into a terrace (through lack of periodic inundaton, scouring and sediment deposition, and the subsequent encroachment of upland plant species) and the formation of islands in the river channel (Andrews 1986, Merritt and Cooper 2000). The two primary woody species Fremont cottonwood and sandbar willow (*Salix exigua*) have responded to these changes in channel morphology in the following ways.

Fremont cottonwood has suffered a severe reduction in recruitment due, primarily, to the elimination of suitable germination sites (Cooper et al. 1999). Currently, cottonwood saplings along the Green River are restricted to recruits from only a few years and only found in close proximity to the main channel whereas the Yampa River has extensive areas of saplings from numerous years associated with point bars and othe land forms. Sandbar willow is abundanta and grows well on both rivers. However, on the Green River willow has shifted its distribution from a primarily bank-oriented species to a bank- and island-oriented species. Islands on the Green River are a new feature that have formed and are growing as a result of flow regulation (Merritt and Cooper 2000). The shift of willow has important implications for beavers.

In riparian ecosystems, beavers can be important because of their ability to cut down trees and remove an exceptionally large amount of biomass (Gill 1971, Johnston and Naiman 1990). In some instances these abilities allow beavers to suppress tree populations and alter the species composition of the riparian ecosystem (Johnson and

Naiman 1990). Understanding when beavers can impact trees can be an important management objective, particularly if the tree species is a critical component of the ecosystem (e.g., cottonwood). The proximity of the two rivers offered a unique opportunity to study how beaver ecology in these contrasting systems and assess whether interactions between beavers and the woody vegetation differ and if that difference can be related to river regualtion.

Importance of Beavers Varies with Environmental Context

An animal's ability to influence the ecosystem is context dependent (Menge et al. 1994, Power et al. 1996). That is, in some situations animals can have a large effect on an ecosystem and have a high community importance. For example, on 2nd-4th ordered streams beavers are able to build dams and have a large impact on a variety of physical and biological traits. Dam building transforms streams from a lotic habitat to a lentic habitat, reducing stream velocity and discharge rates (Gurnell 1998). The altered hydrologic regime affects biogeochemical cycles and the accumulation and distribution of chemical elements (Smith et al. 1991, Naiman et al. 1994, Klotz 1998). For example, beaver ponds trap sediment, increase water depth, accumulate nitrogen, and enhance carbon storage (Naiman et al. 1986). These hydrological and biogeochemical changes can increase or decrease the relative abundance of plants (Mitchell and Niering 1993), aquatic insects (McDowell and Naiman 1986, Clifford et al. 1993), fish (Leidholtbruner et al. 1992, Snodgrass and Meffe 1998), amphibians (Russell et al. 1999), reptiles (Russell et al. 1999), and birds (Grover and Baldassarre 1995, McCall et al. 1996). Taken at a landscape level, beaver dams enhance species richness by creating a diversity of habitat that would not exist in their absence.

In other contexts the same species will have less importance in influencing their ecosystem (e.g., where beavers are primarily bank dwelling and unable to create dams). Applied to this study, the community importance of beavers on the Green and Yampa Rivers was obviously less than the community importance for beavers on small streams where they build dams. In addition, the community importance of beavers between the rivers was likely different because the environmental context had changed on the Green River. Specifically, I predicted that in the absence of flooding on the Green River that beavers would play a greater role shaping their ecosystem than on the Yampa River, primarily through their foraging on key woody species.

Assumption and Objectives

Because direct experimentation was not possible, this study compared and contrasted aspects of beaver ecology on the free-flowing Yampa River to that on the flow-regulated Green River. The key assumption of our study was that prior to completion of the dam, both rivers operated under a similar flow regime and supported similar ecosystems. The following facts support this assumption: 1) mean annual flows between the pre-dam Green and Yampa Rivers were similar (e.g., 65 m^3/s and 61 m^3/s, respectively), 2) annual maximum discharge typically occurred between May 15 and June 15 on both rivers, 3) elevation at our study sites on the Green and Yampa Rivers are similar (1634 m and 1707 m, respectively), and 4) woody vegetation was similar and was characterized by mature cottonwood with willow and tamarisk *(Tamarix ramosissima)* growing immediately adjacent to the rivers (Hayward et al. 1958).

The overall objective was to understand how flow regulation on a large, arid-land river can modify the nature and consequences of beaver-habitat interactions relative to those that would exist in the absence of regulation. The work was premised on the idea that regulation would lead to riparian vegetation changes independent of the presence of beavers. These changes were expected to alter beaver populations and the foraging link between beavers and woody forage (i.e., willow and cottonwood) thereby altering the influence that beavers had on the riparian ecosystem. Specific objectives were:

1) Compare the demography of beavers on the Green and Yampa Rivers as a function of the availability of riparian vegetation.

2) Compare the foraging behavior of beavers as a function of the flow regime along each river.

3) Quantify the impact of beaver herbivory on cottonwood trees and willow.

4) Apply the ideas of community importance and keystone species by comparing work done in systems where beavers build dams to this research where beavers were bank dwelling and could not build dams.

Chapter 2 focuses on the demographic response of beavers due to changes in the availability of vegetation as a result of flow regulation on the Green River. Chapter 3 focuses on willow and the influence of natural and controlled flow regimes on beaver herbivory. Chapter 4 addresses the impact of beavers on cottonwood trees by measuring beaver induced mortality of cottonwood trees as influenced by flooding and the spatial distribution of cottonwood patches. Chapter 5 summarizes the research by applying the notion of community importance of a species and how that changes depending on the environmental context. Chapters 2,3, and 4 were written as independent publications, thus there is some repeated material in the introduction and discussions.

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CHAPTER 2

THE DEMOGRAPHIC RESPONSE OF BANK-DWELLING BEAVERS TO FLOW REGULATION ON THE GREEN RIVER

INTRODUCTION

Annual spring flooding is an important disturbance that regulates the functioning of riparian ecosystems on many arid-land rivers in the western USA (Knopf et al. 1988, Scott et al. 1997). Human alteration of the flood regime through the construction and operation of large dams has caused considerable changes in the distribution and abundance of plants and animals associated with the riparian community (Nilsson et al. 1991, Nilsson and Dynesius 1994, Kingsford 2000). Understanding how and why species respond to flow regulation will be important in the effort to maintain or restore key components of riparian ecosystems on managed rivers.

For example, the decline of cottonwood (*Populus spp.*) across many western rivers (see Cooper et al. 1999) is a major concern because of the unique biological and aesthetic values that cottonwood trees provide (Howe and Knopf 1991, Braatne et al. 1996). Flow regulation affects cottonwoods by altering both abiotic and biotic processes that are required for regeneration (Bradley and Smith 1986, Busch and Smith 1995, Scott et al. 1996, Cooper et al. 1999, Andersen and Cooper 2000). Beaver herbivory is a biotic process that can limit populations of certain tree species (Barnes and Dibble 1986, Johnson and Naiman 1990). Therefore, understanding how beaver populations have responded to flow regulation may be important in the effort to restore cottonwood trees.

Little is known about the impact of flow regulation on the population biology of beavers. Some researchers speculate that stable flows decrease the population of beavers by decreasing the amount of forage (Nilsson and Dynesius 1994). Others predict that stable flows increase beaver populations by increasing the number of denning sites (Lesica and Miles 1999). The validity of these predictions is hard to assess in part because of the lack of autecological knowledge concerning bank-dwelling beavers in large-order rivers. Knowledge of density has been garnered from studies based on trapping data (Vanden Berge and Vohs 1977) and observational data (Strong 1982). But to our knowledge, no study has utilized radio-telemetry to assess important demographic and behavioral parameters (e.g., survival, home range, movement patterns) that are important in assessing and explaining a response to flow regulation.

We used a demographic response design (Garshelis 2000) to attain autecological data on bank-dwelling beavers and assess how beaver populations have responded to specific changes in the riparian ecosystem as a result of flow-regulation. Specifically, we compared beaver body size, density, home range and survival on the flow-regulated Green River to that on the free-flowing Yampa River. Because of the dramatic decline of Fremont cottonwood (*Populus deltoides* Marshall subsp. *wizlizenii*) recruitment on the Green River (Merritt and Cooper 2000, Cooper et al. 1999) and because beavers utilize cottonwood (Strong 1982, McGinley and Whitham 1985), we predicted that: 1) beaver population density would be lower on the Green River, 2) beaver home range size would be larger on the Green River, and 3) adult survival would be lower on the Green River.

STUDY AREA

The Green and Yampa Rivers are major tributaries of the Colorado River system. We conducted our study on alluvial sections of these rivers above their confluence in northwestern Colorado (Figure 1) (see Merritt and Cooper 2000 and Cooper et al. 1999 for a detailed description). On the Yampa River we were constrained to a 10-km section from the confluence of the Little Snake River to the beginning of Yampa Canyon in Dinosaur National Monument. On the Green River (based on aerial photos) we selected a similar 10-km section within Browns Park National Wildlife Refuge that had been studied since 1994 as part of a long-term study of ecological changes as a result of river regulation (Falck 1996, Miller 1998, Cooper et al. 1999, Andersen et al. 2000). Both river sections are sixth-order alluvial systems and neither had been trapped for beavers in at least 3 years prior to, or during, the study.

Our study was an observational field study as described by Eberhardt and Thomas (1991:64-65) with the obvious limitation being the lack of control over allocation of treatments (i.e., unregulated river versus regulated river) to experimental units (rivers). In addition, it was impossible to have replicate rivers, because the Yampa River is the last, relatively unregulated river in the Colorado River system. The primary assumption of this study was that prior to 1962, when Flaming Gorge Dam was completed, the Green and Yampa Rivers had similar flow regimes and maintained similar ecosystems within the study sections. The following facts support this assumption: 1) flow regimes (including peak flows, base flows, and timing of flows) were similar on the pre-dam Green and Yampa Rivers (Figure 2) elevations are similar (1633 m on the Green River and 1707 m on the Yampa River), and 3) woody vegetation was similar and was characterized primarily by Freemont cottonwood and sandbar willow (*Salix exigua*).

Flow regulation (i.e., the reduction of a flood pulse and the increase in base flows, Figure 2) on the Green River has caused a number of changes in the fluvial geomorphology downstream of the dam (Andrews 1986, Merritt and Cooper 2000), including the development of instream islands and loss of point bars in Browns Park National Wildlife Refuge. Because of these changes, sandbar willow has shifted from a primarily bank oriented to an island and bank oriented species, and Fremont cottonwood has suffered a severe decline in recruitment (Cooper et al. 1999).

On the Yampa River, Fremont cottonwood depends on the cycle of spring flooding and is generally prolific along banks and point bars (Cooper et al. 1999). Sandbar willow is also found in large patches primarily along the bank. In late summer the river declines to base flows and remains near that level until the following spring. Base flows expose large sandbars that separate the river from its vegetation.

METHODS

Capture and Radiotelemetry

We used Hancock traps (Hancock Trap Co., Custer, South Dakota) and snares (Gregerson #3 with a 16 inch stop to limit captures of non-target species) to capture beavers during September through November of 1997, 1998 and 1999. The snares were effective at catching adults and occasionally sub-adults but ineffective for juveniles due to the stop. Hancock traps were effective at catching all ages. We minimized the use of snares in this study because of the higher trap mortality associated with snares as opposed to Hancocks (McKinstry and Anderson 1998). In 1997 and 1998, we focused on capturing adult animals for radio implants. In 1999, we attempted to capture all members of each colony within each study area. We trapped 8 to 10 nights on each colony and used 4 or 5 hancock traps and 0 to 40 snares. We trapped for three periods on the Green River (22 Sep-29 Sep, 11 Oct-19 Oct, and 30 Oct-6 Nov) and 2 periods on the Yampa River (1 Oct-9 Oct and 20 Oct-29 Oct) and alternated our trapping sessions between rivers.

All captured animals were weighed and marked with ear tags (monel # 1005-3; National Band & Tag Company, Newport, KY), sexed through external palpation for a baculum (Osborn 1955) and a check of anal sac fluid (Schulte et al. 1995). The following body measurements were taken: total length (from tip of nose to end of tail), width of the zygomatic arch, length of tail (from the base to the end of the tail), width of tail (at the widest part), and thickness of tail (at the mid-line, 2.5 cm distal from the base of tail). Beavers weighing ≥16 kg were considered adults (3+ years old), 8 to 16 kg were considered sub-adults (1-2 years old), and < 8 kg were considered juveniles (<1 year old) (Patric and Webb 1960). We substantiated the 16-kg cutoff for adults by recapturing and weighing 3 animals in 1999 that were caught as juveniles in 1997 (1 from the Green River and 2 from the Yampa River), all weighed over 16 kg in 1999.

We implanted transmitters in 15 adult beavers in the fall of 1997 (8 on the Green River and 7 on the Yampa River). In 1998 we implanted transmitters in 2 additional animals on the Green River and 1 on the Yampa River. We attempted to implant transmitters in adult mating pairs from each colony in our study areas. We used isoflourine and sevoflourine gas anesthesia (a new procedure for beavers-S. Breck unpublished data) for surgery and implanted radio transmitters (Advanced Telemetry

Systems Isanti, MN; 33 mm wide X 109 mm long and 100 g; expected transmitter life = 3 years) in the peritoneal cavity (Davis et al. 1984, Smith et al. 1991). We provided water to individuals post surgery and allowed them to recover for up to 8 hours and then immediately released them at the site of capture. The Colorado State University Animal Care and Use Committee approved our trapping and handling protocol (#97-018A-04).

We monitored radioed animals to estimate both survival and home range size. Monitoring for survival involved locating individuals during the day. Animals in a den were presumed alive; animals outside a den were tracked until status could be determined. To estimate home range we monitored intensely from May through June in 1998 and 1999. During these periods we monitored a single animal or a family pair through the night. Individuals were located before sundown, at which time we attempted to attain a location every 15 minutes. To obtain locations we followed an individual along the shore until the signal was perpendicular to the river. Because we were often unable to determine the precise location of the animal, we plotted the location as a line across the river on a topographic map or a map generated from aerial photographs. We entered these lines into a GIS coverage using Arcview. The line coverage was converted to a point coverage by cropping each line to the river margins and then calculating the middle point of each line (i.e., the points were justified to the middle of the river). The points constituted the Cartesian coordinates that were for the home range analysis described below.

Analysis

Body Size

We used a two-tailed t-test with equal variances (PROC TTEST; SAS Institute 1990) to test for differences in body mass, total body length, tail length, tail width, tail thickness, and zygomatic breadth of beavers between rivers. Adults, sub-adults and juveniles were tested separately. We report actual significance levels.

Density

We estimated density in two ways. First, we attempted to census the number of colonies per linear km in 1997, 1998, and 1999. The designation of a colony was based on the existence of an adult mating pair and the evidence of an active den. This was determined by trapping in 1997, and by trapping and radio telemetry in 1998 and 1999. Second, we summed the mass of all beavers caught in 1999 and divided this by the length of the study area. For adults with radio transmitters that could not be recaptured, we used the mass from the captures in 1997 or 1998. For both measures of density, we used the telemetry data to define the extent of the study area by taking the furthest upstream and down stream telemetry location to define the study area. On the Yampa River we excluded one colony located at the upstream end of the study area just below the confluence of the Little Snake River. Monitoring revealed that they utilized the Little Snake River, but due to logistical constraints we were unable to accurately monitor locations on this river, thus they were eliminated from our analyses of density and home range.

Home Range

Sauer et al. (1999) described a method for analyzing home range size of animals that move in a linear fashion (e.g., river otter, beavers and muskrats restricted to a river). In this procedure the linear length is used as a determinate of home range size rather than the area contained within a contour to avoid the bias of including large areas of land where an animal would not occur. We used a modified version of this technique to calculate the home range size of colonies of beavers on the Green and Yampa Rivers. The locations of adult beavers occupying the same colony were combined but separated by year (1998 and 1999). These Cartesian coordinates were used in the program, The Home Ranger (written by F. Hovey and found at the Illinois Natural History Survey Wildlife Ecology Software server, http://nhsbig.inhs.uiuc.edu/), to generate 95%, 75%, and 50% probability contour intervals. We used the program's fixed kemal estimator with a grid size of 100 x 100 and a smoothing parameter picked by the program based on the least-squares cross validation score. The contour intervals generated by the program were transferred to a GIS to create a coverage that overlaid the original midpoint locations of beavers. Following the line generated by the midpoints, we measured the linear length of river between the points of intersection of the contours and the midline in the river. When there was more than one polygon for a single contour we included the distance between the polygons as part of the home range (Sauer et al. 1999). We calculated a linear home range length for each colony at each probability contour interval (i.e., 95%, 75%, and 50%). Due to the small number of home ranges, we pooled family groups across years and used a t-test (PROC TTEST; SAS Institute 1990) to test whether home range was smaller on the Yampa River.

Survival

We used program MARK (White and Burnham 1999) to model the known fate survival of radioed beaver. A diagram illustrating this model is: Capture and Release -----S(1)----> Encounter 2 -----S(2)----> Encounter 3 -----S(3)----> Encounter 4, where the S between encounter occasions represents survival during that interval.

We used this model to test for differences in survival of adult beavers between rivers. There were a total of 15 encounter occasions, and the intervals between encounter occasions varied from one month to 4 months. Two and 3 radioed beavers, from the Yampa River and Green River, respectively, disappeared without knowledge of their fate. For the survival analysis we censored these animals from the data set at the time of disappearance. Because we implanted transmitters in adult pairs, we suspected lack of independence (a key assumption) which leads to overdispersed data. We corrected for any overdispersion using the quasi-likelihood parameter which can be calculated in program MARK (see program for details).

We generated 6 models *a-priori* for the survival analysis (Burnham and Anderson 1998), each assessing a specific hypothesis:

[S(.)] survival was the same for both rivers,

[S(r)] survival was different between the rivers,

[S(f)] survival was lower when the base flow dropped below 1000 cfs (which occurred only on the Yampa River and was generally when sand bars began to emerge).

[S(y)] survival was different between calendar years,

[S(y+r)] survival was different between years and rivers, or

[S(t)] survival was the same for each river but differed between each of the encounter occasions.

We tested additional models post-hoc that added one of two individual covariates (mass at capture and sex) to the above models.

We used Akiake's Information Criteria (AIC) to select the best (parsimonious) models as supported by the data (Akaike 1973, Burnham and Anderson 1998). We used the small-sample correction of AIC adjusted for overdispersion ($QAIC_c$, see Burnham and Anderson, 1998:53 and Lebreton et al. 1992). Models with the lowest $QAIC_c$ values were considered competing "best" models (Burnham and Anderson 1998:63). In addition, we computed $QAIC_c$ weights ($\underline{\omega_i}$) which provide a measure for the evidence in support of a particular model (Burnham and Anderson, 1998:123-125). To quantify the evidence for the importance of each variable [i.e., (.), (r), (f), (y), (t), (mass) and (sex)], we summed the Akaike weights over the subset of models that included each variable (Burnham and Anderson, 1998:140-143).

RESULTS

Body Condition

Adult beavers on the Green River were larger for 3 of the 6 body measurements: mass, tail thickness, and tail width (p-values < 0.03; Table 1). The other 3 measurements (including the two skeletal measurements, total length and zygomatic breadth) showed little or no difference. Sub-adult beavers on the Green River were larger for 4 of the 6 body measurements: mass, tail thickness, tail length, and total length (p-values < 0.03; Table 1). Tail width and zygomatic breadth showed no difference in size. Juvenile beavers on the Green River were smaller for 2 of the 6 measurements: tail length and zygomatic breadth (p-values < 0.03; Table 1). The other 4 measurements showed no difference.

Density

Based on telemetry, the length of the study reaches over two years, excluding one colony on the Yampa River, were 8.6 km for the Yampa River and 10.1 km for the Green River. Both calculations of density indicated a higher density of beavers on the Green River (0.50 colonies/km and 37.3 kg/km of river) than on the Yampa River (0.35 colonies/km and 27.7 kg/km of river). The number of colonies on the Yampa River, 3, stayed consistent over the 3 fall seasons of trapping and 2 spring seasons of monitoring. On the Green River the number of colonies was at least 5 and there was evidence that in 1999 a 6th colony was becoming established.

We had 1 and 2 trap mortalities in 1997 and 1999, respectively. All mortalities were adult beavers caught in snares on the Green River. In 1999, the trapping effort (trap nights per colony) was similar using Hancock traps (Green River: $\bar{x} = 37.5$, SE = 4.69; Yampa River $\bar{x} = 38.3$, SE = 11.58) but higher on the Green River using snares (Green River: $\bar{x} = 81.0$ SE = 30.4; Yampa River $\bar{x} = 47.5$, SE = 47.5).

Home Range

A total of 5 and 7 home ranges were calculated on the Yampa and Green Rivers, respectively. There was no evidence that the home range length was different between rivers for any of the 3 probability contour intervals (Table 2). Home range length was extremely variable on each river (e.g., range for 95% Contour Interval: Yampa River = 1.55 – 2.95 km, SE = 0.232; Green River = 1.16 – 4.48 km, SE = 0.457).

Survival

Based on the $QAIC_c$ Weights (Table 3) and the summed Akaike weights (Table 4) the data support several candidate models. Therefore, we based our inference on more than one model. Model [S(.)] had the highest $QAIC_c$ weight (0.513, Table 3) and had the highest summed weight (0.443, Table 4), indicating no difference in survival of adult beavers on both rivers (S = 0.87 for the duration of the study, SE = 0.076, Figure 3). However, there was evidence for a lower survival on the Yampa River (model [S(f)], $QAIC_c$ weight = 0.212; model [S(g)], $QAIC_c$ weight = 0.198, Table 3 and Figure 3) probably due to predation.

In the fall of 1998, two of our radioed animals on the Yampa River were killed and eaten by a mountain lion. A third beaver (the mate of one killed) disappeared during this period and was censored from the data set. A fourth adult beaver was killed on the Yampa River in August 1998; it was not part of the survival data set but was suspected to be the mate of a radioed female. All predation events occurred when the Yampa River was near or below 30 m^3/s. On the Green River, no individuals were documented as killed by predators, though 3 disappeared and were censored from the data set.

In our post hoc analysis, the model [S(.) + mass] was a top model in the survival analysis, ($QAIC_c$ weight = 0.174, Table 5) and the mass variable ranked second in the summed Akaike weights (Table 4). Both these results indicated that the mass of beavers was linked to survival. The variable mass had a negative coefficient (-0.62) indicating that smaller adults had a lower survival probability than larger adults. The variable (sex) was generally associated with lower ranking models (Table 3) and had the second lowest summed Akaike weight (Table 4) indicating that sex of beavers had little affect on survival.

DISCUSSION

Vanden Berge and Vohs (1977) compared populations of bank dwelling beavers in bank-stabilized and free-flowing portions of the Missouri River. They found that stabilization decreased the density of beavers and ascribed it to habitat alteration, though they did not discuss what aspect of the habitat was altered. Our original hypotheses followed a similar premise that flow regulation caused a decrease in cottonwood and resulted in a negative demographic response from beaver populations. Instead we found evidence suggesting that flow regulation on the Green River has had a positive influence on the demographic response of beavers in the alluvial section below Flaming Gorge Dam. We believe this was due primarily to changes in distribution and availability of willow as a result of changes in the fluvial geomorphology (Breck Ch. 3).

Body mass and tail size have been used as indicators of body condition in beavers (Aleksiuk 1970, Smith and Jenkins 1997). Smith and Jenkins (1997) demonstrated that the body mass and size of beaver tails decreased during winter and that the amount of decrease varied between years and colonies depending on environmental conditions and the availability of food. Similarly, we demonstrated differences in body size and tail size for adults and sub-adults between rivers, which also may be explained by differences in food availability and environmental conditions caused by flow regulation.

On the Yampa River, sub-adults and adults had lower body mass and smaller tails (2 out of the 3 measurements, Table1) relative to sub-adult and adult beavers on the Green River, indicating that beavers on the Yampa were in poorer condition. This result could be misleading if adult beavers on the Yampa River were generally smaller than beavers on the Green River. However, neither of two adult skeletal measurements (zygomatic breadth and total length) differed between rivers (Table 1), indicating that beavers on the Yampa River were growing to a similar size but not storing as much fat as beavers on the Green River and therefore were in poorer condition.

One factor that may have lowered the condition of beavers on the Yampa River was the higher cost of attaining woody forage during the fall season. Though the abundance of cottonwood and willow was greater on the Yampa River, the availability of cottonwood and willow on the Yampa River dropped every year in late summer through late winter as the river returned to base flow. Each fall we observed beaver trails, varying from a few meters to 50 m, crossing sandy flats and sandbars to access woody forage (S. Breck personal observation). This overland travel to attain forage likely increased beavers energy expenditure (Basey and Jenkins 1995) that otherwise could have been stored as fat. On the Green River, though cottonwood was limited in abundance, the availability of willow was greater due to the stable flows and the redistribution of willow onto islands. Beavers utilized over twice as much willow on the Green River compared to the Yampa River (Breck Ch. 3) which required little or no overland travel and reduced energy expenditure for traveling.

Another explanation for the lower condition of beavers on the Yampa River was that over-winter conditions (namely ice cover) differed strongly between rivers. The surface of the Yampa River froze solid for varying periods each winter during the study, whereas the surface of the Green River remained open because of numerous factors associated with flow regulation. One observed consequence of this difference was that food caches were smaller on the Green River than on the Yampa River (S. Breck personal observation). We can only speculate on the effect that differences in food caching had on the energetics of beavers, but it is conceivable that beavers on the Green River had lower energy expenditure because they were able to forage year round without the energy cost of building a large cache.

In contrast to the older age classes, juvenile beavers on the Yampa River were as large or larger than juvenile beavers on the Green River for all body measurements. This result implies that juvenile beavers on the Yampa River were attaining a positive caloric balance as great or greater than juvenile beavers on the Green River. This result is only partly explained by the greater availability of forage during the flood period on the Yampa River. This is because we trapped and took body measurements in September and October after the Yampa River had been at base flow for 2 or 3 months and thus availability of forage had dropped. Another explanation is that juvenile beavers will maintain growth in the fall and winter by utilizing more of the stored food cache than adults and sub-adults (Novakowski 1967, Smith and Jenkins 1997). If older age-classes were harvesting food for juveniles, as our data support, this would result in even greater energy expenditure for adults on the Yampa River as they would have been expending energy foraging for themselves and juveniles.

Our estimates of density (0.50 and 0.35 colonies per km on the Green River and Yampa River, respectively) were at the lower range of those reported in other studies (see Hill 1982). This may be due to the fact that most studies of beavers occurred on stream systems where beavers were able to build dams and the availability of forage was greater. Strong (1982) provides the only other data concerning density of beavers on a large-order arid-land western river. He reported a density of 1.02 beaver/km on the alluvial sections of the Rio Grande in Big Bend National Park. If we assume that colonies in our study on average contained 5 beavers (Hill 1982), then the Green River had a density of 2.5 beavers/km and the Yampa River had a density of 1.75 beavers/km, nearly 2 to 2.5 times what Strong (1982) found.

Density of beavers is strongly related to the availability of forage (Lawrence 1954 and Rutherford 1955 in Jenkins 1979, Allen 1983, Baker and Cade 1995). On the Yampa River the overall availability of woody forage was much lower than on the Green River. This may explain why beaver densities were lower on the Yampa River, though the abundance of forage was much greater (Breck Ch. 3 and 4). Another explanation is that alternative foods were more abundant on the Green River. Merritt and Cooper (2000) documented the formation of marsh communities on the river margin of the Green River that were not present on the Yampa River. It is possible that these marsh communities provided alternative herbaceous forage for beavers during the spring and summer. However, the availability of herbaceous forage likely decreased in winter when beavers face critical energetic challenges (Dyck and MacArthur 1992). Therefore, even with the presence of alternative herbaceous forages on the Green River, we suggest the availability of willow was likely very important in explaining the higher density as beavers would need to rely on woody forage during the fall and winter.

The distribution and availability of forage may also explain the higher predation rates we documented on the Yampa River. During the base flow period, beavers were often forced to travel large distances across open land to forage on cottonwood and willow (Figure 3), which exposed them to a greater risk of predation (Basey and Jenkins 1995). In contrast, the islands on the Green River provided willow that was adjacent to the river and offered greater protection from predators because of the open water that predators must cross to access the islands. We did document beavers on the Green River traveling on shore to cut cottonwood in the three patches where it was available. However, these patches were close to the river (Breck Ch. 4), thus their use held less predation risk than most patches of cottonwood on the Yampa River at base flow.

Beavers with a smaller mass appeared to have a lower survival than larger beavers as indicated by the "mass" variable in the second to highest model in the survival analysis. It is very likely that this was a spurious result. We documented predation events only on the Yampa River and because beavers, on average, were smaller on the Yampa River, by default a mortality on the Yampa River would be correlated with mass.

Lesica and Miles (1999) speculated that flow regulation might have produced higher populations of beavers on the Marias River. They offered a different explanation for the increased densities, namely that flow regulation enhanced beaver denning habitat. They suggest that flooding is an important cause of beaver mortality and den abandonment (Hill 1982) and thus reduces the density of beavers on rivers that flood. Our data do not support this explanation. We found evidence that survival was higher on the Yampa River during the flood stage (Table 3, model S(f)), when beavers had easy access to preferred foods at minimal risk of predation. Nor was there any indication that juvenile beavers suffered mortality during the spring floods. We found beavers to be very adaptable to floods on the Yampa River by having a spring den that was used during the flood stage and a winter den that was used during base flows. We argue that the greater availability of forage was the primary factor supporting higher densities of beavers on the Green River.

We did not find a difference in home range size between rivers. However, on the

Yampa River we did document large areas between colonies that were not used by radioed beavers and showed very little sign of beaver activity. These unused areas contained woody forage but this forage was made unavailable much of the year by exceptionally large sandbars (over 100 m) that formed during base flows. On the Green River, the gaps between home ranges were much smaller if they existed at all. Consequently, there was no difference in home range size but a lower density of beavers on the Yampa River.

We found large variation in home range size between years for each family group and between family groups on each river. Wheatly (1997) is apparently the only other published study that measured home range size for beavers in a river environment (i.e., where they are unable to build dams). Although she quantified home range differently, making comparisons between studies difficult, she also recorded a great deal of variability. In our study this variability may be partly explained by the removal of individuals, either due to accidental trap mortality or predation events, which allowed beavers in adjacent territories to expand their range. On the Green River, during our first trapping season (fall 1997), one large adult male, presumably from an established territory was killed by a snare. One colony adjacent to this animal had a home range 400 m larger in 1998 (six months after the trap mortality) than it was in 1999. Similarly, on the Yampa River, predators killed the 2 adults from the same colony in the fall of 1998. After this event occurred, we documented the home range of an adjacent colony expanding by nearly 600 m.

Assessing the demographic response of a population of animals to changes in habitat is a difficult process (Garshelis 2000). In this study we measured 4 demographic variables to assess the effect that flow regulation had on beavers. Of the 4 variables, body condition and density provided the strongest evidence that habitat conditions for beavers were better on the Green River than on the Yampa River. Furthermore, there was some evidence that survival was lower for adult beavers on the Yampa River due to predation and that beavers rarely used certain stretches on the Yampa River because of the limited availability of forage. Thus, through weight of evidence, we argue that flow regulation may have benefited beavers and that the primary factor enhancing beaver populations was the greater availability of willow due to its shift in distribution from a bank-oriented to an island-oriented species.

MANAGEMENT IMPLICATIONS

Cottonwood trees are a critical component of riparian ecosystems in western U.S. Flow regulation due to the construction and operation of large dams has caused a severe decline in cottonwood regeneration on many western rivers (Cooper et al., 1999), leaving existing populations of young cottonwood vulnerable to other factors such as herbivory (Andersen and Cooper 2000). Because beavers are able to have a large impact on tree populations through their foraging activities, understanding how beavers respond to flow regulation may be very important for cottonwood restoration efforts. For example, simulated flooding below dams has been proposed as a means of restoring cottonwood recruitment (Bradley and Smith, 1986; Cooper et al., 1999). While flooding may have positive effects on the abiotic processes that encourage seed germination and seedling survival, it may also promote the visitation of beavers to already small cottonwood patches and have a negative effect on older established saplings (Andersen and Cooper 2000, Breck 2000).

On the Green River in Browns Park National Wildlife Refuge we found that beavers have responded positively to flow regulation. The primary reason for the positive demographic response was the greater availability of food (willow) resulting from the development of islands. We predict that as islands continue to form, grow, and support more willow, beaver density will increase. Unless beaver populations are controlled or individuals excluded from certain areas, the restoration of young cottonwood may be jeopardized.

Whether beavers have responded positively to flow regulation on other western U.S. rivers (e.g., the Rio Grande in New Mexico, the Colorado in Grand Canyon National Park, and sections of the Missouri River) is unknown. These rivers, like the Yampa and the Green Rivers, were historically driven by annual spring floods and are now highly controlled. It is known that stabilized flows have altered the riparian plant community. In cases where these alterations have increased the availability of preferred forage species, it is likely that beaver populations have also responded positively to flow regulation. Because of their ability to alter plant community composition, beavers may be having a profound effect on the riparian community on many flow-regulated rivers. More research is needed to determine the response of bank-dwelling beavers to flow regulation and the effect they are having on arid-land riparian ecosystems.

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TABLES AND FIGURES

Table 1. Body measurements of adult beavers captured during the fall of 1997-1999 on the Green and Yampa Rivers, northwest Colorado.

	Green River			Yampa River				
Variable	$\bar{x}$	SE	n	$\bar{x}$	SE	n	t	P
Body mass (kg)	20.91	0.48	20	18.68	0.56	15	3.04	0.005
Tail thickness (cm)	4.15	0.12	20	3.76	0.10	14	2.33	0.026
Tail width (cm)	15.34	0.28	20	14.17	0.27	14	2.88	0.007
Tail length (cm)	28.0	0.39	20	27.78	0.41	14	0.36	0.719
Total length (cm)	111.55	1.06	20	109.2	1.63	14	1.27	0.212
Zygomatic Arch (cm)	10.90	0.22	20	10.96	0.15	14	-0.24	0.812

Table 1. Continued. Subadult beavers.

	Green River			Yampa River				
Variable	$\bar{x}$	SE	n	$\bar{x}$	SE	n	t	P
Body mass (kg)	14.33	0.61	6	12.38	0.28	8	3.21	0.008
Tail thickness (cm)	3.33	0.13	6	2.96	0.08	7	2.59	0.025
Tail width (cm)	12.77	0.75	6	11.79	0.15	7	1.39	0.192
Tail length (cm)	25.85	0.66	6	24.01	0.33	7	2.61	0.024
Total length (cm)	98.58	1.81	6	92.43	1.05	7	3.04	0.012
Zygomatic Arch (cm)	9.97	0.18	6	10.17	0.19	7	-0.76	0.464

Table 1. Continued. Juvenile beavers.

	Green River			Yampa River				
Variable	$\bar{x}$	SE	n	$\bar{x}$	SE	n	t	P
Body mass (kg)	5.58	0.31	8	5.67	0.22	16	-0.24	0.812
Tail thickness (cm)	2.19	0.10	8	2.07	0.06	16	1.10	0.283
Tail width (cm)	8.25	0.38	8	7.85	0.21	16	1.01	0.325
Tail length (cm)	17.36	0.56	8	18.98	0.43	16	-2.24	0.036
Total length (cm)	69.46	1.65	8	71.16	1.00	16	-0.92	0.365
Zygomatic Arch (cm)	7.94	0.11	7	8.33	0.10	16	-2.40	0.026

Table 2. Mean linear home range size of beavers in spring 1998 and 1999 on the Green and Yampa Rivers in northwest Colorado.

Contour	River	Mean (km)	SE	df	P
95%	Green	2.19	0.457	10	0.755
	Yampa	2.38	0.232		
	Difference	-0.19	0.581		
75%	Green	1.81	0.425	10	0.445
	Yampa	2.24	0.225		
	Difference	-0.43	0.543		
50%	Green	1.25	0.464	10	0.702
	Yampa	1.01	0.289		
	Difference	0.24	0.606		

Table 3. Output from the AIC model selection process for the survival analysis of radio-marked adult beavers on the Green and Yampa Rivers in northwestern Colorado.

Model	QAIC	Delta QAICc	QAICc Weight	#Par	Deviance
{S(.)}	7.419	0.00	0.51330	1	31.282
{S(f)}	9.188	1.77	0.21206	2	29.651
{S(g)}	9.328	1.91	0.19772	2	30.459
{S(y)}	11.327	3.91	0.07277	3	30.008
{S(y +g)}	17.065	9.65	0.00414	6	26.213
{S(t)}	36.296	28.88	0.00000	15	17.315

Model Selection Based on c-hat = 5.77

Table 4. Summed QAICc weights of variables from the post hoc survival analysis of adult beavers (Table 3).

Variable	Summed Weight
(.)	0.443
(mass)	0.300
(f)	0.214
(g)	0.165
(sex)	0.138
(y)	0.041

Table 5. Output from the AIC model selection process for the survival analysis of radio-marked adult beavers on the Green and Yampa Rivers in northwestern Colorado. Post hoc variables (mass and sex) were added to models from Table 3.

Model	QAIC	Delta QAICc	QAICc Weight	#Par	Deviance
{S(.)}	7.419	0.00	0.26876	1	31.282
{S(.) + (mass)}	8.285	0.87	0.17431	2	24.410
{S(f)}	9.188	1.77	0.11098	2	29.651
{S(g)}	9.328	1.91	0.10348	2	30.459
{S (.) + (sex)}	9.398	1.98	0.09992	2	30.866
{S(f) + (mass)}	10.295	2.88	0.06381	3	24.025
{S(g) + (mass)}	10.359	2.94	0.06180	3	24.398
{S(f) + (sex)}	11.249	3.83	0.03960	3	29.559
{S(y)}	11.327	3.91	0.03809	3	30.008
{S(g) + (sex)}	11.379	3.96	0.03711	3	30.311
{S(y +g)}	17.065	9.65	0.00216	6	26.213
{S(t)}	36.296	28.88	0.00000	15	17.315

Model Selection Based on c-hat = 5.8

Figure 1. Location of study areas and Flaming Gorge Dam on the Green and Yampa Rivers in Northwestern Colorado 1997-1999.

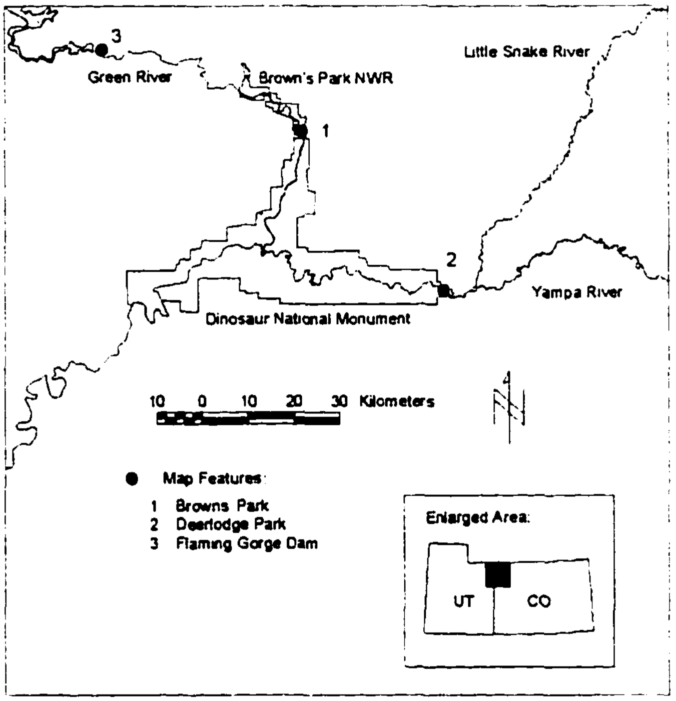


Figure 2. Average yearly flow for the Green River (pre-dam 1923-1962 and post-dam 1962-1994) and Yampa River (1923-1996). Peak and base flows on each river were similar prior to the completion of Flaming Gorge Dam. Flow regulation since 1962 on the Green River has resulted in the elimination of the peak flow and the increase in base flow.

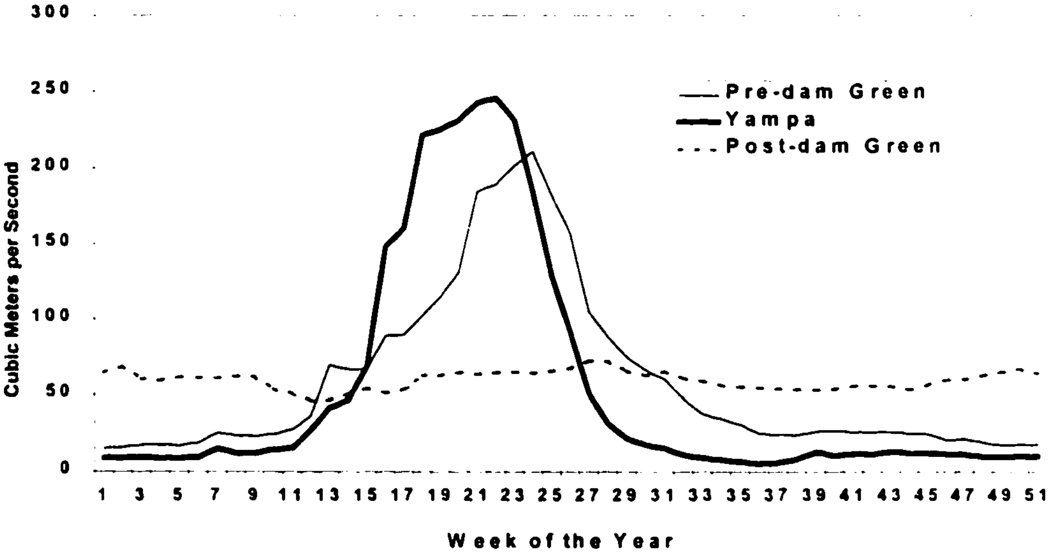
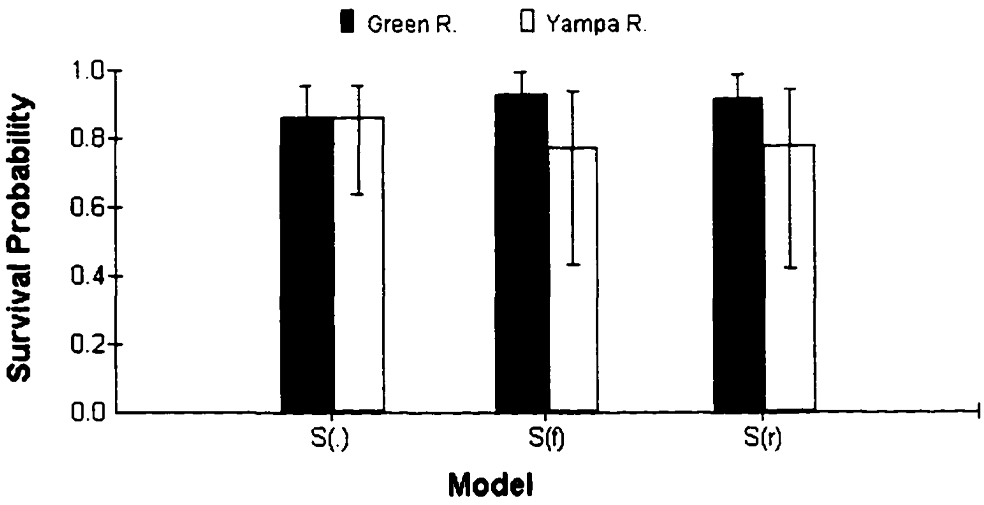


Figure 3. Probabilities of adult beavers surviving the duration of the study (2.5 years); calculated for the top three models from Table 3a. Error bars represent 95% CI.



CHAPTER 3

THE EFFECT OF FLOW REGULATION ON THE INTERACTIONS BETWEEN WILLOW (Salix exigua) AND BEAVERS

INTRODUCTION

Woody vegetation within riparian ecosystems plays an important role in ecosystem functioning and the maintenance of biodiversity, particularly in arid and semi-arid North America (Knopf et al. 1988, Gregory et al. 1991, Naiman and Decamps 1997). Many factors contribute to structuring woody vegetation in western U.S. riparian ecosystems, the most important of which is flow regime (Nilsson et al. 1991, Stromberg et al. 1991, Auble et al. 1994, Stanford et al. 1996, Naiman and Decamps 1997, Poff et al. 1997). Vertebrate herbivores, including livestock (Kauffman and Krueger 1984, Green and Kauffman 1995, Popotnik and Giuliano 2000), native ungulates (Kay 1994, Naiman and Rogers 1997, Singer et al. 1998, Opperman and Merenlender 2000) and smaller mammals (Barnes and Dibble 1988, Johnston and Naiman 1990, Taylor and Grace 1995, Andersen and Cooper 2000) can also affect the structure and function of riparian ecosystems through their selective foraging on plant species. What remains poorly understood is how flow regime influences herbivores and their ability to impact key woody species.

Andersen and Cooper (2000) addressed this issue by studying the impact of mammalian herbivores on Fremont cottonwood (*Populus deltoides* spp. wislizenii) on the free-flowing Yampa River and flow regulated Green River in northwest Colorado. They indicated that a small mammal (*Microtus montanus*) reduced seedling and sapling survivorship on the Green River because flow regulation allowed *M. montanus* populations to escape mortality normally accompanying annual spring floods. Their results highlight the importance of understanding the links between flooding and herbivores that lead to impacts on plant populations.

Willow (*Salix spp.*) are important riparian species that enhance ecological processes (e.g., nutrient cycling) and help maintain biological diversity (Knopf et al. 1988, Kindschy 1989, Snyder and Miller 1992, Baker and Cade 1995). Most Salix species are obligate phreatophytes (Busch et al. 1992), thus their distribution and abundance are dictated by the presence and actions of water (Stromberg et al. 1991). In rivers where flow modification has altered the hydrology and fluvial geomorphology, the distribution of willow is also altered (Stevens and Waring 1985, Merritt and Cooper 2000).

Willow is an important food resource for many herbivores and, in turn, can be affected by the foraging of animals. In general, the susceptibility of a plant population to changes caused by herbivory are a function of characteristics of the plant, the herbivore and factors that mediate the relationship between the herbivore and the plant (Gessaman and MacMahon 1984, Huntly 1991, Augustine and McNaughton 1998). Beavers (*Castor canadensis*) are semiaquatic mammals that can have a large impact on riparian plant communities through their foraging activities (Jenkins and Busher 1979, Johnston and

Naiman 1990, Pastor and Naiman 1992). The distribution and abundance of plants relative to a beaver's place of refuge are important factors dictating their influence on a plant population (Jenkins and Busher 1979, Basey et al. 1988). A strong relationship exits between willow and beavers, especially in aridland rivers where choices for woody forage are limited (Hall 1960, Kindschy 1985, Kindschy 1989, Baker and Cade 1995, Singer et al. 1998). Considering that flow regulation can alter the abundance and distribution of willow and that beavers depend on willow for winter forage, it is likely that the foraging behavior of beavers will respond to these changes and, in turn, that their effect on willow populations will be altered.

Our broad objective was to understand how flow regulation modified the nature and consequences of beaver-willow interactions relative to those that exist in the absence of regulation. We compared beaver and sandbar willow (*Salix exigua*) ecology on a set of matched rivers: the free-flowing Yampa River and the flow-regulated Green River. Our work was premised on the idea that regulation would lead to riparian vegetation changes independent of the presence of beavers. These changes were expected to alter the link between beavers and sandbar willow, thereby altering the influence of beavers on willow. Specific objectives included: 1) quantifying the changes in the distribution and abundance of willow resulting from flow regulation, 2) quantifying beaver herbivory rates on willow and identifying factors that influenced this interaction, and 3) identifying changes in the willow population and community as a result of beaver herbivory.

STUDY AREA

We conducted our study on the Green and Yampa Rivers above their confluence in northwestern Colorado. Our study sites were in alluvial valleys of each river: Browns

Park on the Green River and Deer Lodge Park on the Yampa River (Figure 1). At these locations, both rivers are 6th-order tributaries of the Colorado River and historically featured a meandering form that was influenced by a snowmelt driven spring flood. The Yampa River is free flowing and maintains its meandering form. The Green River has been flow regulated by Flaming Gorge Dam since late 1962 and is in transition to a braided system (Merritt and Cooper 2000).

The main assumption of our study was that prior to completion of Flaming Gorge Dam, the Green and Yampa Rivers featured similar flow regimes (Figure 2) and maintained similar riparian ecosystems. Flow data show the similarity in the historical flow regime, and pre-dam aerial photos demonstrated the similarity of the ecosystems. Both rivers are dominated by Fremont cottonwood and sandbar willow. Details of the ecosystems and the validity of our assumption are in Andrews (1986), Cooper et al. (1999), Andersen and Cooper (2000), and Merritt and Cooper (2000).

On the Yampa River, vegetation is distributed along a gradual, environmental gradient created and maintained by annual spring floods (Merritt and Cooper 2000). Patches of sandbar willow are generally found in the middle of this gradient along the edge of the active channel (i.e., the portion of the channel kept free of perennial vegetation by the spring floods) whereas patches of young Fremont cottonwood (another important forage species for beavers) are generally found on point bars and channel margin bars along the edge of the active channel. During periods of flooding (March-July), the river inundates patches of willow and cottonwood to various extents, depending upon the size of the flood peak. During this period both willow and cottonwood are easily accessible to beavers, because the high waters provide safety from predators

(Breck ch. 2). By August the Yampa River drops to its base flow which exposes large sandbars that separate the river from vegetation. The location of sandbars and subsequently the location of the base flow channel vary from year to year, which in turn influences where beavers can forage.

On the Green River flow regulation has altered the distribution of plants by altering the fluvial geomorphology, hydrology and edaphic conditions (Merritt and Cooper 2000). Two important changes have been the formation of islands in mid channel and the elimination of point bars (Merritt and Cooper 2000). As a result, sandbar willow has shifted from a primarily bank-oriented species to a primarily island-oriented species, patches of young cottonwood trees are rare and associated with old meander bends, and upland vegetation is encroaching to the edge of the active channel (Merritt and Cooper 2000).

METHODS

Willow Abundance and Distribution

We estimated willow abundance on each river, by quantifying the number of patches, total area of patches per km of river, and average density of willow stems. We quantified the number of willow patches by surveying the length of each study area and plotting the location of each patch on aerial photographs taken in July 1997 and August 1995 on the Green and Yampa Rivers, respectively. We estimated the dimension of patches by pacing the length and width of each patch at several locations depending on the size and shape of the patch. We plotted the patch locations and dimensions on GIS coverages of each study area using ArcView. The GIS coverages were developed from the aerial photos mentioned above. We used Arc View to quantify the number of patches and total area of willow on each river. To develop a comparable estimate between rivers, we divided the number of patches and total area of patches by the length of the study reach for each river. We calculated the length of each study reach based on the combined home range size of beavers that were judged to be using each area based on radio monitoring conducted as part of another study (Breck, Ch. 2). Our estimates of willow density were based on data from the exclosures, described below.

Willow Exclosures

In December of 1997, we established 36 exclosures and associated controls on each river. Each exclosure was 1x 2.7x 1 m (WxLxH) and built with 12.5 x 50.0 cm ranch wire fencing. The long side of the exclosure ran perpendicular to the river. The control plots were 1 x 2.7 m (WxL), ran parallel to the exclosures and were randomly placed 1 m away on either side of the exclosures. The exclosures and associated controls were established to monitor beaver herbivory on willow as a function of river (Yampa versus Green) and distance from the river; these exclosures do not prevent small mammals and ungulates from utilizing plants within the exclosures, but did also exclude adult rabbits.

We selected three patches on the Yampa River and 5 on the Green River to contain exclosures. Only three willow patches were selected on the Yampa River because the patches selected were much larger than on the Green River and could hold more exclosures. The main criterion for selecting a patch for exclosures was that the willow patch abutted the active channel. Exclosures were established along transects placed perpendicular to the river. Starting from the upstream end of each willow patch, we randomly selected a point within the first 25 m along the river's edge to begin the first transect. The remaining transects were spaced evenly from this point, with 30 to 70 m separating transects, depending on the patch length. Patches contained at least 2 and up to 6 transects. We established 16 transects on the Green River and 15 transects on the Yampa River.

Each transect contained 1 to 3 exclosures and associated controls, with the mid-point of the exclosure located an average of 1.5, 6, or 10 m from the active channel margin. We attempted to establish 1 exclosure at 1.5 and 6 m on each transect and limited the number of exclosures at 10 m in order to maximize our spatial coverage along the rivers. However, on the Green River 1 willow patch was too shallow to contain exclosures at 6 m. On the Yampa River 6 transects contained exclosures at (1.5, 6 and 10 m), and 9 transects contained exclosures at (1.5 and 6 m). On the Green River 7 transects contained exclosures at (1.5, 6 and 10 m), 5 transects contained exclosures at (1.5 and 6m), and 4 transects contained exclosures at (1.5 m).

We collected data on the diameter of stems and number of stems cut at four points in time (mid-September 1998, mid-April and mid-September1999, and mid-April 2000). During the fall, we measured the diameter of every live willow stem in both the exclosure and control plots. We used dial calipers and measured stems at 3 cm above the ground to the nearest 0.5 mm. Generally, branching of stems did not occur until well above 3 cm above the ground. However, if it did then we measured each branch as a separate stem. Stems less than 4 mm were not measured.

On the Yampa River we commonly found rabbit feces in the willow patches and suspected that they were feeding on smaller diameter willow stems (i.e., <7 mm), see (Figure 3). On the Green River we found no sign of rabbits, probably because rabbits were unwilling to swim to islands where most willow occurred. To remove bias, stems <7 mm were excluded from the analyses. There was sign that ungulates (cows, elk, moose and deer) were utilizing willow on both rivers. We did not measure ungulate herbivory because it was not heavy on either river (S. Breck, personal observation), was not different between the exclosures and controls, and was limited to the leaves and ends of branches which was much different from the affects of beavers.

Stems cut by beaver were also measured at 3 cm above the ground unless the cut was made below this level, then we measured the stem at the base of the cut. Very occasionally a branch was cut and a significant portion of the stem remained. In this case we recorded the diameter just below the cut branch and measured the live stem at the same height as the cut branch. Both of these measurements were used as independent measurements in the analyses. At the spring census, we only measured stems that had been cut in control plots because growth did not occur from September to April.

The density of stems was calculated for each exclosure by counting the number of stems in the exclosure and dividing by the area of the exclosure. This was done once in the spring of 1998 shortly after the exclosures had been built. Average density of willow for each river was estimated by averaging across exclosures.

Total Willow Removed

We applied a model developed by Baker and Cade (1995) to convert sandbar willow measures of stem diameter and density to estimates of the amount of food available (g/m^2) and amount of food used by beaver on each river. The model is a logistic function that relates diameter of stems to oven dried biomass of the bark, phloem and cambium layers of stems 3 mm and greater. Multiplying the predicted biomass (of each diameter class) by the density of willow stems (of each diameter class) estimates the amount of food available per unit area. Similarly, measuring the diameter of cut stems during an interval of time and applying the same procedure estimates the amount of food utilized.

We used the diameter measurements from control plots at the fall 1998 census to calculate the amount of food (g/m^2) available to beavers. We then used the measurements of cut stems from the spring 1999 census to calculate the amount of food that was removed (g/m^2) during the interval fall 1998 to spring 1999. We assumed that all cut stems were utilized for food, which is probably a valid assumption considering that beavers do not build dams on these rivers. Our estimates of the amount of food were comparable between rivers but were likely different than what Baker and Cade (1995) would have calculated. This is because we measured stem diameter lower than they did and we excluded stems <7mm.

Analyses of willow cut and willow growth rates

We performed two analyses on the exclosure/control data. The analyses followed a biologically based modeling philosophy as advocated by Burnham and Anderson (1998), where we collected the data, hypothesized models that explained the data prior to analysis, and then tested for the "best" (i.e., most parsimonious) models using Akiake's Information Criteria (AIC) (Akaike 1973). We used the small-sample correction of AIC adjusted for overdispersion ($QAIC_c$), see (Burnham and Anderson 1998:53 and Lebreton et al. 1992). Models with the lowest $QAIC_c$ values were considered competing best models (Burnham and Anderson 1998:63). In addition, we computed $QAIC_c$ weights ($\underline{\omega_i}$) which provide a measure for the evidence in support of a particular model (Burnham and

Anderson 1998:123-125). The combined weights of all models sum to 1, and larger weights indicate increased model support.

For the first analysis, we used data from the control plots to investigate the relationship between the percent of willow cut by beavers and four independent variables: season (fall/winter or spring/summer), river (Green or Yampa), distance from river (1.5, 6, or 10 m) and diameter of stems. We hypothesized 29 models that were created from various combinations of the four variables and used Proc GENMOD in SAS (1999) to run the models and create output required for the calculation of $QAIC_c$ values.

For the second analysis we used exclosure data to compare growth rates of willow on each river. For this analysis we calculated the average diameter of willow in each exclosure in fall 1998 and fall 1999. We then modeled the difference between these values against three variables: river (Green or Yampa), distance (1.5, 6, or 10.5 m) and transects (16 on Green and 15 on Yampa) nested within rivers. We again used Proc GENMOD of SAS (1999), and model selection was based on $QAIC_c$ values.

RESULTS

Abundance, Distribution, and Amount of Willow Removed

The areal extent of willow patches (m^2/km) was similar between rivers (Table 1), but the abundance of willow was less on the Green River because of the lower mean density of stems (Table 1). The distribution of willow on the Green River has shifted from a primarily bank-oriented species to a bank- and island-oriented species. This shift in distribution combined with the regulated flows resulted in a higher percentage of transects being adjacent to the river channel for the duration of the study on the Green River (100%) than on the Yampa River (60%). The change in distribution on the Green

River has also resulted in a greater number of willow patches and smaller average patch size (Table 1). The amount of biomass available to beavers as food in the fall of 1998 was less on the Green River (167 g/m^2) than on the Yampa River (220 g/m^2). In the following 6 months, beavers on the Green River removed over 2 times more willow (64 g/m^2, 38% of available willow food) than did beavers on the Yampa River (27 g/m^2, 12% of available willow).

Willow Cut

Based on the $QAIC_c$ weights (Table 2), the data support three candidate models that explain the percent of willow cut by beavers. Common to all three models were four variables (River, Season, Average Diameter, and Distance). In addition two interaction variables (River*Distance and River*Average Diameter) were components of the top three models. The proportion of willow stems cut by beavers was over 8 times greater on the Green River (25.8%) than on the Yampa River (3.2%) (Figures 3 and 4) and nearly 5 times greater during the fall and winter months (23.4%) than during spring and summer (5.6%). Large diameter stems (Figure 3) and stems closer to the active channel margin (Figure 4) were preferred.

Growth

Based on the $QAIC_c$ weights (Table 3) the data support several candidate models that explain growth patterns between rivers. The model [growth = (.)] had the highest $QAIC_c$ weight (0.628, Table 3), indicating that the growth rate of willow from fall 1998 to fall 1999 was equal on both rivers. However, there was some support for a greater growth rate (model [growth = river], $QAIC_c$ weight = 0.172) on the Green River (Mean Growth Rate = 0.96 mm SE = 0.23) than on the Yampa River (Mean Growth Rate = 0.49

mm, SE = 0.27), and for an inverse relationship between growth rate and distance of plants from the river (model [growth = distance], $QAIC_c$ weight = 0.133; Figure 5)

DISCUSSION

Although the amount of area containing willow was similar between rivers (Green River: 10,630 m^2/km, Yampa River: 10,607 m^2/km), the amount of willow available as food for beavers was 50 g/m^2 less on the Green River, primarily because of a lower stem density. The lower stem density may be due to the higher rates of beaver herbivory on the Green River (38% of the standing crop or 26% of available stems) versus the Yampa River (12% of the standing crop or 3% of the available stems). A number of studies have demonstrated that beavers are able to lower the stem density of woody species such as *Populus tremuloides*, *Fraxinus* spp., and *Carya cordiformis* (Barnes and Dibble 1988, Johnson and Naiman 1990). In a willow-dominated system similar to the Green River, Nolet et al. (1994) found that beavers did not have a large impact on willow. However, they reported a removal of only 1.5 % of the standing crop of willow, which is markedly lower than the values we found on the Green River. We suggest that beaver herbivory is a primary factor for lowering the stem density on the Green River primarily because of the high rates of removal. Monitoring the exclosures over a longer time period could reveal conclusive evidence about this question.

We detected evidence that willow growth rate was greater on the Green River than on the Yampa River (Table 3 and Figure 6). Important factors that influence the growth rate of willow are available water and nutrients (Busch et al. 1992, Turkington et al. 1998, Singer et al. 1998), air temperature (Kindschy 1989), the age of the stems (Baker and Cade 1995), and the effect of herbivores (Kindschy 1985). Possibly, the higher growth rate on the Green River was caused by a greater availability of water during the growing season. On the Yampa River, spring floods receded in early July, thus lowering the water table. This could have induced water stress and reduced photosynthesis during July and August, when air temperatures were warmest and growth potential greatest. On the regulated Green River the water table remains fairly constant year around because of relatively stable flows of the Green River (Merritt and Cooper 2000). Soils supporting willow remain saturated, or nearly so, throughout the growing season and may provide better growing conditions for willow (D. Cooper, Colorado State University, personal communication). Similarly, the available nitrogen is much higher along the shore of the Green River compared to the Yampa River in part because of higher mineralization rates (Adair 2001). Although these measurements were not taken on islands, it is suspected that available nitrogen on islands is similar to that along shore (C. Adair, Colorado State University, personal communication). A higher availability of nitrogen would help explain the higher growth rates of willow on the Green River.

Alternatively, lower stem density of willow on the Green River may have decreased competition between willow stems and allowed for a greater growth rate. If this was true then beavers may be responsible for increasing the growth rate of willow on the Green River. Kindschy (1985) found a strong correlation between percent of red willow (*Salix lasiandra*) stems cut by beavers and the amount of stem growth the following year. We believe that the difference in growth rate of sandbar willow between the Yampa and Green Rivers is probably a result of both environmental differences and differences in the amount of herbivory by beavers.

We also found evidence that the growth rate of sandbar willow was greater for plants closer to the river on both the Green and Yampa Rivers (Table 3 and Figure 4). We believe that this difference in growth rate is due primarily too herbivory by beavers. We documented that willow stems closer to the river experienced greater herbivory (Figure 4) and that beaver were selecting for larger diameter stems (Figure 3). We hypothesize that removal of older willow stems, which probably have a slower growth rate, were being replaced with younger, faster growing stems. This process was occurring at a faster rate closer to the river because the herbivory pressure was higher close to the river. It is also possible that willow close to the river grew faster because water availability was higher there. This is an area for further investigation.

Many factors, known to influence the feeding behavior of beavers, were also documented in our study. Our finding that beavers selected for larger stems and stems closer to water may be the result of balancing the need for food with the risk of predation (Jenkins 1980, Basey et al. 1988). We also found that beavers cut willow primarily during the fall and winter, which is the result of beavers' dependence on woody forage in the fall and winter months (Jenkins and Busher 1979, Hill 1982). Unique to this study was our finding that flow regulation may alter the interaction between beavers and willow (i.e., more than twice as much willow was cut on the Green River than on the Yampa River).

Three alternative hypotheses might explain the large difference in amount of willow cut between rivers. The first hypothesis is that beaver densities were higher on the Green River, causing a higher rate of herbivory. Breck (Ch. 2) found that beaver densities were indeed higher on the Green River (0.5 colonies/km) than on the Yampa

River (0.35 colonies/km). However, assuming a linear relationship between the density of beavers and the amount of willow cut, the higher densities on the Green River cannot alone account for the two fold increase.

The second hypothesis is that the accessibility of willow to beavers is greater on the Green River because of the shift in distribution of willow and the stability of flows. For beavers, the availability of forage is primarily a function of the proximity of food to water. Willow closer to water is associated with less predation risk and less energetic costs for foraging and therefore is more valuable. The shift in the spatial distribution of willow from primarily bank-oriented to primarily island-oriented, combined with the relatively stable flows, served to increase the quality of willow by making foraging less expensive (energetically) for Green River beavers than for beavers foraging on the Yampa River. Furthermore, because willow grows on islands, the amount of willow area that interfaces with water increased compared to patches on the bank, which further increased the availability of willow to beavers. Other factors that probably increased the availability of forage on the Green River were the size and number of patches. On the Green River, the patch size was smaller and the number of patches was greater than on the Yampa River. These characteristics increased the availability of willow by creating more patch surface area adjacent to water and decreasing the maximum distance of willow from water.

In contrast, the natural flood regime of the Yampa River features dramatic seasonal fluctuations in flow. During the spring and summer flood season (4-5 months), willow was easily accessible to beaver because the river either inundated willow patches or ran adjacent to them. However, during the fall, winter and early spring, when beavers rely on woody forage, the Yampa River had dropped to base flows and exposed extensive sandbars between the river and the willow. These sandbars lowered availability of forage by both increasing risk of predation and increasing energy expenditure associated with traveling to willow patches. The importance of the proximity of willow patches to water is revealed by the fact that 90% of the willow that was cut on the Yampa occurred when the river ran adjacent to willow patches. Furthermore, because patches of forage are not on islands in the river, less of the perimeter interfaces with water which acts to further lower the availability of forage.

The third hypothesis is that the abundance of other woody forage, primarily Fremont cottonwood, has decreased on the Green River, forcing beavers to rely primarily on willow for winter forage. Breck (Ch. 4) documented that total abundance of young Fremont cottonwood was over 5 times greater on the Yampa River than on the Green River and that beavers utilized relatively more cottonwood on the Yampa River than on the Green River. The decrease in cottonwood on the Green River likely contributed to the increase in utilization of willow.

The explanation for higher rates of willow cutting on the Green River probably involves all three hypotheses, though we argue the primary factor is greater availability of willow. Our argument assumes that beavers were able to survive on a winter diet consisting primarily of willow and that willow was regenerating at a rate fast enough to prevent a decline in its availability to beavers. A number of studies support the assumption that beavers can subsist primarily on willow (Hall 1960, Nolet et al. 1994, Baker and Cade 1995). Nolet et al. (1994) found that the winter diet of European beaver (*Castor fiber*) consisted of 90% willow and suggested that non-willow species were probably utilized for their mineral content. Though we did not assess winter diets of beavers, our data on the percent of willow and cottonwood cut indicate that willow was the primary component of their diet on the Green River. Because the amount of available forage strongly influences the density of beavers (Jenkins 1979, Allen 1983, Baker and Cade 1995), this implies a strong positive relationship between amount of willow and density of beavers on the Green River. Willow abundance will likely increase with the predicted increase in number and size of islands (Merritt and Cooper 2000). This should lead to an increase in beaver density. The affect of such an increase on the few existing patches of cottonwood is unclear, but it would almost certainly be negative. Because of the ability of beavers to remove large amounts of biomass from riparian ecosystems, a higher beaver density could have important consequences for the structure and functioning of riparian ecosystems and efforts to maintain or restore stands of cottonwood trees (Nolet et al. 1994).

On the Green River nearly 30% of available willow stems were removed annually within a distance of 10.5 m from shore and this high rate of removal has likely occurred since willow became established on islands. The ability of willow to provide continued sustenance to beavers depends in part on the net primary productivity of sandbar willow and the ability of sandbar willow to replace lost biomass. This rate of removal does not appear to affect willow to the point that stand health is in jeopardy. This is due partly to the ability of sandbar willow to replace lost biomass and partly to the timing of herbivory by beavers. Beavers did most cutting in fall and winter, during a period when willow is least subject to adverse impact (Kindschy 1989). Kindschy (1989) found similar temporal cutting patterns in his study and also found that willow cut while dormant exhibited a more rapid recovery than those cut during the active growing period.

Herbivory by beavers is maintaining sandbar willow in an earlier successional stage, which we hypothesize, is having an impact on other aspects of the community. The rate of nutrient cycling within the willow community has likely been altered. Possibly, the competitive ability of willow has been altered, which may influence the overall species composition. For example, Woods et al. (1996) found that the probability of attack by a galling sawfly (*Euura* sp.) was 10 times greater on 1-year-old sandbar willow ramets than on 2- to 9-year-old ramets. Beaver herbivory promotes suckering and maintains willow stands in a younger phase, and thus may have important consequences on this insect which occurs in Browns Park (B. Kondratieff, Colorado State University, personal communication).

Overall, the nearly doubled rate of herbivory and nearly 8-fold increase in percent of stems removed suggests that beavers have become a much more important force in structuring the riparian ecosystem on the regulated Green River than on the free-flowing Yampa River. Whether this postulated shift in importance among resident riparian herbivores is a general pattern accompanying shifts in flow regimes is unknown. But our assessment of beaver herbivory, together with the shift in importance noted for *Microtus montanus* elsewhere on the Green River (Andersen and Cooper 2000), and the fact that nearly 75,000 rivers and streams in the U.S. are now regulated, suggest this is a critical area for future research.

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TABLES AND FIGURES

Table 1. Amount of sandbar willow on the Green and Yampa Rivers in northwest Colorado, October 1998.

Variable	Green River	Yampa River
Patch Area (m^2)	107,363	91,219
Patch Area / km (m^2/km)	10,630	10,607
Number of Patches	28	22
Number Patches per km (#/km)	3.96	2.91
Mean Patch Size (m^2) [SE]	3700 [1121]	4146 [1670]
Mean Density of Stems (stems/m^2) [SE]	29.04 [1.90]	36.71 [2.82]

Table 2. Top 5 models that explain the percent of willow cut on the Green and Yampa Rivers in northwest Colorado, Sept. 1998-April 2000, selected from 29 models using model selection procedure as suggested by Burnham and Anderson (1998). NPAR is the number of parameters, QAICc is a version of Akaike's information criteria adjusted for overdispersion, ΔQAICc is QAIC differences relative to the smallest QAIC value in the set, WEIGHT is an estimate of the likelihood of each model (Burnham and Anderson 1998). Variables in models are: seas-(September-April and April-September), river-(Green and Yampa Rivers), dist-(1.5 m, 6 m, and 10.5 m), avgdiam-(average diameter of stem in each exclosure), * indicates an interaction between two variables.

MODEL	NPAR	QAICc	ΔQAICc	WEIGHT
Seas river dist avgdiam	5	-6712.27	0.00	0.35
Seas river dist avgdiam river*dist	6	-6712.00	0.28	0.31
Seas river dist avgdiam river*avgdiam	6	-6711.79	0.49	0.28
Seas river dist	4	-6708.71	3.57	0.06
Seas river dist avgdiam river*dist seas*river	7	-6698.94	13.34	0.00

Table 3. Top 5 models that explain the growth patterns on the Green and Yampa Rivers in northwest Colorado, Sept. 1998-April 2000, selected from 8 models using model selection procedure as suggested by Burnham and Anderson (1998). NPAR is the number of parameters, QAICc is a version of Akaike's information criteria adjusted for overdispersion, ΔQAICc is QAIC differences relative to the smallest QAIC value in the set, WEIGHT is an estimate of the likelihood of each model (Burnham and Anderson 1998). Variables in models are: (.)- no difference between rivers or distance, river-(Green and Yampa River), dist (1.5 m, 6 m, 10.5 m), * indicates an interaction between two variables.

MODEL	NPAR	QAICc	ΔQAICc	WEIGHT
Diff = (.)	1	112.75	0.00	0.628
Diff = river	2	115.34	2.59	0.172
Diff = dist	2	115.86	3.11	0.133
Diff = river dist	3	117.95	5.20	0.047
Diff = river dist river*dist	4	119.60	6.85	0.020

Figure 1. Location of study areas and Flaming Gorge Dam on the Green and Yampa Rivers in Northwestern Colorado 1997-1999.

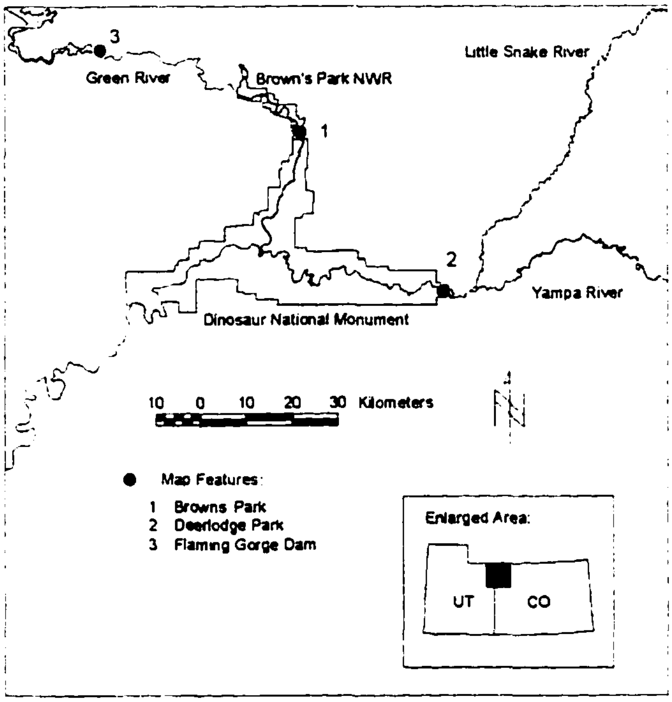


Figure 2. Average yearly flow for the Green River (pre-dam 1940-1962 and post-dam 1962-1995) and Yampa River (1940-1995). Peak and base flows on each river were similar prior to the completion of Flaming Gorge Dam. Flow regulation since 1962 on the Green River has resulted in the elimination of the peak flow and the increase in base flow.

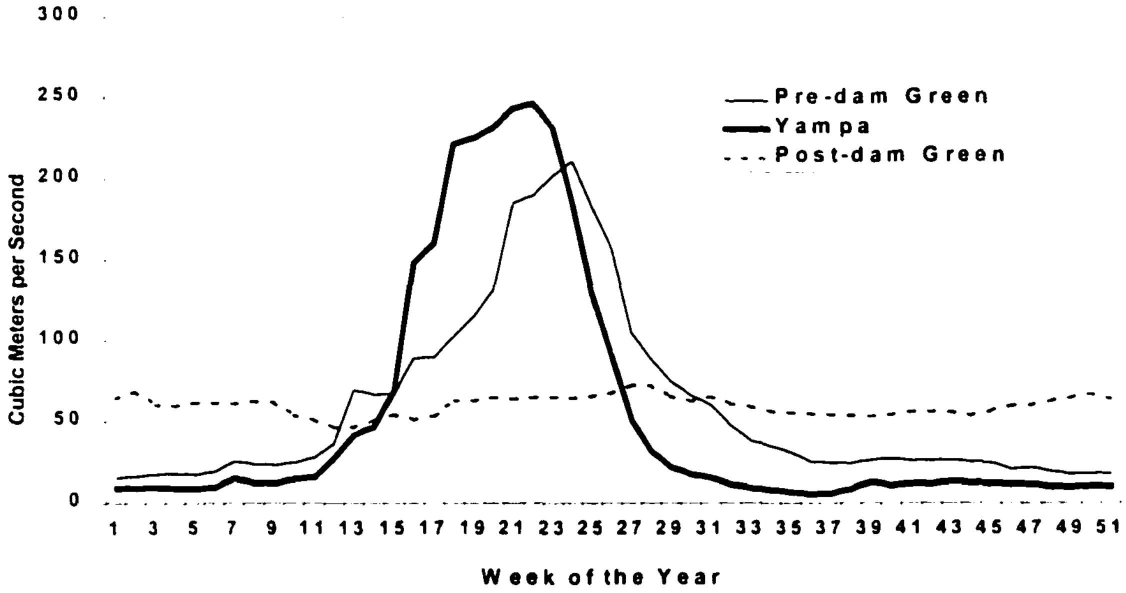


Figure 3. Percent of willow cut by beavers by stem diameter categories on the Green and Yampa Rivers in northwest Colorado, September 1998-April 2000. On the Yampa River we documented a higher rate of herbivory at lower diameters (<7mm), which we believe is due to rabbits. Sign of feeding by rabbits was not documented on the Green River probably because most of the willow was on islands, which rabbits were unable to access.

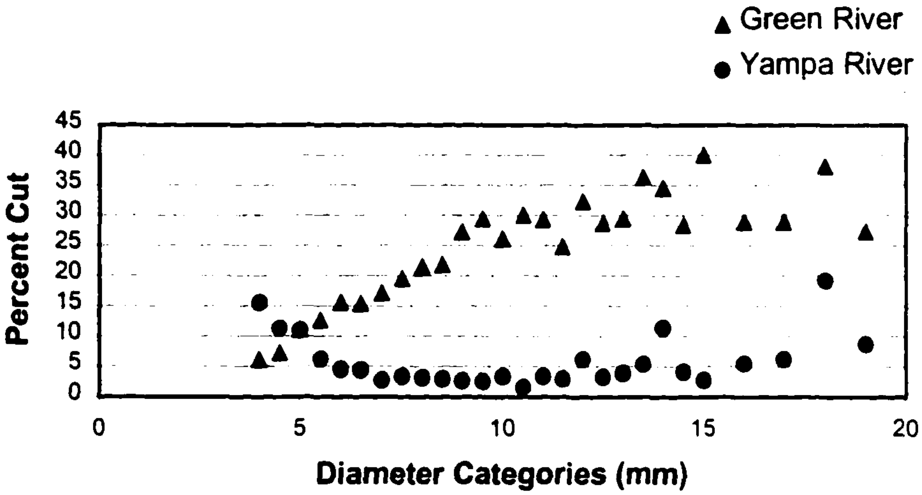


Figure 4. Percent of willow stems cut by beavers at 1.5 m, 6 m, and 10.5 m and SE on the Green and Yampa Rivers in northwest Colorado, Sept. 1998-April 2000.

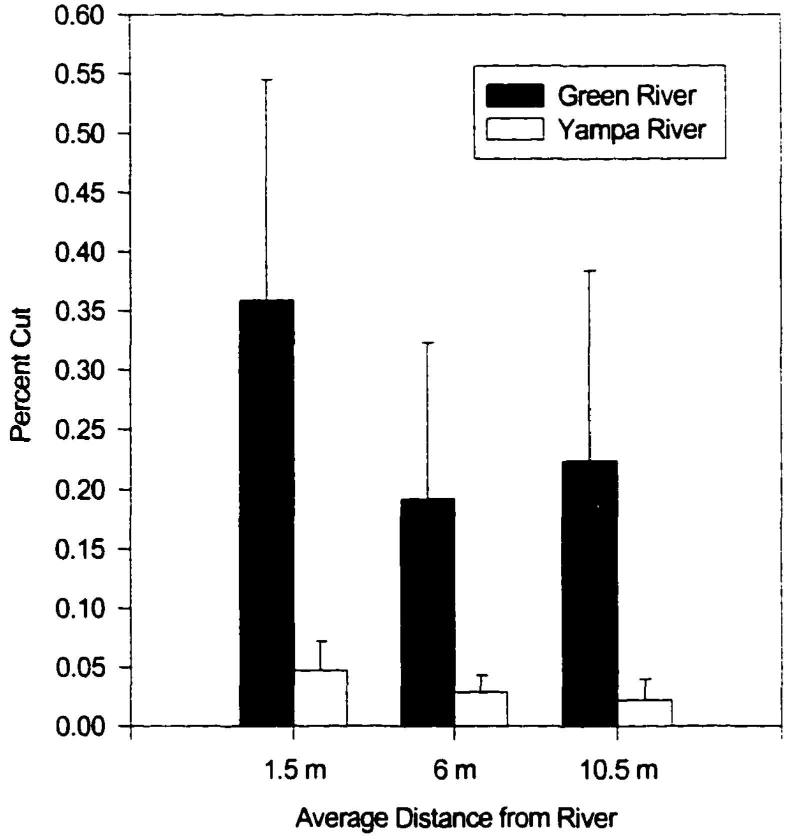
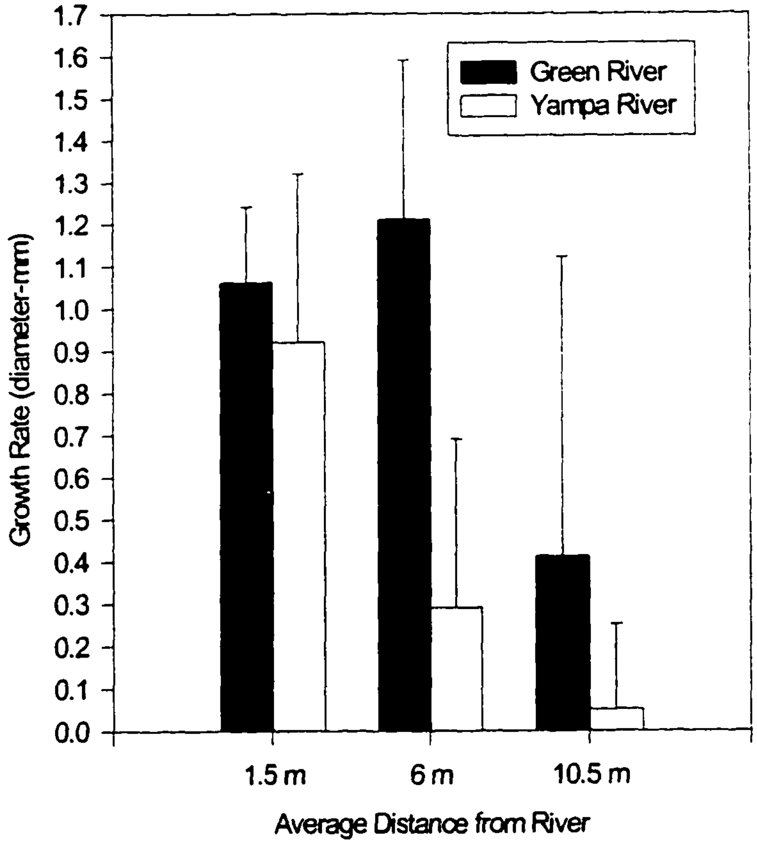


Figure 5. Growth Rate (diameter-mm) and SE of sandbar willow at 1.5 m, 6 m, and 10.5 m on the Green and Yampa Rivers in northwest Colorado, Sept. 1998-April 2000.



CHAPTER 4

FACTORS INFLUENCING HERBIVORY RATE BY BEAVERS AND THE SURVIVAL OF COTTONWOOD TREES ON FLOW REGULATED AND FREE FLOWING RIVERS

INTRODUCTION

Cottonwood forests along arid rivers of western U. S. are often a critical and irreplaceable component of riparian ecosystems (Knopf et al. 1988, Gregory et al. 1991, Braatne et al. 1996). Flow modification due to the diversion of water and operation of large dams is partially responsible for a drastic decline in cottonwood recruitment along many rivers (Reily and Johnson 1982, Fenner et al. 1985, Howe and Knopf 1991, Snyder and Miller 1992, Rood and Mahoney 1995, Busch and Smith 1995, Braatne et al. 1996, Cooper et al. 1999). The reasons for the decline involve both biotic and abiotic processes that are influenced by flow regulation and can vary with geomorphic setting and ecological factors that influence the growth and survival of cottonwood (Braatne et al. 1996, Scott et al. 1996). Most research has focused on abiotic alterations due to flow regulation and their influence on younger stages (seed germination and seedling survival) of cottonwood recruitment (Bradley and Smith 1986, Stromberg et al. 1991, Segelquist et al. 1993, Scott et al. 1997, Cooper et al. 1999). Biotic factors that influence cottonwood recruitment under a flow-regulated regime remain poorly understood but are potentially important, particularly in terms of restoration of cottonwood gallery forests (Braatne et al. 1996, Andersen and Cooper 2000).

Herbivory is a biotic factor that plays an important role in the structure and functioning of many ecosystems (Gessaman and MacMahon 1984, Huntly 1991, Hobbs 1996, Naiman and Rogers 1997). In riparian ecosystems, beavers can be important because of their ability to cut down trees and remove an exceptionally large amount of biomass (Gill 1971, Johnston and Naiman 1990). In some instances these abilities allow beavers to suppress tree populations and alter the species composition of the riparian ecosystem (Barnes and Dibble 1988, Johnston and Naiman 1990, Nolet et al. 1994). Understanding when beavers impact trees is an important management consideration, particularly if the tree species is a critical component of the ecosystem (e.g., cottonwood).

Whether or not a tree species is affected by beavers will depend on a number of factors, including: the ability of the tree species to replace lost biomass, the density of beavers, and rates of herbivory (i.e., number of trees eaten per beaver per unit time) (McGinley and Whitham 1985, Johnston and Naiman 1990, Morgan et al. 1997, Augustine and McNaughton 1998). Herbivory rates are influenced by a number of factors, including: abundance of forage, distance of plants from water, diameter of trees, nutritional quality of forage, presence of alternative forage species, and threats from predators (Jenkins 1980, Belovsky 1984, Basey et al. 1988, Fryxell and Doucet 1991, Doucet and Fryxell 1993, Fryxell et al. 1994).

Much research on beaver foraging has been conducted where beavers create ponds or in artificial settings that simulate beaver ponds. On large rivers where beavers cannot create ponds, less is known about their foraging behavior or how the dynamics of river flow may alter their ability to impact a tree population. With abundant cottonwood recruitment, beaver herbivory likely impacts the growth and survival of trees close to the river (McGinley and Whitham 1985), though it appears to play a minor role in limiting or regulating the cottonwood population (Strong 1982, Andersen and Cooper 2000). On flow-regulated rivers, cottonwood recruitment can be spatially restricted and lead to a situation where trees are more vulnerable to beaver herbivory. For instance, controlled flooding below dams has been proposed as a means of restoring cottonwood recruitment (Bradley and Smith 1986, Molles et al. 1998, Cooper et al. 1999). Although flooding may have positive effects on the abiotic processes that encourage seed germination and seedling survival, the access provided by the flood event could also promote the visitation of beavers to already small cottonwood patches and have a negative effect on older established saplings (Andersen and Cooper 2000).

In this study we asked whether flow regulation and the subsequent changes in cottonwood abundance have altered either the foraging behavior of beavers or their ability to influence cottonwood tree populations. To address these questions we compared herbivory rates by beavers to characteristics of cottonwood and the survival of cottonwood as influenced by beavers on two rivers: the free-flowing Yampa River and the flow-regulated Green River. We report on factors that we found to be important in the interaction, including: cottonwood tree densities, spatial arrangement of cottonwood patches, the depth and duration of controlled floods and the presence of alternative forage. Our work extends that of Andersen and Cooper (2000) who studied the effect of all mammalian herbivores on the survival of cottonwood seedlings on the Yampa and

Green Rivers. We assessed conditions at a different, more regulated site on the Green River that was examined by these authors, focused strictly on beaver herbivory, and measured herbivory during the only two relatively large, controlled floods on the Green River since 1986. These flows, which occurred in 1998 and 1999, were 1.8 and 2.2 times greater than the mean post-dam annual flood.

THE STUDY REACHES

We conducted our study on the Green and Yampa Rivers above their confluence in northwestern Colorado. Our study sites were in alluvial valleys of each river: Browns Park on the Green River and Deer Lodge Park on the Yampa River (Figure 1). The Yampa River is free flowing and the Green River is flow regulated, due to the 1962 completion of Flaming Gorge Dam. Both rivers are 6th-ordered tributaries of the Colorado River and have a spring run off that is snowmelt driven.

The main assumption of our study was that prior to completion of Flaming Gorge Dam, the Green and Yampa Rivers operated with similar flow regimes and maintained similar riparian ecosystems. Flow data show the similarity in the historical flow regime and pre-dam aerial photos demonstrated the similarity of the ecosystems, which consisted primarily of Fremont cottonwood (*Populus deltoides* spp. wislizenii) and sandbar willow (*Salix exigua*). Details of the historic flow regimes and support for our assumption are in Andrews (1986), Cooper et al. (1999), Andersen and Cooper (2000), and Merritt and Cooper (2000).

On the Yampa River recruitment of cottonwood seedlings occurs each spring and is generally relegated to point bars. Moving away from the river and perpendicular to the point bar, cottonwood tree ages increase tracking prior recruitment events. The results are large, dense patches of cottonwood. On the Green River in Browns Park, flow regulation has had an important impact on the fluvial geomorphology, which in turn has impacted the vegetation. Two important changes in the fluvial geomorphology were the formation of mid-channel islands and the elimination of point bars (Cooper et al. 1999, Merritt and Cooper 2000). As a result, sandbar willow has shifted from a primarily bank-oriented species to a primarily island-oriented species and recruitment of Fremont cottonwood has severely declined (Cooper et al. 1999). Current recruitment may best be described as a limited replenishment model characterized by infrequent high flow events that encourage seedling recruitment on low terraces that are close to the river (e.g., abandoned high water channels) (Braatne et al. 1996, Merritt and Cooper 2000).

METHODS

We obtained flow data for the period 1 September 1997 through 1 November 1999 from USGS gauging stations (Figure 1). For Browns Park, we used data from the Greendale, UT gauge (#09234500) located just below the dam. For Deer Lodge Park, we summed discharges of the Yampa River at Maybell, CO (gauge #09251000) and the Little Snake River at Lily Park, CO (gauge # 09260000).

Cottonwood Abundance

We estimated the abundance of cottonwood less than 100-cm diameter at 30 cm above ground on each river by quantifying the number of patches, total area, and density. We quantified the number of cottonwood patches by surveying the length of each study area and plotting the location of each patch on aerial photographs taken in July 1997 and August 1995 on the Green and Yampa Rivers, respectively. We estimated the dimension of patches by pacing the length and width of each patch at several locations depending on the size and shape of the patch. We plotted the patch locations and dimensions on GIS coverages of each study area using ArcView. The GIS coverages were developed from the aerial photos mentioned above. We used ArcView to quantify the number of patches and total area of cottonwood on each river. To develop a comparable estimate between rivers, we divided the number of patches and total area of patches by the length of the study reach, measured on channel centerline, for each river. We calculated the length of each study reach based on the combined home range size of beavers that were judged to be using each area based on radio monitoring conducted as part of another study (Breck Ch 2). Our estimates of cottonwood tree density were based on data from belt transects, described below.

Belt Transects

In May 1998, we established sets of 1-m and 2-m wide, respectively, belt transects in three cottonwood patches on the Yampa River (YDE, YCM, and YCB) and two patches on the Green River (GAB and GU5). Our goal was to place transects in 3 patches on each river. However, on the Green River there were only 2 patches of cottonwood within our study area. Due to a lower density of trees on the Green River, transects were 2-m wide to increase the sample size of marked trees. Perpendicular-to-the-river transects were placed by first calculating parallel-to-the-river length of each patch and dividing this length by 10; this determined the distance between transects. A random starting point for the first transect was chosen within the first 25 m of the upstream end of the cottonwood patch. Parallel-to-the-river length ranged from 300-470 m on the Green River and from 150-900 m on the Yampa River. Most patches resulted in 9-10 transects except for one small patch on the Yampa River (YCB) that had 4 transects.

We estimated the mean density of cottonwood trees on each river by calculating the density for each belt transect (number of trees/area of transect), and then averaging the transect densities for each river.

All trees in each transect were tagged and the diameter recorded at 30 cm above ground. Trees with a diameter less than 7 mm were not included because observations indicated that beavers did not cut below this diameter (S. Breck, personal observation). From May 1998 to November 1999 we assessed condition of each tagged tree (i.e., encounter occasion) a total of 8 times on the Yampa River and 9 times on the Green River (Figure 2), including the initial marking occassion. We added an extra interval on the Green River to isolate the effect of the peak flow during the large controlled flood of 1999. The intervals between encounter occasions varied in length from 1 month to 4 months (Figure 2). For each encounter occasion, we recorded each tree as either alive and uncut, cut by beaver, dead and not cut by beaver, or not found. How we used these distinctions is explained in the survival analysis below.

Distance of Patches from River

We measured the distances from the river of every tree tagged in the belt transect. On the Yampa River the distance from trees to the river was difficult to quantify because the varying water levels created varying distance of trees to water. Thus we assigned a value of 0 to trees in each transect that were closest to the river. Distances of the remaining trees in each transect were relative to the first tree. During base flow (August-March – Figure 2) large sandbars formed between the trees and river, making the trees farther from the river than our measurement reflected. To attain a more accurate measure of the distances we plotted the belt transects on the GIS image of the Yampa River, which reflects base flows in 1995, and measured the distance from the end of each transect to water. We added this value to each tree in each transect. On the Green River, distance from trees to water was a straightforward measure because of relatively stable flows and generally steeper banks. On both rivers, flood waters confounded the distance measure by inundating cottonwood patches and effectively making the distance from the river to each tree = 0. Consequently, we weighted the distance of each tree by the number of months it was not inundated by water (11/12 for the Green River and 8/12 for the Yampa-see Figure 2). We used these weighted means for each individual tree to calculate the mean distance of each patch from the river.

Herbivory Rate

First, we estimated total number of cut stems on each river by dividing number of trees cut by the proportion of cottonwood area sampled (i.e., total # of cut stems = # of cut trees / proportion of cottonwood area sampled). The herbivory rate was calculated by dividing the above result by the estimated kg of beaver per river section (i.e., total # cut stems / kg of beaver). The kg of beaver per river was estimated by intensive trapping in the fall of 1999 (Breck ch2).

Analyses

We estimated the probability of a tree being cut down by a beaver during each interval. We used the known fates option in program MARK (White and Burnham 1999) to perform the analyses. Known fates is a model based on capture-recapture methodology where individuals are marked and then followed through time. Each "recapture" occasion allows survival to be estimated for that interval and assumes that the probability of detecting each individual is one. Marked trees are ideal for the known fates model because there is a high probability of finding all marked individuals on each search occasion. Those trees that died or could not be found were censored from the data set at the interval when they were recorded as dead or lost. Censuring prevents the individual from continuing to contribute to the analysis from that point. "Survival" in this case is a measure of the probability of not being cut down by a beaver and does not reflect the true survival of the tree. For example, a tree could have been cut down but survived and re-sprouted.

Each analysis followed a biologically-based modeling philosophy as advocated by Burnham and Anderson (1998), where we collected the data, hypothesized models that explained the data prior to analysis, and then selected the "best" (i.e., most parsimonious) models using Akiake's Information Criteria (AIC) (Akaike 1973). We computed the small sample correction, AIC_c, except when overdispersed data was indicated, at which time we computed $QAIC_c$ (Burnham and Anderson 1998). Overdispersion was likely because herbivory events on individual trees likely were not independent. An overdispersion correction factor was calculated from the fully parameterized model (Burnham and Anderson, 1998) and applied to all models. Further, we computed AIC_c or $QAIC_c$ weights ($\underline{\omega_i}$) which provide a measure for evidence in support of a particular model (Burnham and Anderson 1998: 123-125); the sum of all model weights equals 1. For each analysis, we report the models with the lowest AIC_c or $QAIC_c$ values and largest weights; these are considered the "best" models based on the data (Burnham and Anderson 1998).

We first compared the probability of beaver cutting cottonwood on the Green River versus the Yampa River. For this analysis we eliminated the extra encounter occasion (interval 7, Figure 2) from the Green River so that intervals were equal between rivers. We hypothesized 10 models a priori to analysis:

[S(.)] survival was the same for all 5 patches and all time intervals,

[S(r)] survival differed between the rivers,

[S(t)] survival differed for each time interval,

[S(p)] survival differed for all 5 patches,

[S(p+t)] survival differed for all 5 patches and for each time interval,

[S(f)] survival was lower during the flood intervals only,

[S(p)+(f)] survival differed between patches and was lower during the flood intervals,

[S(fall)] survival was lower during the fall intervals only,

[S(p)+(fall)] survival differed between patches and was lower during the fall intervals,

[S(p) + (flood,fall)] survival differed between patches and was lower during the fall and flood intervals.

In addition, we added two covariates (distance and diameter), separately, to each of the 10 base models before the analysis, i.e., 20 models in total. These models tested whether size or distance from water influenced a tree's likelihood of being cut by beaver (Jenkins 1980). Our data indicated a weak relationship for the variables, therefore, we performed a post-hoc analysis using the Kolmogorov-Smirnov goodness of fit test to test whether the diameters and distances of cut trees had the same distribution as available trees. We performed this test separately for each variable and each river.

For the second survival analysis, we focused on the Green River to investigate how controlled flooding affected beaver herbivory of cottonwood. There were two patches (GU5 and GAB) and 8 time intervals. We hypothesized the following models a priori to analysis:

[S(.)] survival was the same for both patches and all time intervals,

[S(t)] survival differed for each time interval,

[S(p)] survival differed for patches,

[S(p+t)] survival differed for patches and time intervals,

[S(p+s1)] survival differed for patches, the mean of the two spring time intervals, and the mean of all other time intervals,

[S(p+s2)] survival differed for patches, the 1st spring, the 2nd spring, and the mean of all other time intervals,

[S(flood)] survival differed only during the flood intervals.

RESULTS

Abundance, Density, Distance of Patches and Herbivory Rate

The weighted distance of patches from the river were 1.5 to 3 times greater on the Yampa River (YDE: 117 m, SE = 1.67 m; YCM: 107 m, SE=1.41 m; YCB: 86 m, SE = 1.03 m) than they were on the Green River (GAB: 59 m, SE = 1.74 m; GU5: 42 m, SE = 1.29 m). The average diameter of trees was smaller on the Green River (GU5: 17.4 cm, SE= 0.76; GAB: 28.5 cm, SE= 2.92) than on the Yampa River (YDE: 36.5 cm, SE= 1.63; YCM: 25.3 cm, SE= 0.64; YCB: 29.7 cm, SE=1.59). The cottonwood area/km, number of patches/km and density (stems/m^2) were all much lower on the Green River compared to the Yampa River (Table 1). We sampled 1.3% and 12.5% of the total area of young cottonwood patches on the Yampa and Green Rivers, respectively. Beaver biomass was 238 kg on the Yampa River and 380 kg on the Green River. Beavers cut 42 of 934 marked stems on the Yampa and 199 of 561 marked stems on the Green River during a

17-month period. The herbivory rate (number of trees cut/kg of beaver) during the 17 month interval was over three times greater on the Yampa River (13.6 trees cut/kg of beaver) than on the Green River (4.2 trees cut/kg beaver).

Survival: Yampa versus Green River

When the probability of not being cut (survival) was compared on the Yampa and Green Rivers, the model component [S(p+t)] was common to the top three models strongly indicating that survival was different in each of the 5 patches and for each of the 7 time intervals (Table 2). Both patches on the Green River showed a lower survival rate for the duration of the study (17 months) (GU5= 0.66 and GAB = 0.88) than the patches on the Yampa River (YCB = 0.95, YCM = 0.99, YDE = 0.99) (Figures 3). In addition, survival varied by time (Figure 4) largely because large sample sizes (GU5: n = 156, GAB: n = 399, YCB: n = 239, YCM: n = 349, YDE: n = 339) made it possible to detect small differences between intervals. The covariates, distance and diameter, were in 2 of the top 3 models. Both were negative and slight (diameter = -0.477 distance = -1.243), indicating that there was only weak evidence that beavers selected for smaller trees and those closer to the river. The Kolmogorov-smirnov tests supported this finding by showing that there was little difference between distributions of cut stems and available stems for the variable diameter on either river (Yampa River: ks = 0.156, p = 0.226; Green River: ks = 0.075, p = 0.376) (Figure 5) and for the variable distance on the Green River (ks = 0.098, p = 0.119) (Figure 6). Only the variable distance on the Yampa River showed a strong difference in distributions of cut versus available stems (ks: 0.399, p = 0.001) (Figure 6).

Survival: Controlled floods on the Green River

The model [S(p+t)] was again in the top three models (Table 3), indicating that the probability of not being cut by beaver (survival) differed between the two patches and 8 time intervals on the Green River (Figure 7). The mean survival rate for GU5 was S = 0.95, 95% CI = 0.919-0.981, n = 156 and for GAB was S = 0.985, 95% CI = 0.975-0.995, n = 399. Interval 7 (1999 flood interval) had the lowest survival for both patches (GU5: S = 0.699, 95% CI = 0.629-0.762; GAB: S = 0.889, 95% CI = 0.855-0.916). Interval 2, the high flows during 1998, did not show a decrease in survival (Figure 7). In all intervals, survival was lower in patch GU5 than in GAB (Figure 7).

DISCUSSION

Our results were consistent with experimental work that found harvest rate by beavers was sensitive to the abundance of trees, spatial distribution and size of trees, and presence of alternative forage species (Jenkins 1980, Fryxell 1992, Doucet and Fryxell 1993, Fryxell 1999). Unique to this study was the demonstration that a controlled flood on a regulated river can also increase harvest rate by decreasing the distance of forage from water. Furthermore, our results demonstrated that beavers are a significant source of mortality for cottonwood on the Green River, which we suggest is primarily due to the low abundance of cottonwood, the tree's closer proximity to water, and the maintenance of a large beaver population by alternative forage (Breck Ch.2, Breck Ch.3).

Harvest Rate

For the 17 month study period, the harvest rate of cottonwood trees by beavers was > 3 times less on the Green River compared to the Yampa River. The rate of consumption by a consumer can be affected by the abundance of prey (Holling 1959).

Presumably at lower prey abundance the search time increases which decreases the number of prey the consumer are able to process. Our results support this theory as the Green River had a lower harvest rate and a much lower abundance of cottonwood trees compared to the Yampa River (Table 1). However, we believe there are other factors (i.e., alternative forage, diameter of trees, distance of trees from water, and flooding) in addition to abundance that potentially help explain the difference in harvest rate between rivers.

Few consumers use only a single resource type, thus the harvest rate associated with one forage species can be dependent upon the abundance, availability and nutritional quality of other forage species (Fryxell and Doucet 1993, Fryxell 1999). On the Green River, willow has responded to flow-regulation by shifting its distribution from a bank-oriented species to an island-oriented species (Merritt and Cooper 2000, Breck Ch3). This shift has decreased the distance of willow to water, which implies that energetic costs and risk of predation associated with searching and harvesting have decreased compared to willow on the Yampa River (Basey and Jenkins 1995). Willow is a good food source for beavers, and although cottonwood may be preferred (Breck, personal observation), the costs associated with searching for and harvesting willow have decreased (Breck Ch 3) relative to the costs associated with cottonwood trees. Thus the harvest rate of cottonwood trees was likely lowered by the greater availability of willow on the Green River.

Andersen and Cooper (2000) speculated that depth and duration of flooding strongly influences the harvest rate by beavers. We can demonstrate this was true on the Green River by substituting the number of cut stems during the 1999 flood interval with the number of cut stems during the same period in 1998 and recalculating the harvest rate. Beaver cut 64 stems during the controlled flood of 1999 but only 20 stems during the same period in 1998 on the Green River. Substituting 20 for 64 gives a harvest rate of 3.2 stems cut/kg of beaver, which lowers the harvest rate by almost 25% for the 17-month interval.

The difference in the rate of herbivory between floods was likely the result of differences in magnitude and duration of flood events between years. We assessed depth of water in one cottonwood patch (GU5) during the controlled floods in 1998 and 1999. In 1998 only a small portion of the cottonwood patch was inundated to a depth of approximately 0.5 m, the remaining patch had no standing water. Furthermore, the peak (182-198 cms) only lasted 8 days (Figure 2). In contrast, the 1999 flood inundated all of GU5 to a depth of 0.5 – 1 m and lasted for 34 days (Figure 2). In essence the depth of the flood in 1999 made the distance to patches equal 0, decreasing predation risk and energetic costs of foraging and allowing adequate time for beavers to forage and increase their harvest rate.

There was also strong evidence that the harvest rate by beavers increased during flood intervals on the Yampa River. In this case we can estimate the effect of flooding on the harvest rate by substituting the average rate of removal for non-flood intervals into the flood intervals. The result is a simulated total of 25 marked stems cut during the 17-month interval versus a real total of 42 marked stems cut. The harvest rate is lowered to 8.01 stems cut/kg of beaver, which is nearly a 40% difference in the harvest rate and indicates that beavers on the Yampa, like on the Green River, take advantage of the higher water levels to forage on cottonwood.

Jenkins (1980) demonstrated that beavers cut smaller diameter trees and a smaller size-range of trees the further trees were from water. In our study, the parameter "diam" in the third model of Table 2, indicated that beavers were selecting smaller trees. However, the results of the Kolomogorov-Smirnov test indicated that this selection was weak if present at all (Figure 5). The reason for the discrepancy is due to the large sample sizes (n = 1482) in our survival analysis that enabled us to detect small differences in what was cut versus what was available. Our biological interpretation is that beavers did not discriminate amongst trees based on diameter size on either river.

The negative value for the parameter "dist" in the model [S(p+t)+dist] (Table 2) indicated that survival of individual trees was higher the further they were from water. However, this relationship was only present on the Yampa River (Figure 6). On the Green River there was little evidence that beavers selected trees based on the distance of trees from water (Figure 6). Furthermore, there was little indication that beavers selected trees based on their diameter on either river (Figure 5).

The reason we did not detect a relationship between beaver foraging and distance from water or size of trees was likely due to the influence of the controlled flood in 1999. Of the 199 stems that beavers cut on the Green River, 64 (32%) of them were cut during this flood event (Figure 7). Because flooding eliminated the distance of trees to water, trees became equally available and the high rates of herbivory during this period may have eliminated any patterns of selection based on distance that were present before the flood. In addition, flooding should also have acted to increase the size-range of trees that beavers cut (Jenkins 1980), which could have eliminated patterns of selection based on the diameter of trees.

Impact of Beaver Herbivory on Cottonwood

Despite a lower herbivory rate on the Green River, our survival analysis indicated that the probability of a cottonwood tree being harvested by a beaver was much higher (Figure 3). Lower survival probabilities of cottonwood on the Green River were primarily due to a decrease in abundance of cottonwood, without a concomitant decrease in abundance of beavers. The theory of a "predator pit" (Messier 1994, Krebs et al. 1995, Krebs 1996) states that predators are able to regulate or limit a prey population in situations where forces other than predators lower abundance of prey to the point that prey numbers become sensitive to predation events. On the Green River flow regulation has caused the amount of area that contains young cottonwood and density of cottonwood within patches to decrease nearly 5 fold compared to the Yampa River. In contrast, beaver populations have increased slightly on the Green River (Breck Ch2) because of increased presence and availability of willow (Breck Ch4). Although beavers do not utilize as much cottonwood on the Green River compared to the Yampa River, they are able to have a greater impact because of increased sensitivity of cottonwood to herbivory events.

The sensitivity of cottonwood trees to beaver herbivory on the Green River is most clearly demonstrated by contrasting how survival probabilities changed with changes in the harvest rate. On the Green River we demonstrated that harvest rate increased by approximately 25% during the controlled flood in 1999. The mean survival rate for non-flood intervals on the Green River reveals a 19% decrease in survival (0.79 mean survival during flood intervals, 0.97 mean survival during non-flood intervals) (Figure 7). On the Yampa River we demonstrated that harvest rate increased by 40%

because of flooding. However, the mean survival rate during flood intervals only decreased by about 0.5% (0.993% mean survival during flood intervals, 0.998 mean survival during non-flood interval) (Figure 4).

Typically the term survival refers to a life or death situation, however in this study we use the term as the probability of a tree not being cut down by a beaver. It is possible that stumps of trees cut by beavers lived and sprouted more shoots, but we did not follow the fates of stumps. However, even if stumps did sprout shoots, their ability to reach reproductive maturity and develop a mature canopy was set back by many years (McGinley and Whitham 1985), making beavers an important biological agent.

Linking flow regime to beaver herbivory

The linkage between river regulation and patterns of beaver herbivory are contrasting in the literature. Bradley and Smith 1986) reported that beavers did not affect survival of plains cottonwood (*Populus deltoides* var. *occidentalis* Rydb.) differentially between a flow-regulated and free-flowing portion of the Milk River. Andersen and Cooper (2000) reported the probability of saplings being cut by a beavers to be similar on the Yampa River (0.019/yr) and partly flow-regulated Green River (0.043/yr) at a site called Island Park-below the confluence of the Green and Yampa Rivers. Their data were based on sets of small diameter saplings (<20 cm) in ≤ 3 locations at each site they examined. In contrast, our data, gathered over a larger area and including a greater size range, show the probability of a cottonwood tree being cut was 0.032/yr and 0.250/yr on the Yampa River and Green River at Browns Park. Nolet et al. (1994) reported that beavers heavily impacted tree species such as Alnus, Corylus, Fraxinus, Populus and Prunus because the attenuated river flows decreased their populations and made them susceptible to herbivory. Similarly, Lesica and Miles (1999) reported that plains cottonwood (*Populus deltoides* Bartr.) was prevented from developing a mature canopy because the low abundance caused by flow regulation allowed beavers to suppress the recruitment into larger size classes.

These apparently conflicting results can be explained by the degree to which flow regulation affects the populations of tree species preferred by beavers. In rivers where regulated flows result in low tree recruitment (e.g., Green River at Browns Park), beavers will be important herbivore because of the sensitivity of the tree population to each stem removed. In rivers with variable flows and abundant cottonwood, like the Yampa River and the Green River at Island Park (Andersen and Cooper 2000) flooding produces an abundance of cottonwood, which buffers the effect of foraging by beavers.

Management implications

Merritt and Cooper (2000) predict that channel widening, currently occurring on the Green River, will cease by mid-century and speculate that cottonwood may be able to establish along channel margins. Our results indicate that beavers could limit the establishment of cottonwood especially if recruitment areas are close to the river and the absolute abundance of cottonwood remains low. We recommend, if possible, encouraging the recruitment of cottonwood in areas that are over 100 m from the river, a distance that appears to maximize survival (Figure 6). Beavers are territorial and territoriality probably lowers maximum harvest rate by maintaining beavers at a lower density. Because of this, we recommend establishing trees in a few large patches with a high density of individuals versus many smaller patches. Doing so would enhance the probability that some trees are able to grow large and escape the threat of beaver herbivory.

Controlled flooding is proposed as a management technique for restoring riparian ecosystems on many regulated rivers (Stanford et al. 1996). Our results suggest that a threshold of discharge exists that allows beavers greater access to riparian vegetation. If plant species are both preferred forage for beavers and rare (e.g., cottonwood) a discharge above this threshold will promote higher rates of foraging on this plant. Managers should be cognizant of this relationship and be willing to protect these species during such events.

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TABLES AND FIGURES

Table 1. Characteristics of young cottonwood patches on the Green and Yampa Rivers in northwest Colorado, 1999. Variables include: total area, total area/km of study reach, number of patches, number of patches per study reach, density of trees within patches.

River	Area (m^2)		Number of Patches		Density	
	Total	Per km	Total	per km	Mean	SE
Yampa	87,992	10,232	17	1.98	1.01	0.17
Green	20,336	2,707	3	0.30	0.22	0.04

Table 2. Results of the AIC model selection procedure comparing survival (probability of not being cut by a beaver) of cottonwood on the Green and Yampa Rivers. Only the top 4 models out of a candidate of 17 are shown. Variables in models are: p- 5 patches (3 on the Yampa River and 2 on the Green River), t- 7 time intervals (see Fig 1), diam and dist are covariates that represent the diameter of each tree and the distance of each tree from the river. chat = 1.13

Model	AICc	Delta AICc	AICc Weight	# Par	Deviance
[S(p+t)]	1503.49	0.00	0.423	11	1674.1
[S(p+t) + diam]	1503.66	0.18	0.387	12	1671.9
[S(p+t) + dist]	1505.08	1.59	0.191	12	1673.6
[S(p) + (t-flood,fall)]	1532.33	28.85	0.000	8	1713.5

Table 3. Results of the AIC model selection procedure comparing survival (probability of not being cut by a beaver) of cottonwood in two patches on the Green River. Only the top 4 models out of a candidate of 9 are shown. Variables in models are: p- 2 patches (Gu5 and GAB), t- 8 time intervals (see Fig II), c-hat = 2.44

Model	QAICc	Delta QAICc	QAICc Weight	# Par	Deviance
[S(p+t)]	564.34	0.00	1.000	9	1332.9
[S(t)]	589.10	24.77	0.000	8	1398.3
[S(p + s2]	593.42	29.08	0.000	4	1428.4
[S(p + s1)]	609.57	45.23	0.000	3	1472.7

Figure 1. Location of study areas and Flaming Gorge Dam on the Green and Yampa Rivers in northwestern Colorado 1997-1999.

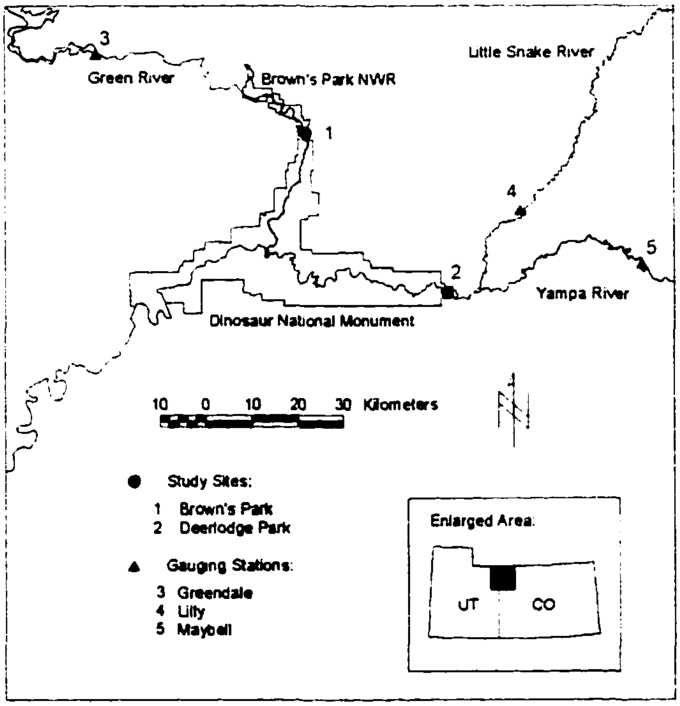


Figure 2. Daily mean discharge for the period October 1997 – November 1999 for the Yampa River in Deerlodge Lodge Park and the Green River in Browns Park in northwest Colorado. The vertical bars represent encounter occasions in the survival analysis of cottonwood. The periods between the bars are the survival intervals. There were 7 survival intervals on the Yampa River and 8 on the Green River.

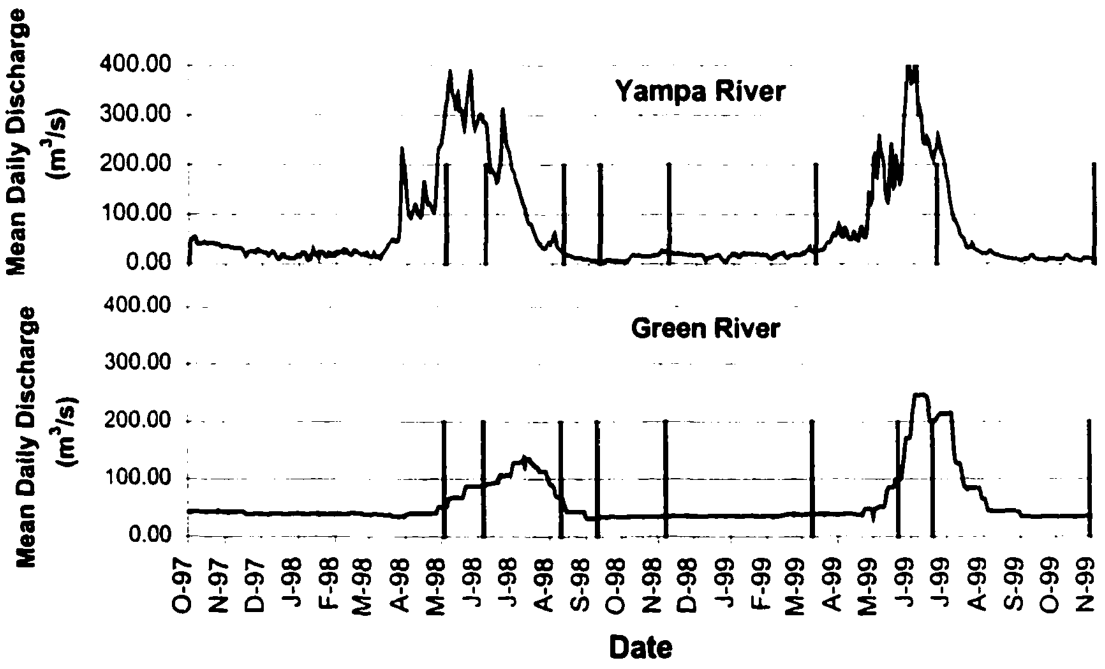


Figure 3. Probability of not being cut by a beaver (survival) from May 1998 to November 1999 (17 months) and SE for cottonwood trees in 5 patches, 3 on the Yampa River (YCB, YCM, YDE) and 2 on the Green River (GU5 and GAB). Survival estimates for each patch and each time interval were taken from the model [S(p+t)], the most parsimonious model in the AIC model selection procedure (Table I).

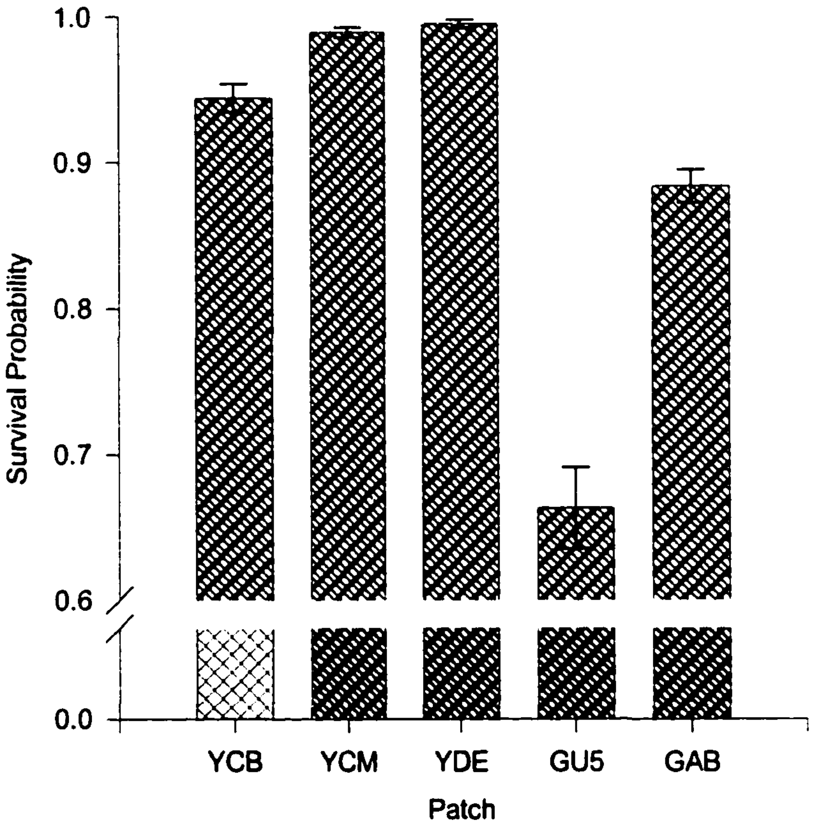


Figure 4. Mean probability of not being cut by beaver (survival) and SE for cottonwood trees from May 1998 to November 1999 on the Green River in northwest Colorado. Mean survival for each time interval was calculated by averaging survival estimates across patches, 3 on the Yampa River and 2 on the Green River. Survival estimates for each patch and each time interval were taken from the model [S(p+t)], the most parsimonious model in the AIC model selection procedure (Table I).

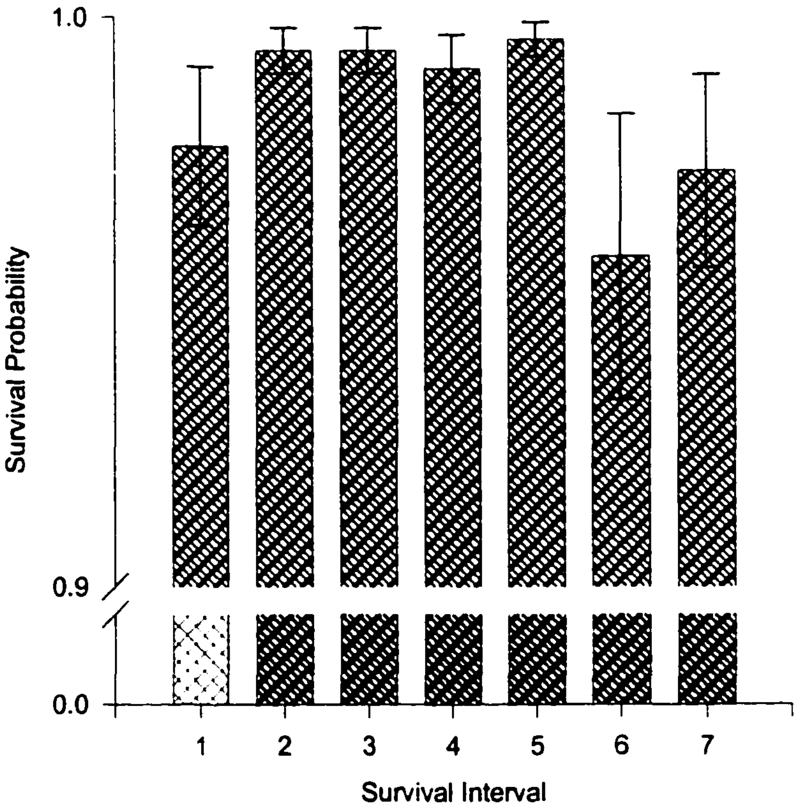


Figure 5. Number of available and beaver-cut cottonwood trees in relation to their diameter (cm) on the Green and Yampa Rivers in northwest Colorado, May 1998 – November 1999.

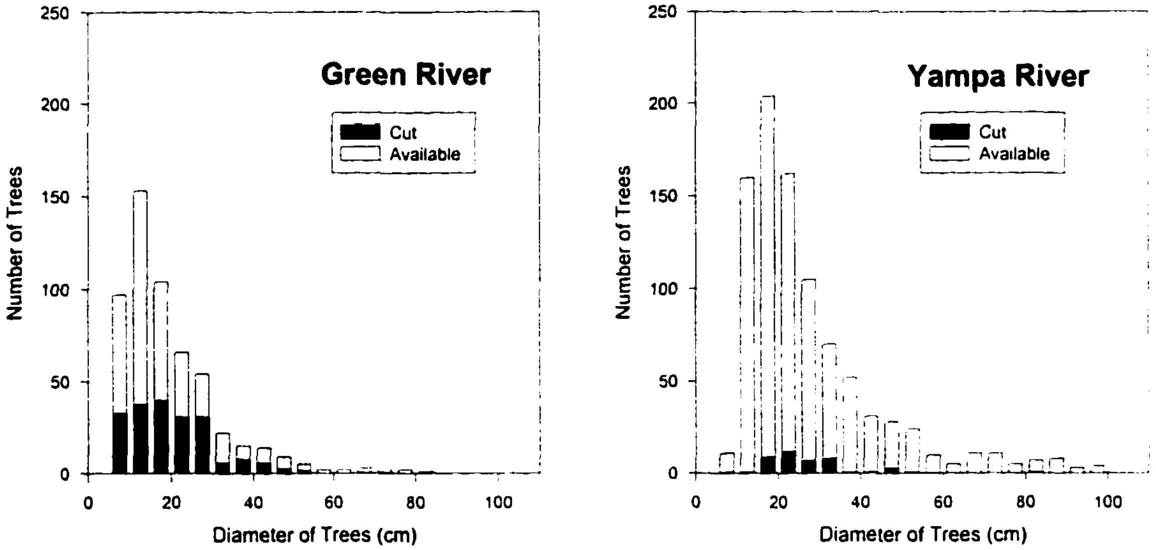


Figure 6. Number of available and beaver-cut cottonwood trees in relation to their weighted distance from water on the Green and Yampa Rivers in northwest Colorado, May 1998 – November 1999.

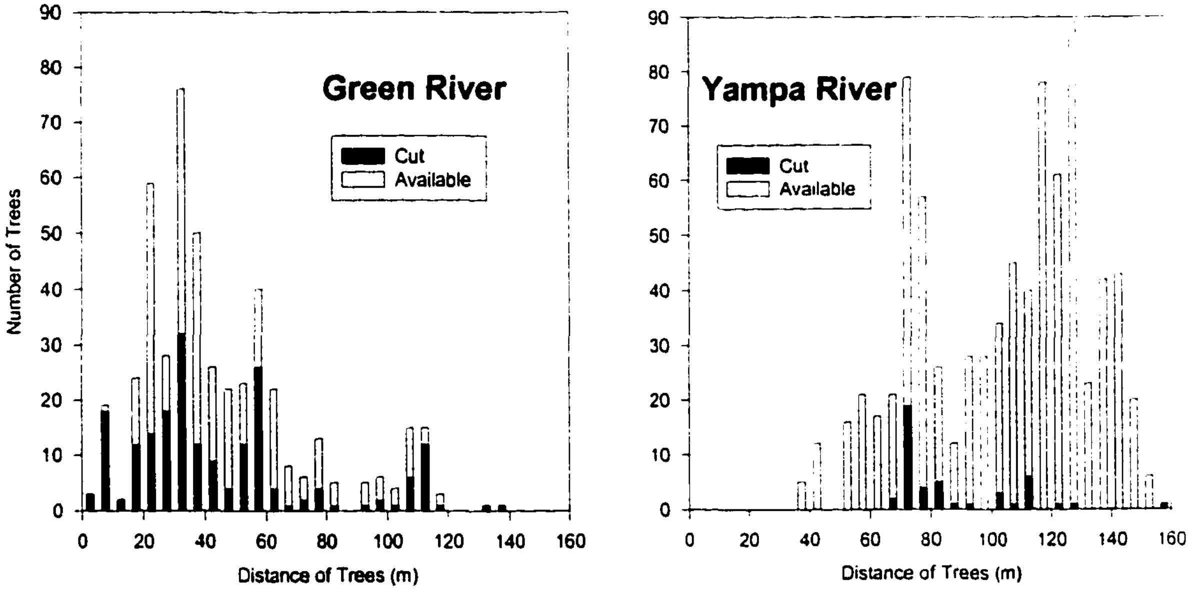
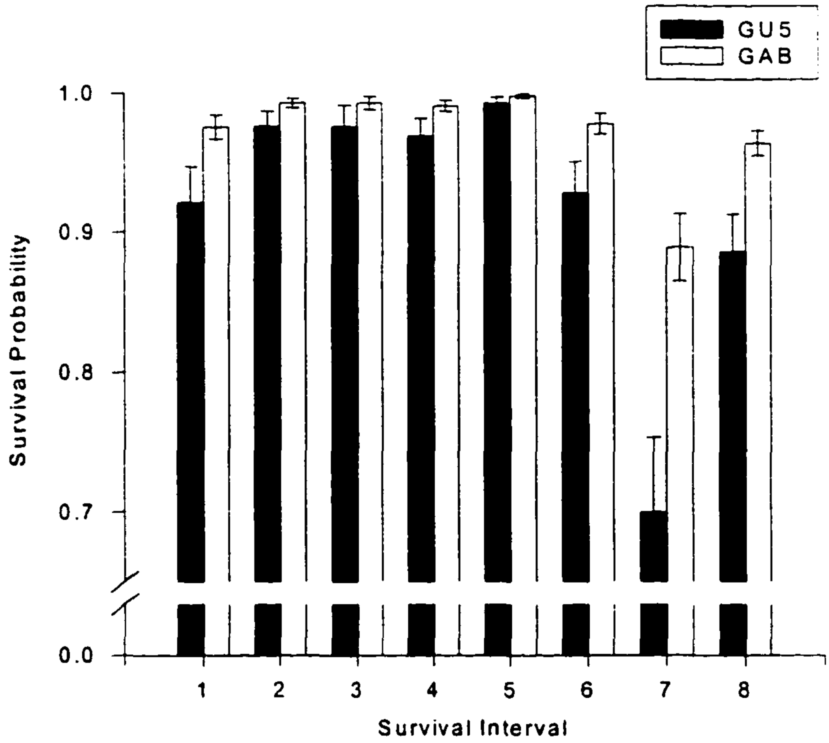


Figure 7. Probability of not being cut by beaver (survival) and SE for cottonwood trees from May 1998 to November 1999 on the Green River in northwest Colorado. Survival estimates for each patch and each time interval were taken from the model [S(p+t)], the most parsimonious model in the AIC model selection procedure (Table II). There are 2 groups (GU5 and GAB) and 8 intervals. Interval 2 was the flood in 1998 and interval 7 was the flood in 1999.



CHAPTER 5

CONTEXT DEPENDENCY OF COMMUNITY IMPORTANCE AS APPLIED TO BEAVER

INTRODUCTION

Paine (1969) initially formalized the concept of a keystone species to describe the effect of predatory activities of a starfish (*Pisaster ochraceus*) on species composition of a rocky intertidal community. The concept gained popularity and its use was expanded to include a wide variety of species affecting a broad array of ecological processes and ecosystem attributes (e.g., species richness, nutrient cycling, and species diversity). In subsequent years the concept was criticized as being vague and undefined and therefore misapplied (Mills et al. 1993). Power et al. (1996) helped revive the concept by providing a more precise definition of a keystone species and a way of quantifying the importance of a species in a community. Their paper emphasized that a keystone species was one with a high community importance (CI), meaning the species has a large influence on an important aspect of the community or ecosystem that is disproportionate to the species' abundance.

To calculate CI of a species, Power et al. (1996) provided the following equation:

$$C_i = \left| \left(\frac{t_N - t_D}{t_N} * \frac{1}{p_i} \right) \right|,$$

where t_N is the community or ecosystem trait when species i is present (e.g., species richness, rate of nutrient cycling, or the abundance of a dominant species), t_D is the trait in the absence of species i, and p_i is the proportional biomass of species i before removal relative to the total biomass of all other species in the community. Properly quantifying p_i is critical to CI but has proven very difficult to accomplish. Part of the problem is that the proportional abundance of a species depends on the scale of measurement and the organisms included for calculating the proportion. For example, in riparian systems p_i for beavers will differ depending on the spatial scale and whether or not plants and/or animals are included in the calculation.

Another criticism of the keystone species concept is that often researchers search for a false dichotomy (i.e., either the species is keystone or not). In fact the strength of connections between species in ecological assemblages (i.e., interaction strength) likely varies in space and time, depending on environmental context. For example, Menge et al. (1994) demonstrated that predation pressure of *P. ochraceus* (the original keystone species) was strong in wave-exposed habitats but very weak in wave-sheltered habitats, thus making it a keystone species in one environment but not in the other. Discovering factors that influence a species' interaction strength and understanding why they do is touted as a more interesting and valuable pursuit than trying to artificially classify a species as either keystone or not (Mills 1993, Menge et al. 1994, Power et al. 1996, Hurlbert 1997, Kotliar 2000).

Beavers have been labeled keystone species by many investigators (Naiman et al. 1986). In this chapter we explore how environmental context can dictate interaction strength of beavers at two scales. First, we qualitatively assess differences in interaction strength between pond-dwelling beavers (able to build dams in 2^{nd}-4^{th} order streams) and bank-dwelling beavers (not able to build dams in 5^{th}-7^{th} order rivers). Second, we quantitatively assess interaction strength of bank-dwelling beavers between two comparable rivers with contrasting flow regimes (the Green and Yampa Rivers). Our goals are threefold: 1) to evaluate the keystone role of beavers and how it changes with environmental context, 2) to summarize research presented in Chapters 2-4 by demonstrating how regulated flows influence the interaction strength of beavers, and 3) to speculate on the role of energy (i.e., environmental disturbance) for dictating interaction strength of beavers.

METHODS

To qualitatively assess interaction strength between pond-dwelling and bank-dwelling beavers, we searched peer-reviewed literature for papers addressing the impact of beavers on community and ecosystem traits. We selected a variety of traits (Table 1), and for each trait we ranked the beaver's influence as none, low, medium, or high in both a pond situation and a bank-dwelling situation. Ranking the beaver's influence on a trait was subjective and based on the number of studies with similar data, validity of methodology, and strength of results. Most research examining the effect of beavers on aspects of the community or ecosystem has occurred primarily where beavers are pond-dwelling, therefore we relied on our research observations and biological intuition to rank many traits where beavers were bank-dwelling.

To compare interaction strength for beavers on the Green and Yampa Rivers we used the formula for CI provided by Power et al. (1996). We selected two traits, survival of cottonwood as influenced by beavers and the amount of willow removed by beavers on each river. Details of calculations of these traits are in Breck (Ch. 3 and 4). Using the equation by Power et al. (1996) requires data on an ecosystem trait in the presence and absence of beavers. We did not have data on cottonwood tree survival in the absence of beaver and therefore assumed that all cottonwood trees harvested by beavers would have survived. For the amount of willow harvested by beavers we used data from beaver exclosures to compare with control areas that beavers could access (Breck Ch. 3). The most difficult aspect of utilizing Power et al.'s (1996) equation was determining a reliable estimate for the proportional abundance of beavers. To do so required quantifying the total biomass of each community, which we were unable to do. Instead, we used arbitrary values of p_i that varied between rivers based on the known biomass of beavers in each river as described below.

Beaver biomass was determined by trapping in the fall of 1999 and is expressed as kg of beaver/km of river (Breck Ch. 2). We arbitrarily choose a value of 1% to represent the proportional abundance of beavers on the Yampa River, which is probably a liberal value considering the abundance of willow, cottonwood, elk, moose, deer, small rodents, and other plants and animals. We then calculated the total biomass/km of riparian ecosystem by dividing known biomass of beavers by 1% (i.e., the arbitrary value of proportional abundance). To calculate proportional abundance of beavers on the Green River, we divided the known biomass of beaver/km on the Green River by the total biomass/km calculated for the Yampa River.

The key assumption was that the total biomass of each ecosystem was similar. This assumption was likely valid prior to completion of Flaming Gorge Dam as the Green and Yampa Rivers operated with similar flow regimes and maintained similar riparian ecosystems (Andrews 1986, Cooper et al. 1999, Merritt and Cooper 2000, Andersen and Cooper 2000). Since completion of the dam many changes in the riparian ecosystem have occurred, most notable of which is the drastic decline in abundance of cottonwood on the Green River (Breck ch4). However, higher abundance of other species such as tamarisk, grasses, and wetland species that are currently more plentiful on the Green River may have compensated (Merritt and Cooper 2000).

RESULTS

Of the 10 ecosystem traits that we evaluated, beavers had the highest impact on 2nd-4th order streams. In all cases the primary mechanism by which beavers affected these traits was through construction of dams (Table 1). Herbivory by beavers primarily influenced plant abundance and species composition, which in some cases indirectly influenced insect abundance (Table 1). Beavers may influence erosion on large-ordered rivers because of their burrowing habits, though this has not been documented.

Biomass of beavers was 34% greater on the Green River (37.3 kg/km) than on the Yampa River (27.7 kg/km). Based on a 1% proportional abundance for beavers on the Yampa River, total biomass of the ecosystem was 2,770 kg/km. The proportional abundance of beavers on the Green River was 1.34%. For the trait cottonwood survival, the CI was 21.1 and 3.1 on the Green and Yampa Rivers, respectively. For the amount of willow removed the CI was 46.4 and 14.0 on the Green and Yampa Rivers, respectively. Beaver biomass on the Yampa River would have to increase 3 to 7 times (depending on the trait) to achieve a value of CI equal to that of beavers on the Green River.

DISCUSSION

Interaction strength of beavers is strongly influenced by environmental context. On 2nd-4th ordered streams beavers are able to build dams and have a large impact on a variety of physical and biological traits. Dam building transforms lotic habitat to lentic habitat, reducing stream velocity and discharge rates (Gurnell 1998). The altered hydrologic regime affects biogeochemical cycles and the accumulation and distribution of chemical elements (Smith et al. 1991, Naiman et al. 1994, Klotz 1998). For example, beaver ponds trap sediment, accumulate nitrogen, and enhance carbon storage (Naiman et al. 1986). These hydrological and biogeochemical changes can increase or decrease the relative abundance of plants (Mitchell and Niering 1993), aquatic insects (McDowell and Naiman 1986, Clifford et al. 1993), fish (Leidholtbruner et al. 1992, Snodgrass and Meffe 1998), amphibians (Russell et al. 1999), reptiles (Russell et al. 1999), and birds (Grover and Baldassarre 1995, McCall et al. 1996). Taken at a landscape level, beaver dams enhance species richness by creating a higher level of habitat diversity than would exist in their absence. Although beavers are not the only biological agents of disturbance on small streams, the magnitude of their disturbance compared to their proportional abundance makes them unique in their community and justifies them being labeled a keystone species.

On large order rivers (5th-7th), interaction strength of beavers is diminished considerably because they are unable to create dams. Despite this, in certain environmental situations, their interaction strength can be high because they are able to cut down trees and remove an exceptionally large amount of plant biomass relative to their abundance (Gill 1971, Johnston and Naiman 1990a). These abilities potentially enable beavers to suppress tree populations and alter species composition of the riparian community (Barnes and Dibble 1988, Johnston and Naiman 1990a, Nolet et al. 1994), which could in turn could have important implications for biogeochemical cycles and species diversity (Pastor and Naiman 1992). Available research indicates that the beaver's ability to affect tree populations varies considerably depending on environmental context. In situations where a preferred tree species has a low abundance, beavers have a strong impact on the tree population (Nolet et al. 1994, Lesica and Mills 1999, Breck Ch. 4), whereas in situations where preferred species are abundant their interaction strength is weak (Strong 1982, McGinley and Whitham 1985, Bradley and Smith 1986, Breck Ch. 4).

To determine the keystone status of beavers on the Green and Yampa Rivers we used Power et al.'s (1996) formula. A CI > 1 indicates that a species has a greater effect on an ecosystem trait than would be predicted if its effect was in direct proportion to its abundance (Power et al. 1996). However, how much greater than 1 the CI should be to classify a species as keystone is not provided, possibly because no value would consistently equal the same "importance" in all situations. Labeling a species as keystone should be based on confidence in estimates of proportional abundance and on how important the trait is for affecting other components of the community. Below we use data from the Green and Yampa Rivers to elaborate on these points.

Community Importance

The CI for beavers on both the Green and Yampa was well above 1 for both traits, indicating that interaction strength of beavers was greater than their relative abundance. More importantly the CI value was over 3 to 7 times higher for beavers on the Green

River than on the Yampa River indicating beavers played a stronger role in the survival of cottonwood and removal of willow on the Green River. For cottonwood tree survival, the greater interaction strength of beavers on the Green River was probably due to a lower abundance of trees, which made the survival parameter more sensitive to each herbivory event (Breck Ch. 4). In fact the number of trees harvested by beavers was higher on the Yampa River, but a greater abundance of trees buffered the population and lowered the interaction strength of beavers (Breck Ch. 4). For amount of willow removed, the greater interaction strength of beavers on the Green River was possibly due to a doubling in willow consumed by beavers and a slightly lower abundance of willow on the Green River (Breck Ch. 3). Increased consumption of willow was probably a result of a greater density of beavers on the Green River (Breck Ch. 2) and an increase in accessibility of willow (Breck Ch. 3).

Community Traits

Willow is an important plant because it provides food and shelter for a variety of wildlife (Knopf et al. 1988, Kindschy 1989, Snyder and Miller 1992, Baker and Cade 1995). Sandbar willow's rapid growth rate potentially makes it a competitive and dominant plant affecting species richness and abundance of other plants in the community (Dulohery et al. 2000). High rates of herbivory cause greater changes in other communities (Augustine and McNaughton 1998), and could reduce the competitive abilities of sandbar willow and allow other plant species to establish and increase in abundance. It may also keep willow in an earlier successional state, thus providing a greater diversity of habitats for insects and food for mammals (Woods et al. 1996, Breck Ch. 3). Currently it is unknown whether beaver herbivory causes such changes in the community. If they did it would increase the beaver's potential to be labeled a keystone species. My data does support the idea that if willow herbivory by beavers does affect species composition, then it will more likely be expressed on the Green River because of the higher percentage of willow removed.

Cottonwood trees are important species on the Green and Yampa Rivers because they are essentially the only tree species at lower elevation alluvial reaches, create forage for animals, provide 3-dimensional structure to the ecosystem, aesthetic value to humans, and enhance species diversity (Knopf et al. 1988, Gregory et al. 1991, Braatne et al. 1996). Maintaining processes that lead to adult trees is important for overall diversity on these rivers. On the Green River seedling recruitment of cottonwood has decreased dramatically due to flow regulation, causing concern that as older trees die there will be no new trees to replace them and benefits of cottonwood trees will be lost from the ecosystem. Because of changes in fluvial geomorphology due to flow regulation, only a few areas on the Green River contain young cottonwood (Cooper et al. 1999, Merritt and Cooper 2000). These patches tend to be closer to the river and have a lower density than cottonwood patches on the Yampa River (Breck ch4). Because of the low abundance, the population is more susceptible to agents of mortality, creating a situation where beavers can decrease survival and suppress the population of young cottonwood on the Green River.

On the Yampa River, assuming that a natural flood regime is maintained, there probably would be little difference in abundance of cottonwood with or without beavers. This is because beavers play a minor role in affecting survival of young cottonwood trees and the mortality that they cause is likely compensatory. On the Green River, mortality of cottonwood trees from beaver herbivory is probably additive (Breck Ch. 4). Thus, in the absence of beavers, young cottonwood trees would have a much better chance of maturing to an adult stage and forming a mature canopy.

Does the above information justify labeling beavers as keystone species on the Green or Yampa Rivers? The values of CI suggest that beavers have high interaction strength for two important traits, particularly on the Green River. However, even if the data were not speculative, it would be difficult labeling beavers as keystone species on either river as there are so many other traits (Table 1) that beavers on the Green and Yampa Rivers do not affect at all. This highlights a consideration we think is important when using Power et al.'s (1996) formula. Instead of deciding whether a species is keystone based on one trait, we believe the formula should, when possible, be expanded to include the sum of many community and ecosystem traits.

The formula for CI would be:

$$C_{ij} = \sum_{j=1}^{n} \left| \left(\frac{t_{Nj} - t_{Dj}}{t_{Nj}} \frac{1}{p_{ij}} \right) \right|,$$

where everything is the same as Power et al.'s (1996) formula except that C_{ij} is over all traits, j, from 1 to n. This formula does not solve the problem of calculating an accurate proportional abundance, but it is a more realistic model. If we used this formula to compare beavers in small ordered streams versus large ordered streams we could quantify and compare the influence of beavers for a variety of factors as I did qualitatively (Table 1). Doing so would eliminate confusion in designating beavers as keystone species. For example, Naiman et al. (1986) designated pond-dwelling beavers as keystone species in boreal forests but Donkor and Fryxell (1999) doubted the keystone role of pond-dwelling beavers in boreal systems. The difference is that Donkor and Fryxell (1999) only considered the impact of beavers on one aspect of the community, whereas Naiman et al. (1986) considered a variety of traits.

Role of Physical Disturbance

We demonstrated that the interaction strength of beavers was variable not only from small ordered streams to large ordered rivers but also between two comparable, large ordered rivers featuring similar flow regimes. Understanding the causes of this variation is more important to our understanding of beavers and the systems than classification of a species as keystone or not. Interaction strength of beavers is strongly influenced by their ability to build dams. The primary factor preventing beavers from constructing dams is the hydraulic energy associated with the stream. Two primary components that influence hydraulic energy are gradient and water volume. Where the gradient is low (generally less than 2%) and volume of water small (2^{nd}-4^{th} order streams), hydraulic energy is low enough for beavers to construct dams. As gradient increases or water volume increases, hydraulic energy increases and prevents beavers from building dams, therefore lowering their interaction strength.

Variability in hydraulic energy is also important in that it tends to decrease interaction strength of beavers. On 2^{nd}-4^{th} order streams, variability in hydraulic energy (i.e., flooding) can destroy beaver dams. Though beavers rebuild the dams, interaction strength is decreased because dam removal temporarily returns the stream to a lotic system. Sediment and nutrients are washed downstream, hydrology is altered until the dam is rebuilt, and animal and plant populations are likely disrupted and moved toward what is found in undammed portions of the stream.

On large ordered rivers variability in hydraulic energy can decrease interaction strength of beavers by influencing abundance and availability of forage. For example, on the Yampa River, flooding is responsible for producing the abundance of cottonwood, which buffers the effect of foraging beavers and thereby decreases their interaction strength. Low flows on the Yampa River decrease interaction strength of beavers by increasing effort required to gather forage due to the exposure of large sandbars that separate river from forage. Overland travel across these sandbars increases energy expenditure and risk of predation for beavers, which decreases the number of trees that they harvest and lowers their interaction strength (Breck Ch. 2 and 3). On the Green River, low variation in hydraulic energy increases interaction strength of beavers by decreasing the abundance of cottonwood and forcing cottonwood and willow closer to water. For example, willow has shifted from a primarily bank-oriented species to an island- and bank-oriented species, which makes willow easily accessible to beavers year around (Breck Ch. 3). The accessibility lowers the energy costs of foraging and risk of predation thereby allowing beavers to harvest more willow, and increases their interaction strength.

The idea that amount and variability of hydraulic energy influences interaction strength is applicable to other animals on the Green and Yampa Rivers and to beavers in other systems. Andersen and Cooper (2000) found that interaction strength of a small mammal (*Microtus montanus*) increased on the Green River because stable flows allowed (*M. montanus*) populations to escape mortality normally accompanying annual spring floods and enabled them to have a greater impact on cottonwood survival. For bank-dwelling beavers in other systems, interaction strength appears to be higher on rivers with low hydraulic variability (Nolet et al. 1994, Lesica and Miles 1999), than on rivers with high hydraulic variability (Strong 1982, Bradley and Smith 1986).

To help clarify the variation in interaction strength of beavers, or of any species, we recommend using the formula for CI in a comparative way. As stated earlier, it is difficult to obtain proportional abundance estimates for a species, but it is often possible to obtain reliable abundance (or relative abundance) estimates which would facilitate comparison using CI. For example, we found it useful for distinguishing the relative difference in interaction strength of beavers between the Green and Yampa Rivers. The central idea that interaction strength of a species should be based on its proportional abundance in the ecosystem is an important one, and allows a valid comparison between two or more systems assuming that proportional abundance can be reliably estimated. Unfortunately, trying to base a decision about the keystone status of a species on the CI value of one trait seems limited. There is no cut off value that distinguishes a keystone species nor are there any rules to determine which traits are worthy for determining a keystone species.

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Table 1. Ability of beavers to impact various community and ecosystem traits on small streams (2nd -4th order) and larger rivers (5th-7th order). Rankings are None, Low, Medium, and High and are based on results from peer-reviewed literature and subjective determination where nothing was published about the trait. Beavers affect traits primarily by building dams or felling trees.

Trait	Potential of Beaver to Impact Trait 2nd-4th ordered stream	 5th-7th ordered river	Mechanism
Hydrology	High[1]	None[a]	Dams
Patch formation	Med.-High[2]	None[a]	Dams
Soil erosion or deposition	Med.-High[3,4,5]	Low[a]	Dams/Burrowing
Nutrient abundance and turnover time	Med.-High[3,4,5]	None to Low[a]	Dams/Herbivory
Insect abundance, composition or diversity	High[6,7]	Low[14]	Dams/Herbivory
Amphibian abundance, composition or diversity	Low[8]	None[a]	Dams
Reptile abundance, composition or diversity	Med.[8]	None[a]	Dams
Fish abundance, composition or diversity	Med [9,10]	None[a]	Dams
Plant abundance, composition or diversity	High[11,12]	Low-Med.[11,15]	Dams/Herbivory
Landscape alteration	High[13]	None-Low[a]	Dams/Herbivory

1. Gurnell 1998
2. Johnston and Naiman 1990b
3. Smith et al. 1991
4. Naiman et al. 1994
5. Klotz 1998
6. McDowell and Naiman 1986
7. Clifford et al. 1993
8. Russel et al. 1999
9. Snodgrass and Meffe 1998
10. Leidholtbruner et al. 1992
11. Mitchell and Niering 1993
12. Johnston and Naiman 1990a
13. Johnston and Naiman 1990c
14. Schlosser and Ebel 1989
15. Breck (Ch. 3 and 4)

a) We relied on research observations and biological intuition.