1-1-2001

The ecological role of beavers (Castor canadensis) in a Southwestern desert stream

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THE ECOLOGICAL ROLE OF BEAVERS (*CASTOR CANADENSIS*)

IN A SOUTHWESTERN DESERT STREAM

by

Bryan James Harper

Bachelor of Science
Arizona State University
1995

A thesis submitted in partial fulfillment
of the requirements for the

Master of Science Degree
Department of Biological Sciences
College of Sciences

Graduate College
University of Nevada, Las Vegas
May 2001

UMI Number: 1405106

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

UNLV

Thesis Approval
The Graduate College
University of Nevada, Las Vegas

Feb. 27th , 2001

The Thesis prepared by

Bryan J. Harper

Entitled

The Ecological Role of Beavers (Castor canadensis) in a Southwestern Desert Stream

is approved in partial fulfillment of the requirements for the degree of

Master of Science

Examination Committee Chair

Dean of the Graduate College

Examination Committee Member

Examination Committee Member

Graduate College Faculty Representative

PR/1017-53/1-00

ABSTRACT

The Ecological Role of Beavers (*Castor canadensis*) in a Southwestern Desert Stream

by

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The ecological impact of beavers on a stream in the southwestern United States was investigated to determine if beavers have impact on community and ecosystem level processes in a manner similar to what has been documented in more mesic regions. Specifically, my goals were to determine (1) whether beaver pond densities differ in an arid Mojave Desert system from densities reported for those of more mesic regions, (2) what riparian plant species beaver are foraging on most frequently in this system, and (3) to determine if beaver ponds alter the system retention of nitrogen, a nutrient that often limits primary production in streams of the western United States.

The spatial prevalence of beaver ponds along Meadow Valley Wash, a perennial stream in southeast Nevada, was determined by surveying 31.5 kilometers of the streams length. I found that approximately 80% of the stream's length contained riparian vegetation usually associated with beavers and that beavers impounded nearly 8% of the stream's length. A total of 26 ponds were located along the study reach. Surveys of the

vegetation surrounding ponds, and the foraging preference of beavers, showed that beavers preferentially feed on *Populus fremontii*, *Salix lasiolepis*, and *Fraxinus velutina* to a greater extent than other resident species.

At the ecosystem level, stream nitrogen retention was measured using solute injection methods designed to estimate the uptake length (the distance an inorganic nutrient molecule travels downstream before becoming incorporated into the biota) coupled to investigations of the abundance of particulate organic matter in beaver pond sediments relative to unimpounded stream reaches. Results indicate that beaver ponds along Meadow Valley Wash have almost three times the sediment organic matter per unit relative to unimpounded reaches, suggesting that ponds are retaining particulate organic nitrogen to a greater extent than unimpounded stream reaches. The results of the solute injections showed that inorganic nitrogen retention in the spring was much higher for ponds than unimpounded stream reaches. In addition, sediment mineralization and nitrification rates did not differ between impounded and unimpounded stream reaches.

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ACKNOWLEDGMENTS

Numerous individuals contributed to the completion of this work. The UNLV Graduate Student Association and the Department of Biological Sciences Aquatic Biology Endowment provided much of the funding for this project. I would also like to thank my wife, Stacey Harper, for her patience and unending support. I would like to thank all of the members of my graduate committee, Peter Starkweather, Stan Smith and Lars Walker as well as James Deacon and former committee members that contributed to the development of this project and my scientific education. I would like to also thank Carl Reiber for emotional support and guidance during the tougher times and for providing resources critical to the completion of this work

CHAPTER 1

INTRODUCTION

Beavers are modifiers of the ecological processes occurring in streams because they affect their environment directly through foraging and indirectly through the construction of dams and the resulting impoundment of water. The foraging and impoundment of water by beavers changes the habitat available for both aquatic and riparian species and alters the rate at which energy is transformed and exported from the ecosystem. Desert streams differ in many ways from streams in more humid regions (i.e., type and frequency of disturbance, nutrient dynamics, rates of primary productivity) and the majority of research on beavers has been conducted in mesic temperate regions. Very little research on beavers has been conducted in arid or semiarid regions such as the southwestern United States. In this work I present findings that have addressed three research goals: (1) to determine if the spatial prevalence of beaver ponds in xeric regions is similar to pond densities reported for mesic regions, (2) to understand how riparian community structure is potentially changed by beavers in a southwestern stream; and (3) to understand how the rates of processes involved with nitrogen biogeochemistry are affected by the presence of beavers is such a system.

Background

Two species of beavers exist worldwide, the North American beaver (*Castor canadensis*) and the Eurasian beaver (*Castor fiber*). Although beavers may have been close to extinction due to extensive trapping in both the United States and Europe around the turn of the century (Anderson 1964, Nolet and Rosell 1998), reintroductions have been successful and beaver populations are now thriving in many streams throughout both continents (Naiman et al. 1988, Snodgrass 1997, Nolet and Rosell 1998). Currently an estimated 6-12 million beaver inhabit streams throughout North America (Anderson 1964, Naiman et al. 1988). The continually growing numbers of beavers and the expansion of beavers into regions where they had once been eradicated have shown that the magnitude of the effects of past beaver removal on stream ecosystems is only beginning to be understood (Naiman et al. 1986). The field of stream ecology developed in the early part of the 20th century, well after beaver populations were removed from most streams (Anderson 1964). Only recently have studies such as this one begun to clarify the importance of beavers in the ecology of streams.

The Ecological Role of Beavers

Beavers are a keystone species in many ecosystems in which they are common (McDowell and Naiman 1986). Keystone species provide a unique contribution to the community or ecosystem; thus, removing a keystone species results in a significant change in community structure, ecosystem function, or both (Paine 1969). The activity of beavers in some regions has led to increases in stream biodiversity and alterations in the rate of invertebrate and vertebrate production (McDowell and Naiman 1986). In addition, studies have shown that in some environments beavers create heterogeneity in

stream ecosystems through the sequence of pond formation and abandonment (Snodgrass 1997). An individual beaver can cut up to a metric ton of wood each year for food and dam construction (McGinley and Witham 1985, Johnston and Naiman 1987). When foraging, beavers selectively feed on preferred species (Kindschy 1985, Barnes and Dibble 1988, King et al. 1998). Thus, the foraging of beavers can lead to dramatic shifts in riparian community structure compared to streams without beavers present, altering the trajectory of vegetative succession along riparian corridors.

The heterogeneity in flow associated with beaver impoundments has concomitant effects on ecosystem level processes such as organic matter retention and microbial activity (Naiman et al. 1986). Ponds are important locations for accelerated nutrient transformations (Bilby and Likens 1980, Bilby 1981, Naiman et al. 1986, Hedin 1990). For example, the accumulation of organic matter in beaver ponds dramatically increases sediment microbial activity (Songster-Alpin and Klotz 1995, Rosenfeld and Hudson 1997), thus often increasing levels of anoxia within pond sediments. Increased anoxia elevates rates of anaerobic microbial metabolism, which in turn affects oxidation-reduction reactions that govern nutrient cycling within the ecosystem (Tiedje et al. 1989, Bridgham et al. 1998). Beaver ponds often have rates of CO_2 and CH_4 emissions higher than surrounding stream reaches (Ford and Naiman 1988, Naiman et al. 1991, Updegraff et al. 1995), suggesting an increased processing of nutrients and organic matter. Thus, beaver ponds serve as important locations for organic matter retention and conversion of organic matter into inorganic nutrients.

The Need to Study Beavers in the Southwest

Although Naiman et al. (1986) suggested that drainage networks with beavers present are substantially different in their biogeochemical economies than those without beavers, only a handful of studies have addressed the role of beaver ponds in altering nutrient transformations, retention or export, and almost no research has been conducted on beaver ponds in the southwestern United States. In north temperate regions, beaver ponds significantly modify nitrogen retention in streams and play an important role in altering rates of denitrification and nitrogen fixation rates relative to unimpounded reaches (Naiman and Melillo 1984, Francis et al. 1985). On the Maryland coastal plain, beaver ponds reduced the annual discharge of total nitrogen and phosphorus; however, the effects of the single pond studied varied seasonally and with stream discharge (Correll et al. 2000). Beaver ponds often modify the phosphorus concentration of temperate zone streams as well, yet no predictable trends have been shown (Devito et al. 1989, Klotz 1998). As such, previous studies have not clearly defined any specific hypotheses that consistently explain how beaver ponds affect nutrient availability to stream biota in mesic regions, and have never investigated these factors in southwestern streams.

The availability of inorganic nutrients, particularly nitrogen and phosphorus, often structure ecosystems through the regulation of photosynthesis and bacterial production. Streams in arid regions of the southwestern United States often have rates of primary production exceeding rates in wetter climates (Busch and Fisher 1981, Fisher 1986) and thus require large amounts of inorganic nitrogen and phosphorus to support primary

production. In streams of the Sonoran Desert, primary production has been shown to be limited by the availability of nitrogen (Grimm and Fisher 1986a, 1986b) and preliminary evidence indicates nitrogen limitation exists in streams of the Great Basin as well (J. B. Jones and B. J. Harper, unpublished data). Because secondary productivity is dependent on the rate of primary productivity, the overall productivity of desert stream ecosystems is inherently regulated by the availability of nitrogen.

Research Objectives

Spatial Prevalence of Beaver Ponds

In order to assess the impact of beaver ponds on the ecosystem as a whole, it is necessary to estimate how prevalent beaver ponds are in a southwestern stream. Dam frequency along streams varies widely throughout North America (Butler 1995). In Oregon, coastal stream frequencies are reported to be 1.2 dams per kilometer (Leidholt-Bruner et al. 1992), while the semiarid regions of eastern Oregon have frequencies of 0.15 dams per kilometer (McComb et al. 1990). Surveys in Quebec have shown that beaver ponds are present along 30 – 50% of the stream length, with a frequency of 10.6 dams per kilometer (Naiman and Melillo 1984, Naiman et al. 1988). Butler and Malanson (1994) encountered more than 25 dams per kilometer in the Rocky Mountains of northwestern Montana. Of all the surveys conducted, only the survey by McComb et al. (1990) was conducted in a semiarid environment, so information I present here on the frequency of beaver dams in a southwestern stream of the arid Mojave Desert is both novel and important to future research efforts.

In this portion of the study, I investigated the possibility that the lack of upland and occasionally riparian trees needed to support beaver activity in semiarid regions limits the abundance of beavers relative to more heavily forested regions. Howard and Larson (1985) have developed a stream habitat classification system for beaver in mixed coniferous-deciduous habitats. Their model suggests positive correlations between beaver colony density and the amount of non-coniferous (hardwood) trees, the watershed size, and stream width. Howard and Larson (1985) defined a colony as a group of beavers (inhabiting one or more ponds) that share a common food source. Jenkins (1980) suggest that the maximum distance a beaver will travel away from its pond when foraging is 100 meters; thus, I defined a beaver colony as a group of ponds with less than 100 meters between ponds. Using this definition, I conducted a survey of 31.5 km of desert stream for the presence of beaver ponds to determine if the model of Howard and Larson (1985) is applicable to beavers along a Mojave Desert stream.

Riparian Vegetation and Foraging Preference of Beavers

In a second survey, I investigated the types of riparian vegetation present along reaches inhabited by beaver and the components of this vegetation being used for food and dam construction. The goal was to determine what vegetation exists in habitats chosen by beavers in the Southwest and to determine which types of vegetation beaver are foraging on. In addition, I was interested in testing the hypothesis that beavers prefer to feed on native species. The riparian corridors of streams in the Southwest are being rapidly invaded by *Tamarix ramosissima* (DiTomasso 1998). *Tamarix ramosissima*, also known as saltcedar, is a salt-tolerant phreatophyte that secretes salts from its foliage. The salts then enter riparian soils as leaves are deposited onto the soil surrounding the tree

(DiTomasso 1998, Smith et al. 1998). The salinization of the soil is so extensive that native riparian species are often displaced by *Tamarix* (Smith et al. 1998). My field observations suggest that beaver do forage on *Tamarix*, although not to the same extent as the native species. In order to quantify this general observation, I estimated the foraging preference of beavers for both native and invasive riparian.

Impact of Beavers on Inorganic Nitrogen Availability

In this portion of my thesis I investigated the effect of beaver ponds on the nitrogen biogeochemistry of stream reaches. Since desert stream primary production is often limited by nitrogen availability (Grimm and Fisher 1986a, b), my efforts were focused on understanding how beaver activity alters the processing and retention of nitrogen within the watershed. My goal was to determine if beavers modify the amount of nitrogen being retained by the ecosystem, and if there are any seasonal patterns in the effect of beaver ponds on nitrogen retention. I was also interested in understanding how beavers affected the mineralization of organic matter and the subsequent microbial nitrification of ammonium produced from mineralization. I hypothesized that beaver ponds would have higher rates of organic matter mineralization and nitrification than unimpounded reaches (due to increased amounts of sediment organic matter in ponds relative to unimpounded reaches) and that flooded riparian soils would contribute to these difference should they exist.

CHAPTER 2

THE SPATIAL PREVALENCE AND FORAGING PREFERANCE OF BEAVERS ALONG MEADOW VALLEY WASH, NEVADA

Abstract

I conducted two surveys along Meadow Valley Wash, a perennial stream in southern Nevada, to determine the prevalence of beaver ponds and what types of vegetation beaver prefer to forage upon in desert streamside environments. Numerous surveys of beaver pond abundance and foraging preference have been conducted in mesic regions, but information on the activity and habitat of beavers in arid and semiarid regions is lacking. Ground surveys revealed 26 ponds that clustered into 9 groups or colonies of ponds. Based on the mean length of the ponds (95 m) beaver ponds occur along almost 8% of the stream length within the 31.5 km study reach, with an average of about 0.8 ponds per kilometer of stream. In addition, I found that approximately 21% of the stream's length lacked the riparian vegetation usually associated with beaver ponds and likely would not serve as suitable habitat for beavers. Dominant riparian vegetation foraged upon by beavers was *Populus fremontii* (Fremont cottonwood), *Fraxinus velutina* (velvet ash), *Salix lasiolepis* (arroyo willow), *Baccharis glutinosa* (seep-willow) and *Tamarix ramosissima* (saltcedar). Surveys of beaver foraging preference based on

chewed stems indicate that beavers preferentially feed on *Salix*, *Populus* and *Fraxinus* species, followed by *Tamarix* and *Baccharis*.

Introduction

The North American beaver (*Castor canadensis* Kuhl) is becoming widely recognized as an important agent of ecological change in aquatic ecosystems (Naiman et al. 1988, Smith et al. 1989, Naiman et al. 1994, Jones et al. 1997). Beaver activity modifies the hydrology and morphology of stream reaches, with concomitant effects on organic matter transport, nutrient cycling, and community production and diversity (Naiman and Melillo 1984, McDowell and Naiman 1986, Naiman et al. 1986, Snodgrass and Meffe 1998). The terrestrial foraging activity of beavers leads to changes in the structure and dynamics of the riparian community along streams with beavers present (Kindschy 1985, Barnes and Dibble 1988, Donkor et al. 1999). In northern regions of the United States, beaver have been shown to cut at least a metric ton of wood annually (McGinley and Whitham 1985, Johnston and Naiman 1987). The cutting of wood by beaver for food and dam construction can lead to changes in the species composition of the riparian zone, with species preferred by beaver being virtually removed (Naiman et al. 1988, Johnston and Naiman 1990). Non-preferred species thus may gain a competitive advantage and become more prevalent (Barnes and Dibble 1988), although some preferred species have been shown to be unaffected or even benefit from the foraging activity of beaver (Kindschy 1985, King et al. 1998). Thus, it is important to document which species are preferred by beavers for food and dam construction.

Much of the research that has been conducted on beaver foraging has taken place in mesic, heavily forested regions and little is known of the food preference of beavers in more arid environments (McComb et al. 1990). Before extensive beaver trapping occurred in the United States, beavers were present as far south as the deserts of northern Mexico; however, trapping and removal drove beavers to near extinction throughout North America around the turn of the century (Anderson 1964, Naiman et al. 1988). Beaver populations have since rebounded, and currently an estimated 6-12 million beaver are thought to inhabit streams in North America (Naiman et al. 1988). Beaver are once again found in desert regions such as the Great Basin and northern Mojave Desert. Habitat models that have been developed for beavers in north temperate regions do not work well in arid climates (McComb et al. 1990). In addition, aerial survey techniques developed for estimating beaver populations rely on visual counts of food caches in the ponds, which do not exist in beaver ponds found in warmer climates (Swenson et al. 1983). All of these factors have lead to a poor understanding of beaver population growth and foraging activity in the southwestern United States.

This study was designed to provide information on current beaver population size and foraging preferences in a stream of the southwestern United States. My goals were to try and determine (1) how prevalent beaver colonies are in streams of the Mojave Desert, (2) which riparian species are preferred by beaver for food and dam construction, and (3) if beaver are playing an important role in the invasion of exotic riparian species in the Southwest through selective foraging on native species.

In order to assess the overall impact of beaver ponds on the ecosystem as a whole, it is necessary to understand how prevalent beaver ponds are along streams in the

Southwest. Dam frequency along streams has been shown to vary widely throughout North America (Butler 1995). In Oregon coastal sites, frequencies are reported to be 1.2 dams km^{-1} (Leidholt-Bruner et al. 1992), while streams in semiarid regions of eastern Oregon have frequencies of 0.15 dams km^{-1} (McComb et al. 1990). Surveys in Quebec have shown that beaver ponds are present along 30 – 50% of the streams length, with a density of 10.6 dams km^{-1} (Naiman and Melillo 1984, Naiman et al. 1988). Butler and Malanson (1994) encountered more than 25 dams km^{-1} in the Rocky Mountains of northwestern Montana. Of all the surveys conducted, only the survey by McComb et al. (1990) has been conducted in a semiarid environment, thus more information on the density of beaver in southwestern streams is warranted. The lack of abundant riparian and upland vegetation to support beavers in arid regions, such as the Mojave Desert, leads to the hypothesis that beavers will not be as prevalent along desert streams as in more heavily forested regions.

The second portion of this study investigates the types of riparian vegetation present along reaches inhabited by beaver, and the components of this vegetation being used for food and dam construction. Understanding what vegetation exists and which types of vegetation beaver are foraging upon is important in the Southwest, as the species present differ dramatically from more temperate regions. In addition, riparian corridors of streams in the Southwest are being rapidly invaded by *Tamarix ramosissima* (saltceder) (DiTomasso 1998). *Tamarix* is a salt-tolerant phreatophyte which secretes salts from its foliage, which then enters riparian soils as leaves are deposited onto the soil surrounding the tree (DiTomasso 1998, Smith et al. 1998). The salinization is so extensive that native riparian species are often displaced by *Tamarix* (Smith et al. 1998).

Field observations have found that beaver do forage on *Tamarix*, and so a study of foraging preference relative to native species was warranted. If beavers selectively feed on *Tamarix*, then beavers could serve as a type of biological control for its invasion. In contrast, if beaver preferentially feed on native species, then beaver may actually aid in the invasion of *Tamarix*, assuming *Tamarix* suffers from beaver foraging.

Methods

Study Site

I conducted this study along Meadow Valley Wash, Nevada. Meadow Valley Wash is a perennial stream located in Lincoln County, Nevada, about 125 km northeast of Las Vegas in the transition between the Mojave and Great Basin Deserts. Annual precipitation averages 23 cm and is bimodal, with maximum precipitation occurring in the summer and winter (French 1983). Meadow Valley Wash is a ca. 5th-order stream draining a 4300-km^2 basin. In spite of the large drainage area, a mean annual precipitation of 23 cm generates a mean annual baseflow of only 170 L s^{-1} and summer flows average only 45 L s^{-1} (USGS Nevada NWIS-W data). The catchment ranges in elevation from 950 to 2300 m, with the study sites located in the lower elevation portions.

The dominant riparian flora along Meadow Valley Wash is a mixture of riparian and desert vegetation. Stream banks are dominated by *Populus fremontii* (Fremont cottonwood), *Fraxinus velutina* (velvet ash), *Salix lasiolepis* (arroyo willow), *Baccharis glutinosa* (seep-willow), *Chilopsis linearis* (desert willow), and *Tamarix ramosissima* (saltedar). On the upland edge of the stream, the vegetation changes rapidly into a plant community dominated by either *Artemisia* spp. (sagebrush) or *Larrea tridentata*

(creosotebush). Dominant aquatic macrophytes, when they exist, are predominantly *Typha* spp. (cattail).

Spatial Prevalence of Beaver Habitat and Pond Abundance

In order to gain an estimate of the spatial prevalence of beaver ponds along Meadow Valley Wash, I surveyed 31.5 km of the southernmost portion of Meadow Valley Wash for the presence of beaver ponds. The northern extent of the survey reach began at Choke Cherry Canyon, 18 km south of Caliente, Nevada (37.53 °N, 114.59°W, 1250 m elevation). Upstream of Choke Cherry Canyon the majority of stream flow is through privately owned cattle ranches, thus anthropogenic impacts are much greater. The southern end of the study reach was 1 km south of Cottonwood Canyon, approximately 10 km southeast of Elgin, Nevada (37.29°N, 114.46°W, 950 m elevation), where a decrease (and often a loss) of surface flow occurs due to a deepening of the alluvial bed. Because the upper portion of the stream flows through cooler, wetter, and more heavily forested regions, the southernmost portion of Meadow Valley Wash was selected to gain a conservative estimate of beaver pond abundance. Surveys were conducted by a combination of driving along Union Pacific Railroad maintenance roads and hiking those portions of the stream not accessible by the maintenance roads. Beaver ponds were logged with a hand-held GPS device and recorded onto a map of the stream. Portions of Meadow Valley Wash that lacked riparian trees necessary to support beavers were also recorded to get an estimate of how much suitable habitat exists for beaver along Meadow Valley Wash. Because beavers rely primarily on riparian woody species for food and dam construction, unsuitable habitat was defined as any habitat that lacked

riparian trees (regions where *Artemisia* or *Larrea* are continuous from upland to the streams edge).

Riparian Vegetation and Foraging Preference

I conducted surveys of woody species surrounding 4 ponds in April 2000 by randomly selecting plots along the banks of beaver ponds. Along Meadow Valley Wash, there is a rapid transition from riparian vegetation into upland communities due to the arid nature of the environment, and there is no evidence of beaver foraging on upland vegetation. Circular plots with a 4.9 m radius (75 m^2) were laid out adjacent to the waters edge and often extended close to (but never beyond) the upland edge of the riparian corridor. The first plot was located within ten meters of the upstream side of the dam. I selected additional plots by choosing random distances upstream, such that the plots did not overlap, until the top of the pond was reached. Four ponds were surveyed in this manner with at least 5 plots surveyed for each pond. The bank that was chosen to survey was randomly selected for each pond (odd or even random number selected for first plot location determined which bank was surveyed). Three of the four ponds were large enough to randomly select 6 plots, while one pond only allowed for the selection of 5 plots with the survey design. Data from individual plots for a given pond were averaged to get a mean value for that pond.

Only woody vegetation that could be used by beavers for either food or dam building was surveyed. Each species within a plot was scored in two ways. First, the percent cover was visually estimated and scored using the Braun-Blanquet scale (Table 1), which has six cover classes with smaller partitions near the bottom of the scale (Kent and Coker 1992). After I assessed the percent cover, I then conducted a second estimate

of the amount of that species foraged by beavers. The same Braun-Blanquet scale was used to record the visual estimate of the percent of a given species cover that had been foraged based on cut stems or trunks.

Mean percent cover and percent foraged for each species was calculated by using the median value for each cover class to calculate a mean across plots. Preferences for individual species were determined by calculating an electivity index (Jacobs 1974, Barnes and Dibble 1986). The electivity index (E) is calculated using the formula of Jabobs (1974) where $E = \ln (r(1-p) / p(1-r))$; where r represents the proportion of a given species foraged by beavers and p represents the proportion of that species which is available to beavers. Thus, an electivity index greater than 0 represents a preference for that species and an electivity index less than 0 implies avoidance.

Results

Spatial Prevalence of Beaver Ponds

Of the 31.5 km of stream surveyed for the presence of beaver ponds and beaver habitat, 6.5 km (20.6%) lacked the riparian species that could be utilized by beavers in this region, and as such, would not be suitable habitat for beaver colony establishment (Fig. 1). The remaining 25.0 km (79.4%) had some type of riparian species utilized by beavers. A total of 26 ponds were located that clustered into nine different colonies (ponds within 100m of each other) along the 31.5 km of stream surveyed. I mapped four ponds in detail and the resulting mean length of those four ponds (92.5 m) was used to calculate an estimate of the total length of beaver impounded stream. Beaver impounded approximately 2.4 km (7.6%) of the surveyed portion of the stream. The frequency of

ponds along Meadow Valley Wash was 0.8 ponds per kilometer. When groups of ponds close to one another were grouped into colonies as described above, the density of colonies was 0.3 colonies per kilometer of stream.

Vegetation Surrounding Beaver Ponds

I conducted vegetation surveys on 23 plots surrounding the 4 southernmost beaver ponds. I found that plots extending 10 meters from the edge of the pond were suitable along Meadow Valley Wash, as very little evidence of beaver foraging was ever found beyond the upland side of the plots.

The species with the highest percent cover within the plots were *Baccharis glutinosa* covering 13%, *Populus fremontii* with 11% cover, *Fraxinus velutina* with 11% cover and *Tamarix ramosissima* with 8% cover (Fig. 2). Other species that occurred with a lesser frequency include *Chrysothamnus nauseosus* (4% cover on average), *Salix lasiolepis* with 3% cover, *Artemisia* spp. covering 2% of the plots, *Chilopsis linearis* with 1% cover and *Gutierrezia microcephala* with less than 1% cover. Raw data for individual plots and genera can be found in the Appendix.

Beaver Foraging Preference

Populus had the highest proportion of individuals showing signs of beaver foraging (75% foraged) (Fig. 2). Following *Populus*, the order of foraging percentage was *Salix* (60%), *Fraxinus* (34%), *Tamarix* (21%), *Baccharis* (18%), and *Chrysothamnus* (10%). All other species had no signs of beaver foraging (Figure 2). Electivity indices for each species are shown in Table 2. Based on the proportion of individual species present and the amount of foraging observed for each species, beavers prefer *Salix* (E = 3.8), followed closely by *Populus* (E = 3.2). Other species showing preferred status

included *Fraxinus* (E = 1.4), *Tamarix* (E = 1.1), *Chrysothamnus* (E = 1.1) and *Baccharis* (E = 0.4). Beavers avoided foraging on *Artemisia* spp., *Chilopsis* and *Gutierrezia*. The electivity indices showed a high degree of variation between ponds due to natural variation coupled to the inherent bias of the Bran-Blanquet techniques for certain plant morphologies.

Discussion

Beavers are found more frequently than expected along Meadow Valley Wash, given the semiarid nature of the environment. My estimated dam density of 0.8 dams km^{-1} is much higher than the 0.15 dams km^{-1} found for semiarid regions of Oregon by McComb et al. (1990), yet much lower than densities reported for mesic regions (Naiman and Melillo 1984, Naiman et al. 1988, Liedholt-Bruner et al. 1992, Butler and Malanson 1994, Butler 1995). The average number of dams per kilometer may not be the appropriate measure for Meadow Valley Wash, as dams are clustered into colonies of beavers with several ponds, which often flow from one right into the next. The approach of Busher et al. (1983) and Howard and Larson (1985), which looks at a group of ponds together as a colony of beavers, is perhaps a more accurate way to assess beaver density in this environment.

The need for migration up and down stream by beavers has been documented by Pollock et al. (1995) and theoretically defined by Gurney and Lawton (1996) based on mesic region vegetative growth characteristics. Because the riparian corridor containing the vegetation necessary to support beavers is fairly narrow along Meadow Valley Wash (approx. 10 – 30 meters on each side of the stream), beavers likely build dams and reside

in a given pond only a short amount of time, then are forced to build further up or downstream of the initial pond. Thus, the average number of dams per kilometer could be an overestimate of beaver density. A colony density of 0.3 colonies km^{-1} is closer, yet still higher than the density of 0.15 dams km^{-1} found for the semiarid regions of eastern Oregon by McComb et al. (1990).

There appears to be a lot of habitat still available for beavers along Meadow Valley Wash, however this estimate takes into account only the presence of food and dam building material as criteria. Several studies have shown that other factors such as geomorphology may play an equal, if not larger, role in beaver habitat choice (Howard and Larson 1985, Bier and Barret 1987, Johnston and Naiman 1990, McComb et al. 1990, Barnes and Mallik 1997, Suzuki and McComb 1998). Consequently, there may be much less suitable habitat than I have reported here.

The lack of trees beyond the riparian corridor may constrain the carrying capacity of the ecosystem beyond the 1 colony km^{-1} estimate of Howard and Larson (1985). Beavers can easily cut years worth of tree growth down in only a few months, and since forage is limited along Meadow Valley Wash, the current density may represent a maximum density for the environment. Numerous researchers have shown that beaver populations fluctuate dramatically over time, perhaps due to population growth exceeding the carrying capacity of the system (Buster et al. 1983, Kindschy 1985, Busher 1987). Although discussions with local landowners along Meadow Valley Wash suggest that beavers have been quite prevalent along the study reach for over 30 years, long-term population surveys are unavailable, and as such, estimating the carrying capacity of the system is not possible.

Barnes and Mallik (1996) suggested that beavers in their region cut *Alnus* spp. (alder) for dam construction only; given that *Baccharis* was often foraged but had a low electivity index, and that the dams are constructed of a large number of *Baccharis* stems, it is possible that this is the case for *Baccharis* as well. Foraging on *Chrysothamnus* was reported. However due to the narrow stem diameter of *Chrysothamnus*, it was impossible to rule out the possibility that this species was foraged upon by some other animal (cattle, deer or rabbits). The electivity index shows that beavers forage on the exotic invasive *Tamarix*; thus, the foraging activity of beavers may be affecting the rate at which *Tamarix* is invading Meadow Valley Wash. Researchers have been successful at using beavers to help restore riparian ecosystems (Brayton 1984); however, my findings suggest that the interaction between beavers and invasive species may complicate restoration efforts.

Beavers create patchiness along the riparian corridor by building dams that flood riparian vegetation and by foraging on floodplain vegetation (Snodgrass 1997). Ponds can only provide habitat for beavers for a limited amount of time, after which beavers deplete riparian food stocks and move to new locations. I observed the creation and abandonment of ponds several times over two years along Meadow Valley Wash, in support of this hypothesis. Thus, there is a continual cycle of disturbance by both flooding and foraging, followed by a succession of riparian species along the stream corridor. All species capable of living along the riparian corridor may be established at the same time, or at any time (Barnes and Dibble, 1988), and as such, species that become established along the banks of a pond are likely not species that are dependent on

pioneer species, but rather species that can tolerate the flooded, anoxic environment created by beaver ponds, and those that can tolerate or avoid being foraged by beaver.

As beaver populations continue to grow throughout Europe and North America, it is important to continue to investigate the role of these keystone species in the ecology of streams and their floodplains. It is clear that in the Southwest, as elsewhere, beavers play a key role in the ecology of the riparian community and the ecosystem as a whole. Future research should be designed to take advantage of habitats, such as those in the Southwest, that are soon to be or recently have been colonized by beavers. Long-term population trends need to be documented if accurate carrying capacities are to be determined, and if a thorough understanding of how beaver activity impacts riparian ecosystems is going to be achieved. Studies of the temporal impact of foraging and dam construction will be key to determining the sustainability of riparian corridors that have evolved without the presence of beavers.

Table 1. Braun-Blanquet cover scale (as described in Kent and Coker, 1992) used for estimating plant species cover and the proportion of each species foraged by beaver.

Assigned Value	Cover Scale
+	Less than 1% cover
1	1 – 5% cover
2	6 – 25% cover
3	26 – 50% cover
4	51 – 75% cover
5	76 – 100% cover

Table 2. Electivity Index scores for individual woody plant species surrounding beaver ponds. A score greater than 0 indicates a preference for that species, while a score less than 0 indicates avoidance. Electivity Index is calculated based on the formula of Jacobs (1974); where r is the proportion of cut trees of a given species and p represents the available proportion of a given species.

Species	r	P	E
Artemisia spp.	0.000	0.020	-5.34
Baccharis glutinosa	0.182	0.126	0.43
Chilopsis linearis	0.000	0.011	-4.74
Chrysothamnus nauseosus	0.103	0.037	1.10
Fraxinus velutina	0.338	0.110	1.42
Gutierrezia microcephala	0.000	0.004	-3.77
Populus fremontii	0.759	0.111	3.23
Salix lasiolepis	0.601	0.032	3.83
Tamarix ramosissima	0.213	0.082	1.11

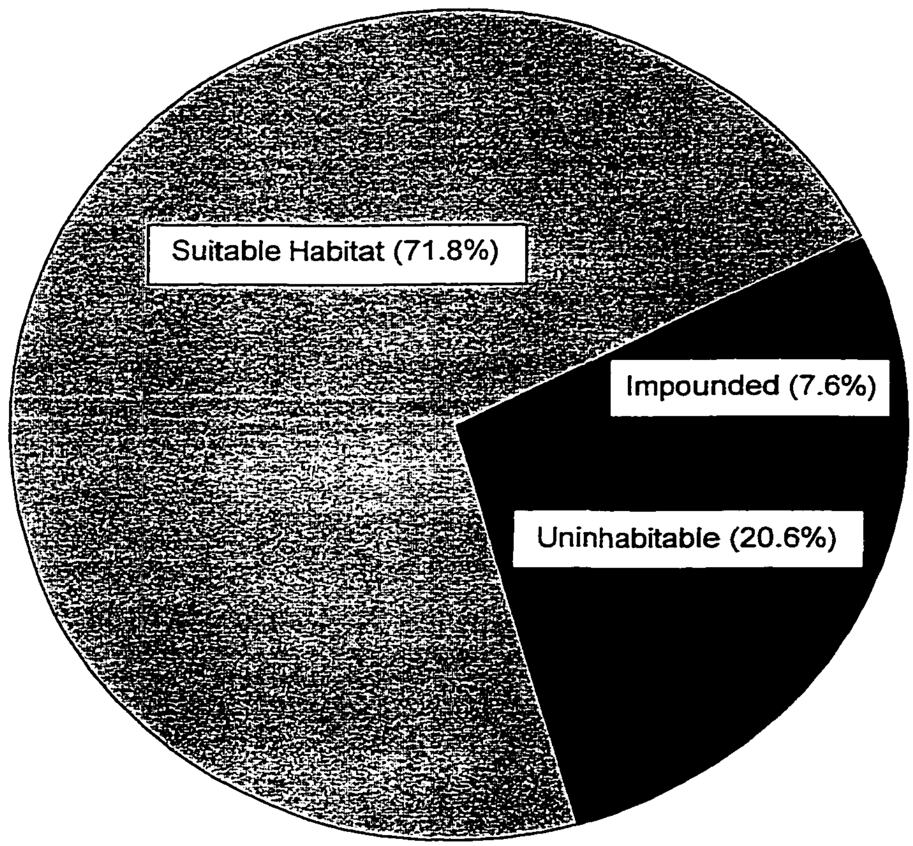

Fig. 1. Proportion of available habitat for beaver along Meadow Valley Wash, Nevada based on the presence of riparian trees, as well as the proportion of the 31.5 km of surveyed stream impounded by beaver dams (23 ponds). The unihabitable portion was defined based on the lack of woody riparian vegetation.

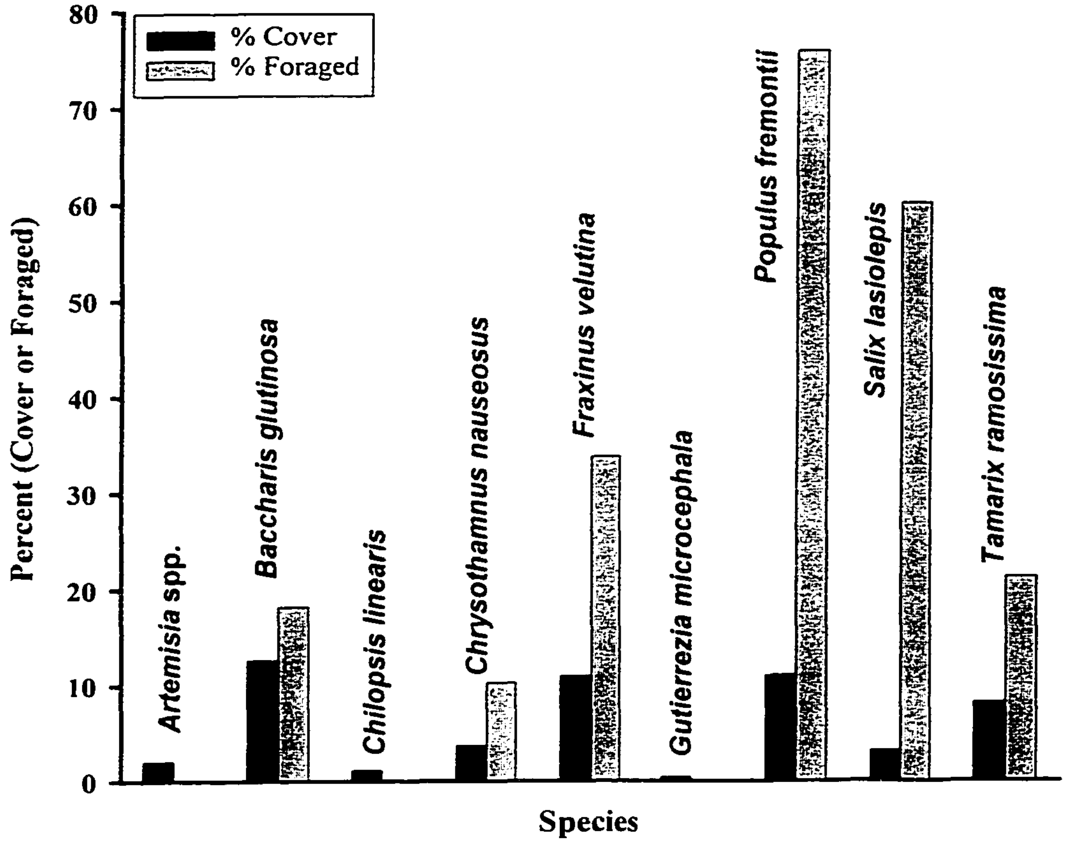

Fig. 2. Average percent cover and the mean proportion of each species foraged by beaver for woody trees and shrubs surrounding beaver ponds along Meadow Valley Wash, Nevada. Data represent the mean of 23 plots ($75m^2$ each) surrounding 4 ponds.

CHAPTER 3

THE IMPACT OF BEAVERS ON THE NITROGEN DYNAMICS OF DESERT STREAMS

Abstract

Nitrogen retention in a southwestern beaver pond was measured (1) by estimating the accumulation of particulate organic matter in beaver pond sediments relative to the unimpounded stream reaches surrounding ponds, and (2) by conducting a simultaneous injection of inorganic nitrogen (NO_3-N and NH_4-N) and a conservative tracer. I found that beaver pond sediments contain significantly higher amounts of organic matter than sediments of unimpounded reaches surrounding ponds. In late spring, the beaver ponds had higher nutrient uptake rates (U) and longer uptake distances (S_w) than unimpounded reaches. By late summer, and on the one winter date, the beaver ponds had much lower nitrogen uptake rates than unimpounded reaches just above the pond; however, nitrogen uptake distance remained similar between pond and non-pond reaches highlighting the impact of the differential surface area of ponds versus unimpounded reaches. Combined, these results show that beaver ponds increase net ecosystem nitrogen retention. Net mineralization and nitrification rates did not differ between ponds and unimpounded reaches. Assuming Meadow Valley Wash is representative of southwestern streams, the

presence of beavers along desert streams may help to increase overall ecosystem nitrogen retention in these nitrogen-limited systems.

Introduction

Stream nutrient retention and the efficiency with which organic matter is processed (the rate at which organic matter is retained and broken down through microbial action) differ between impounded and unimpounded stream reaches (Mulholland et al. 1984, Naiman et al. 1986). The dam-building activity of beavers (*Castor canadensis*) leads to heterogeneity in the physical structure of stream ecosystems that, in turn, leads to differences in the biogeochemical cycles of impounded and unimpounded stream reaches (Johnston and Naiman 1987, Naiman 1988). Beavers have been described as a keystone species (Naiman et al. 1986) and as "ecosystem engineers" (Jones et al. 1997) due to the extensive modification of their surrounding environment and the accompanying effects on community production and diversity (McDowell and Naiman 1986, Schlosser 1995, 1998), as well as the retention of organic matter and nutrients by the ecosystem (Naiman and Melillo 1984). The increased accumulation of organic matter in beaver pond sediments can increase microbial activity (Songster-Alpin and Klotz 1998) and, in turn, change the redox potential of pond sediments (Johnston et al. 1995). This leads to alterations in the rate of biogeochemical processes regulating organic matter processing and nutrient availability to instream biota (Bridgham et al. 1998).

Although several studies have developed nutrient budgets for beaver ponds or examined seasonal variation in the export of nutrients from beaver ponds, only limited

generalizations can be made as to the role of beaver ponds in the biogeochemistry of streams (Correll et al. 2000). Many studies have looked at individual nutrients in single ponds, often neglecting changes to ecosystem nitrogen dynamics. An exception is the study of Naiman and Melillo (1984), who found that beaver ponds in Quebec retained approximately 10^3 times more nitrogen after beaver impoundment occurred. In colder climates such as Quebec, however, beavers cache nitrogen in the form of food in the bottom of their ponds for the winter months when the pond is frozen, a behavior that is not exhibited by beavers in warmer climates (Swenson et al.1983). In addition, Francis et al. (1985) found that rates of nitrogen fixation in Quebec ponds were higher than rates for unimpounded stream reaches. Thus, beaver ponds have the potential to alter the nitrogen retention of stream ecosystems by causing the sequestering of organic nitrogen and increasing its processing efficiency (Naiman and Melillo 1984), yet many of the processes involved in nitrogen cycling (mineralization of organic matter, nitrification, denitrification) have not yet been studied in beaver ponds.

Nitrogen may play a more critical role in southwestern desert streams than in mesic regions (where the majority of research on beaver ponds has been conducted) because primary production is often limited by the availability of nitrogen (Grimm and Fisher 1986a, b). Since secondary productivity relies on primary productivity, nitrogen, in effect, may limit the overall productivity of desert stream ecosystems. The nitrogen biogeochemistry of desert stream ecosystems is often dependent on autochthonous production (Holmes et al. 1994, 1998; Jones et al. 1995). Thus, understanding the seasonal impact of beaver ponds on the amount of nitrogen available to support primary

production and microbial metabolism is essential in order to begin to understand the tight coupling between the biogeochemistry and energetics of desert streams.

The nutrient spiraling concept (Newbold et al. 1981, Elwood et al. 1983) describes the simultaneous processes of nutrient cycling and downstream transport of nutrient molecules in abiotic (dissolved in the water column) and biotic (incorporated into biota) forms (Mulholland et al. 1990). Nutrient spiraling distance is the distance a dissolved nutrient molecule travels in the water column, plus the distance the nutrient molecule travels while incorporated into biota, before mineralization and release back into the stream in inorganic form. Since the distance a nutrient molecule travels in the biota can only be measured through extensive radiotracer studies, a component of nutrient spiraling, the uptake length (S_w), is often used as an estimate nutrient retention. S_w is the distance a nutrient molecule travels in the water column before being taken up by the biota, and as such, is a measure of the rate of removal of a nutrient from the water relative to its downstream flux, or the efficiency with which the stream ecosystem utilizes an available nutrient (Mulholland et al. 1990). S_w is the major component of spiraling length and, as such, is a good index of ecosystem nutrient retention that can be calculated by injecting nutrients into streams in conjunction with a conservative tracer (Mulholland et al. 1990, Marti and Sabater 1996, Webster and Ehrman 1996).

This study tested the hypothesis that the construction of beaver ponds leads to increases in ecosystem inorganic nitrogen retention by altering the uptake distance of inorganic forms of nitrogen (S_w). In addition, I addressed the hypothesis that the impoundment of water by beavers and the resulting changes in the physical environment, lead to an increase in overall particulate organic nitrogen retention and processing

efficiency, measured as the accumulation and mineralization of organic matter within the stream ecosystem.

Methods

Study Site

This study was conducted between June 1999 and January 2000 along Meadow Valley Wash, Nevada. Meadow Valley Wash is a perennial stream located in Lincoln County, Nevada, about 125 km northeast of Las Vegas in the Mojave Desert. Annual precipitation averages 23 cm, with maximum precipitation occurring in the winter (French 1983). Meadow Valley Wash is a ca. 5^{th}-order stream draining a 4300-km^2 basin. Mean annual baseflow averages 170 L s^{-1} and summer flow averages only 45 L s^{-1} (USGS Nevada NWIS-W data). Geological substrate consists primarily of volcanic tuffs, tuffaceous sediment and rhyolite with smaller outcrops of quartzite, limestone, shale and dolomite (Tschanz and Pampeyon 1970). The catchment ranges in elevation from 930 to 2300 m, with the study sites located in the lower elevation portions (950 to 1100 m).

Dominant riparian flora include *Populus fremontii* (Fremont cottonwood), *Fraxinus velutina* (velvet ash), *Salix lasiolepis* (arroyo willow), *Baccharis glutinosa* (seep-willow), *Chilopsis linearis* (desert willow), and *Tamarix ramosissima* (saltcedar). On the upland edges of the stream the vegetation changes rapidly into a plant community dominated by either *Artemisia* spp. or *Larrea tridentata*.

Sediment Organic Matter

Although the accumulation of organic matter has been shown to occur in beaver ponds in wetter temperate regions (Naiman et al. 1986), there is no research that

estimates organic matter accumulation in beaver ponds of the southwestern United States. I collected several sediment organic matter cores from both beaver-impounded and unimpounded reaches along Meadow Valley Wash. Sediment cores were collected from the center of the pond (in order to avoid organic matter associated with the inundated riparian soil) using a circular core with a 2.5 cm radius to a depth of 5 cm. Cores were collected every 10 m from 40 m below the outflow of the dam to 50 m above the pond, thus, the number of impounded and unimpounded samples collected for each pond were similar. Mean sediment organic matter for impounded and unimpounded regions of an individual pond was calculated and used as a single estimate of sediment organic matter for comparisons among ponds. Sediment samples were returned to the lab and dried at 40°C for 48 hours and weighed (dry weight). After dry weight was determined, samples were combusted at 550°C for four hours and then re-weighed for Ash Free Dry Mass (AFDM) determination.

Nutrient Retention

To estimate the rate at which beaver ponds (in comparison to unimpounded reaches) retain dissolved inorganic nitrogen, I conducted a series of nutrient injections on a medium-sized pond along Meadow Valley Wash, and calculated the uptake rate (U) and uptake length (S_w) of inorganic nitrogen. A solution of ammonium nitrate and a conservative dye tracer (FWT Red Tracing Dye, Ben Meadows Cat. #221491) were simultaneously added to the stream at a constant rate from a Marriotte bottle located 50 m above the most upstream sampling point to allow for thorough mixing to occur. Dye concentration was measured in the stream with a Turner Model 10 Fluorometer fitted with a Turner 10-1056 excitation filter and a Turner 10-052 emission filter.

Concentrations and injection rates were adjusted to achieve twice the background concentration of NH_4-N and NO_3-N and one hundred times background fluorescence at steady-state conditions.

Calculations were based on the techniques presented in the Stream Solute Workshop (1990). Final nutrient concentrations were corrected for background levels by calculating a normalized nutrient concentration as follows:

$$C_N = (C_t - C_b) / Co \quad (3.1)$$

where C_N is the normalized nutrient concentration, C_t is the final nutrient concentration at a specific site, C_b is the background (initial) nutrient concentration, and C_o is the steady state tracer concentration at each sampling point. Steady-state (plateau) nutrient concentrations can then be used to calculate the nutrient uptake rate as,

$$ln(C_N x) = ln\ (C_{NO}) - k_C x \quad (3.2)$$

in which $C_N x$ is the normalized nutrient concentration at distance x and k_C is the uptake rate per unit distance. Using the uptake rate (k_C) as well as the velocity of the reach (v), the uptake length (S_w) can be calculated as,

$$S_w = v / k_C \quad (3.3)$$

and the uptake rate on an areal basis (U) can be calculated as,

$$U = (CQ / S_w w) \quad (3.4)$$

where v is the stream velocity, Q is discharge and w is the stream width. Because the beaver pond had varying stream width, pond U was calculated as the mean uptake value for each 10-m pond reach.

Sampling points were marked every 10 m from 50 m above the pond to the outflow of the pond, such that at least 5 points within the unimpounded stream reach just above the pond were obtained to calculate uptake coefficients for the upstream reach to compare to beaver pond values. Prior to beginning the injection, initial samples were collected for background nutrient concentrations and fluorescence. Fluorescence (dye concentration) was monitored every 15 minutes at the most downstream point until a plateau dye concentration had been reached, at which time each sampling location was re-sampled for final nutrient concentrations and fluorescence. Initial samples were analyzed for inorganic nutrients (ammonium, nitrate and soluble reactive phosphorus) and total dissolved nitrogen (TDN). Soluble reactive phosphorus (SRP) was measured with the molybdate-antimony method (Murphy and Riley 1962). Changes in initial and final SRP concentration was used as an indicator of steady state conditions in stream flow and nutrient uptake. Ammonium was analyzed using the phenolhypochlorite method (Solorzano 1969), nitrate through the cadmium reduction method (Wood et al. 1967) and dissolved organic matter by persulfate digestion (Pujo-Pay and Raimbault 1994). Final samples were analyzed for inorganic nutrients only.

Organic Matter Mineralization and Nitrification of Ammonium

The spatial variation in the net rates of organic matter mineralization and the microbial nitrification of ammonium were measured for sediments collected from three beaver ponds along Meadow Valley Wash in June 2000, when high rates of mineralization and nitrification would be expected. The three ponds were sampled on the same day in June to allow for direct comparisons to be made between ponds. Beginning 10 m upstream of the dam, transects were laid out every 20 meters until the upstream end of the pond was reached. Along each transect, three sediment cores were collected from the center of each third of the ponds width. This sampling design allowed for comparisons to be made between bank and thalwag sediments. In addition to pond samples, sediment cores were collected from three upstream locations, each at least 10 m apart, to serve as controls for comparison with pond sediment mineralization and nitrification rates.

Sediment cores were collected as 2.5 cm radius circular cores by inserting a piece of acrylic tubing 5-cm into the sediment and excavating the core. Cores were placed into plastic containers and stored on ice during transport to the lab. In the lab, sediments were placed into sterile disposable filter funnels attached to a filter flask with a glass fiber filter (~0.7 μm pore size, VWR Grade Number 151) separating the sediments from the filter flask. The design of these chambers was adapted from the design of Nadelhoffer (1990). Initially, sediments in the funnel were rinsed with 50 ml of distilled water, which was then suctioned through the filter and discarded. After rinsing, another 50 ml of distilled water was added to the sediments, and the sediments were allowed to incubate at room temperature for 48 hours in the dark. After 48 hours, the water was suctioned through the

sediments into the filter flask and analyzed for NO_3-N and NH_4-N. The entire process (with the exception of the rinsing step) was repeated three more times. Net mineralization and nitrification rates were calculated as follows:

$$NH_{4\,after\ 48\ hours} = NH_{4\,mineralization} - NH_{4\,nitrified} = \text{Net Mineralization}$$

$$NO_{3\,after\ 48\ hours} = NO_{3\,nitrification} - NO_{3\,denitrified} = \text{Net Nitrification}$$

Thus, slope of the accumulation of NH_4 and NO_3 over the three sampling periods represents the net mineralization rate and net nitrification rate, respectively.

Results

Sediment Organic Matter

104 sediment cores were analyzed from 4 different beaver ponds on 6 dates (two of the ponds were sampled on two dates) between June and September 1999. T-test comparisons showed no significant differences between sediments collected upstream of ponds and sediments collected downstream of a pond ($P = 0.13$, $n = 6$, SigmaStat version 2.0) (Table 3). In addition, Mann-Whitney Rank Sum Test showed no significant differences between dates for the two ponds sampled on two dates ($P=0.86$ for pond 2, and $P = 0.38$ for pond 3). Thus, by combining all unimpounded reach samples and conducting a Mann-Whitney Rank Sum Test, we find that pond sediments have significantly higher amounts of organic matter than unimpounded reach sediments ($P = 0.002$, $n = 6$) (Fig. 3).

Nutrient Concentrations In Ponds

Concentrations of ammonium (NH_4-N), nitrate (NO_3-N), and soluble reactive phosphorus (SRP) varied seasonally along Meadow Valley Wash (Fig. 4). NO_3-N and

NH_4-N showed greater variation than did SRP from June through September 1999. Variation also existed between upstream and pond nutrient concentrations for individual dates. The percent change in the mean upstream nutrient concentration was calculated from the mean pond nutrient concentration in order to make comparisons between ponds that were independent of ambient nutrient concentrations (Fig. 5). One-way analysis of variance (Sigma Stat version 2.0) found no significant changes in NH_4-N, NO_3-N or SRP concentration as water moved through ponds (Table 4). Dissolved organic nitrogen (DON) showed similar variation and did not change consistently as water flowed through ponds (Table 4).

Nutrient Uptake Rate and Uptake Distance

Nutrient uptake rates (U) and uptake lengths (S_w) were calculated for a medium sized pond (Pond #2, length = 88 m, mean width = 12 m, mean depth = 0.5 m) on four dates. In late spring (17 June 1999), the beaver pond had higher calculated nutrient uptake rates than the unimpounded reach just above the beaver pond (330, 106 $\mu g\ N \cdot m^{-2} \cdot min^{-1}$, respectively) (Fig 6a). Inorganic nitrogen uptake rates were lowest for the pond and the unimpounded reach on 5 August 1999 (1 $\mu g\ N \cdot m^{-2} \cdot min^{-1}$ for both), perhaps due to the low in-stream NO_3-N and NH_4-N concentrations, which were at or below detection limits. In late summer the trend was reversed, with the beaver pond having lower inorganic nitrogen uptake rates than the unimpounded reach (156, 472 $\mu g\ N \cdot m^{-2} \cdot min^{-1}$, respectively). On the one winter date (11-Jan-2000), the unimpounded reach had a higher uptake rate than the beaver pond (229, 105 $\mu g\ N \cdot m^{-2} \cdot min^{-1}$, respectively).

Differences in the nutrient uptake length (S_w) were greatest on 17 June 1999 (unimpounded reach = 613 m, pond reach = 122 m), the only date in which the beaver

pond had a shorter uptake length than the unimpounded reach (Fig. 6b). The unimpounded reach had its shortest uptake length on 5 August (87 m) whereas the beaver pond had the shortest uptake length on 19 September (113 m). Winter uptake distances were 5-fold higher than at any other time of the year, and similar between ponds and unimpounded stream reaches (unimpounded reach = 1423 m, pond = 1443 m).

Sediment Mineralization and Nitrification

Organic matter mineralization rates for the three ponds were highly variable and did not differ significantly from unimpounded reach mineralization rates (Fig. 7). Left and right bank sediment samples had slightly higher mean mineralization rates than the center of the pond, however one way analysis of variance shows no significant differences in mineralization rate between any pond samples and samples from the unimpounded reaches ($P = 0.83$, $F = 0.286$, SigmaStat version 2.0). Similarly, Kruskal-Wallis analysis of variance on ranks showed that sediment nitrification rates did not differ within the ponds or between ponds and unimpounded reaches ($P = 0.68$, $H = 1.513$). Thus, there appears to be no consistent differences between beaver impounded and unimpounded stream reaches in either sediment net mineralization or nitrification rates.

Discussion

Beaver ponds impacted the retention of nitrogen along Meadow Valley Wash. Data presented here show that beaver ponds along Meadow Valley Wash not only increased nitrogen retention (relative to unimpounded stream reaches) through the accumulation of sediment particulate organic matter, but also increased nitrogen retention

through higher per unit inorganic nitrogen uptake rates during the spring, relative to unimpounded reaches. Although inorganic nitrogen uptake rates decreased in the pond and increased in the unimpounded reach in late summer and winter months (Fig. 6), the beaver pond maintained similar uptake lengths across dates, perhaps as a result of the increased surface area and decreased flow velocity of the pond.

Not surprisingly, the amount of sediment organic matter was three times higher in beaver ponds than in unimpounded reaches (Fig. 3). Sediments collected just downstream of beaver ponds have similar organic matter contents as sediment samples from upstream of beaver ponds (Table 3). Thus, beaver pond sediments may be receiving some of their organic matter from the decomposition of organic matter in the riparian bank after inundation. Otherwise, we would expect to see a decline in sediment organic matter abundance immediately below ponds if the organic matter in pond sediments was the result of the decreased flow velocity of ponds.

Dissolved inorganic nutrient (NO_3-N, NH_4-N and SRP) concentrations were extremely variable across different dates, highlighting the seasonal nature of nutrient availability in stream ecosystems. The lack of consistent trends in nutrient concentration as water flowed through ponds is similar to the findings from several other beaver pond studies in other regions (Dodds and Castenholz 1988, Devito et al. 1989, Cirmo and Driscoll 1993, Naiman et al. 1994, Klotz 1998, Correll et al. 2000). Thus, it appears that the role of beaver ponds in the nutrient dynamics of streams may vary seasonally, and studies such as this, which measured specific rates of nutrient uptake seasonally, can provide insight into the factors controlling these seasonal patterns.

The shorter nitrogen uptake lengths for the pond, relative to the unimpounded reach in the spring, suggest that beaver ponds are increasing nitrogen retention during this time. However, later in the summer ponds become less retentive of nitrogen relative to unimpounded reaches and this trend holds throughout the fall and winter. It should be noted, however, that the rates reported here are areal measures and that pond and unimpounded reach surface areas differ dramatically. Thus, during late summer and winter unimpounded stream reaches have dramatically higher nitrogen uptake rates, but similar uptake lengths. For example, along Meadow Valley Wash, beavers impound 7.5% of the stream's length, and the width of beaver ponds is approximately three times the unimpounded stream width (Chapter 2). Thus, beaver ponds represent over 20% of the surface area of the stream and their effects on overall ecosystem inorganic nitrogen retention should not be overlooked. Higher nutrient uptake rates for the ponds in the spring correspond to an observed increase in macrophyte and algal abundance during this time, as well as riparian tree leaf production. Thus, future studies should address the partitioning of nutrients taken up from the water column, perhaps by conducting injections of nutrients as stable isotopes.

Sediment net mineralization and net nitrification rates were found to be variable but constant between beaver pond sediments and unimpounded reach sediments, despite the increased organic matter available in beaver pond sediments. For all locations, the net mineralization of organic matter produced more NH_4-N than was nitrified; however, NH_4-N concentration never increased significantly in ponds (Fig. 5). Thus, NH_4-N is being produced from the mineralization of organic matter that is not being nitrified and must be either assimilated or bound to beaver pond sediments.

Net nitrification rates were close to the rates for ammonium production through mineralization, suggesting a close coupling between these processes in stream sediments. Pond NO_3-N concentrations did not differ despite the prevalence of nitrification, likely due to assimilation and denitrification, as well as hyporheic removal. The impoundment of water behind dams creates an increased hydraulic head, forcing water down through the pond sediment into the hyporheic zone of the stream. Conservative tracer concentrations remained remarkably constant in beaver ponds, suggesting that little or no hyporheic upwelling occurred. Thus, NO_3-N produced in pond sediments is likely forced down through low-oxygen hyporheic flowpaths, where denitrification rates are high (Holmes et al. 1998). The increased sediment organic matter and warmer temperatures of desert stream beaver ponds could lead to higher rates of denitrification relative to unimpounded stream reaches and rates of denitrification in temperate region ponds. Thus, future studies need to quantify the role of denitrification in order to fully understand nitrogen cycling in beaver ponds.

It is clear that beaver ponds in desert streams retain more particulate nitrogen than unimpounded stream reaches, thus increasing ecosystem nitrogen retention. In addition, during the spring months it appears that beaver ponds also increase inorganic nutrient uptake, and these seasonal patterns of inorganic nitrogen uptake may be driven by factors such as temperature that are affected by the differential surface area and hydrology of ponds. Overall, the presence of beavers along desert streams may help to increase overall ecosystem nitrogen retention in these nitrogen-limited systems, allowing the ecosystem as a whole to be more productive.

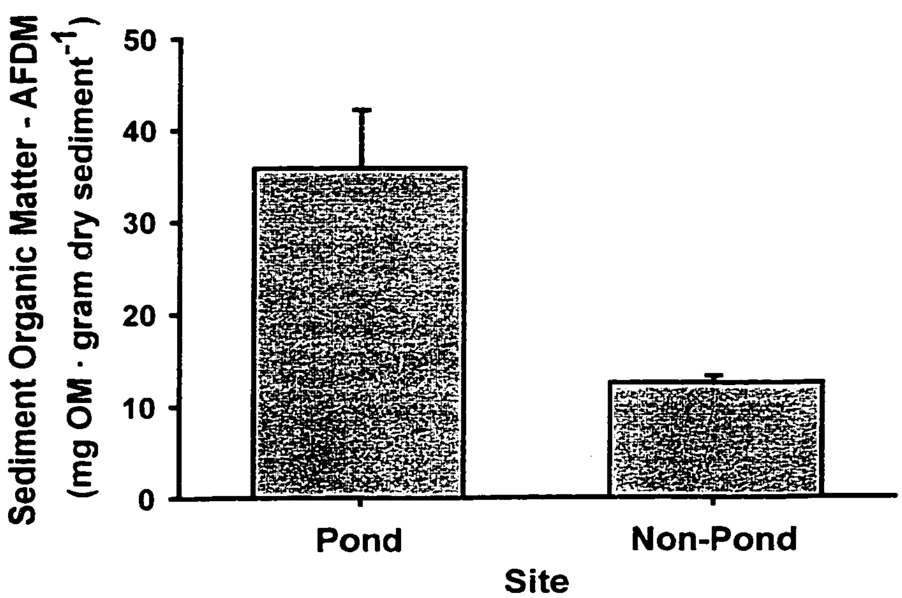

Figure 3. Quantity of sediment organic matter in cores collected from beaver-impounded (pond) and unimpounded (non-pond) stream reaches. Bars indicate the standard error of the mean.

Table 3. Sediment organic matter, as determined by Ash-Free Dry Mass, for sediment cores collected upstream of beaver ponds, within beaver ponds, and below beaver ponds. Organic matter concentrations are expressed as mg • gram dry sediment^{-1} • hour^{-1}.

Date	Location	Upstream	Pond	Downstream
2-June-99	Pond #1	13.5	59.9	12.3
17-Jun-99	Pond #2	10.5	26.7	10.7
7-Jul-99	Pond #3	12.3	46.8	16.7
22-Jul-99	Pond #3	13.5	38.0	13.7
19-Aug-99	Pond #4	8.9	25.1	11.3
17-Sep-99	Pond #2	9.7	18.5	18.9
	Mean	**11.4**	**35.8**	**13.9**

Table 4. Results of one-way analysis of variance between nutrient concentrations and location. Three locations were tested, samples collected upstream of beaver ponds, within beaver ponds, and below beaver ponds.

Nutrient Type	**F**	**P**	**N**
NO_3-N	0.095	0.91	8
NH_4-N	0.579	0.57	8
SRP	0.015	0.99	8
DON	0.190	0.83	7

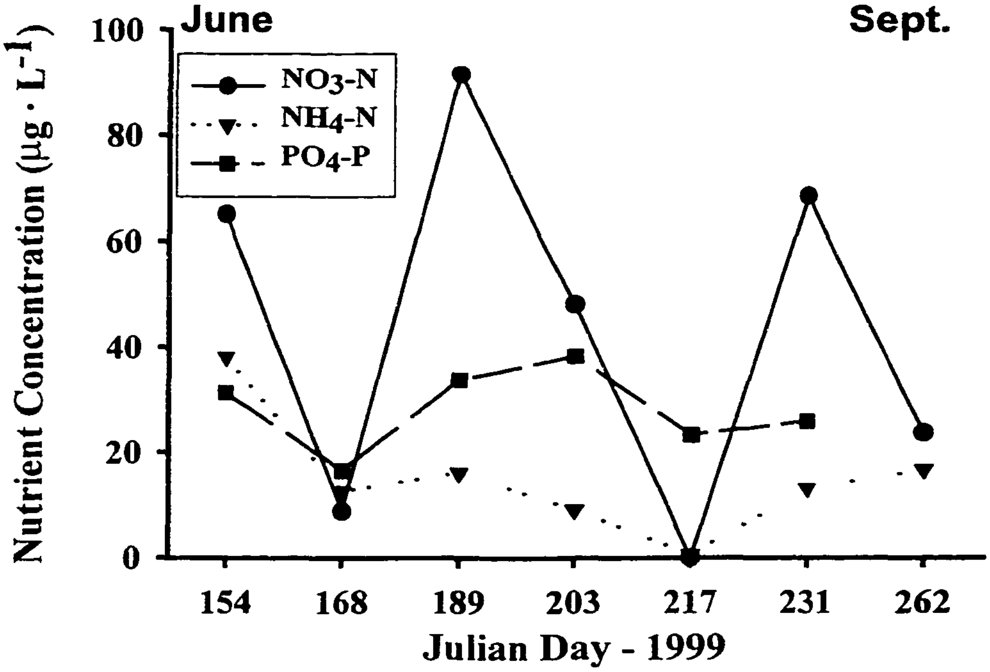

Figure 4. Seasonal variation in nutrient concentrations along Meadow Valley Wash for samples collected between June and September 1999.

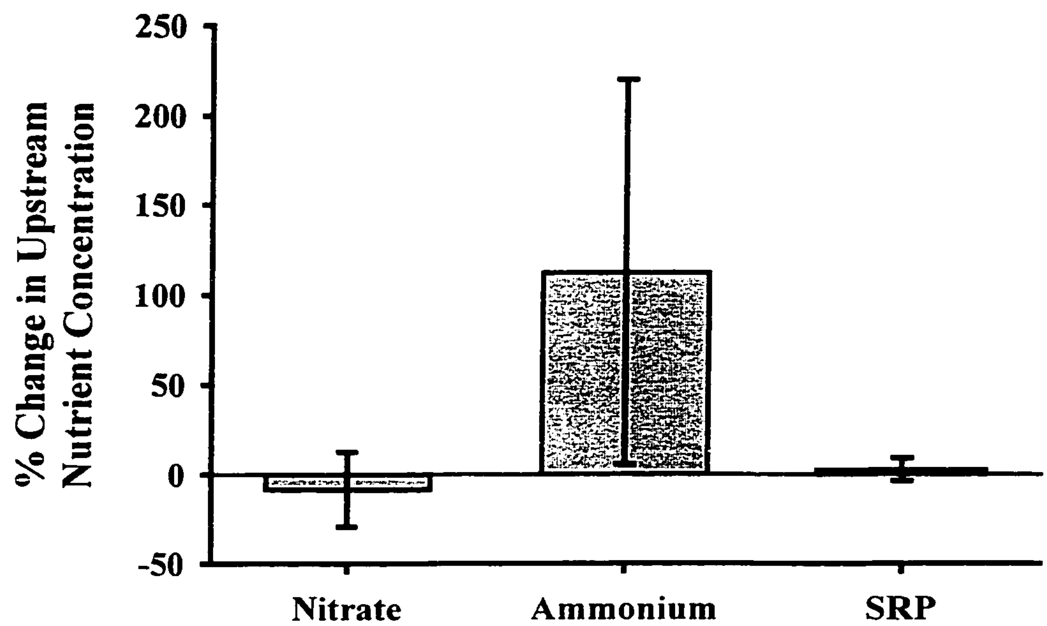

Figure 5. The percent change in beaver pond nutrient concentrations, relative to upstream (unimpounded) reach nutrient concentration. SRP is used to represent soluble reactive phosphorus. Bars indicate the standard error of the mean.

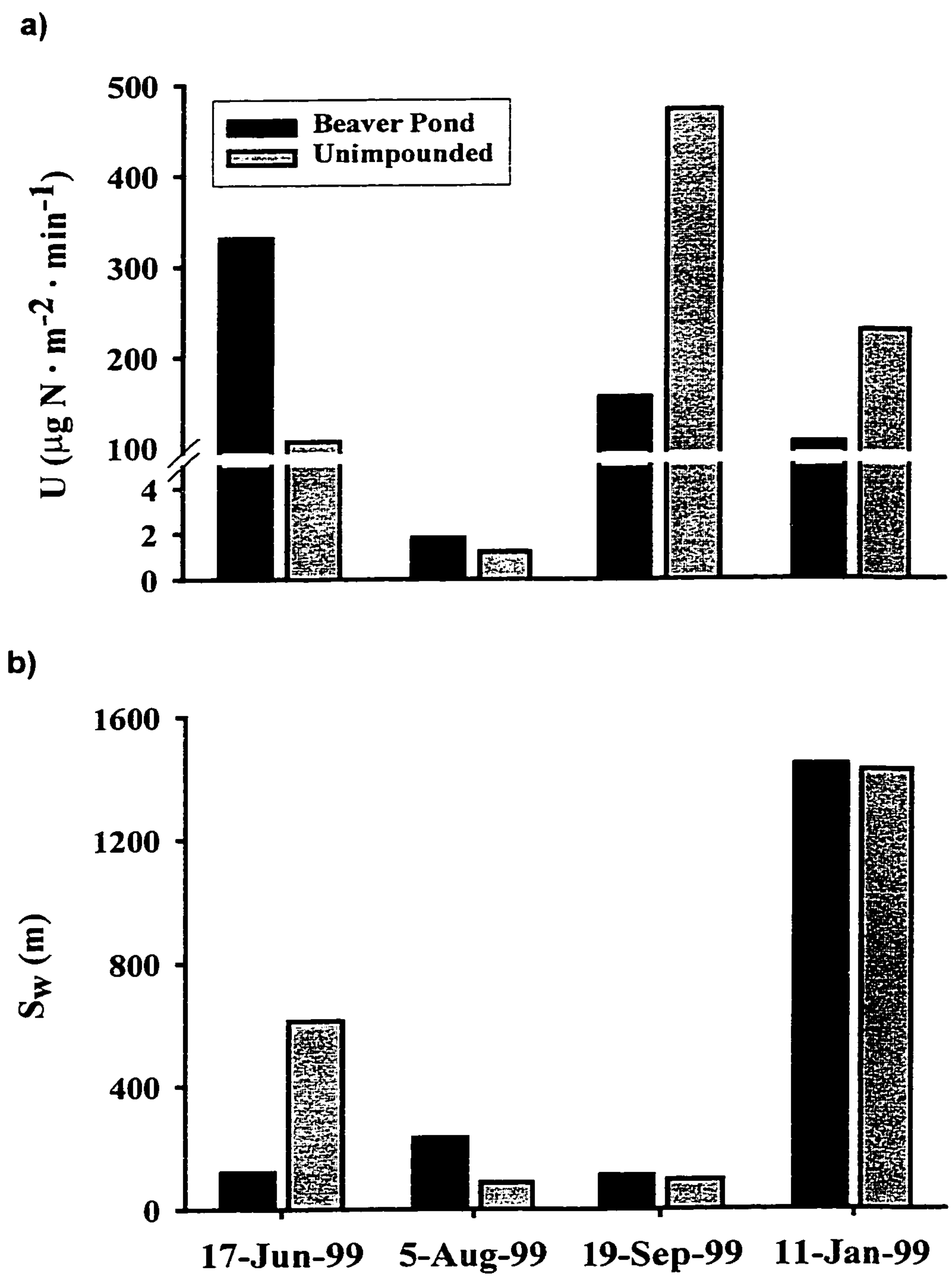

Figure 6. a) Calculated uptake rates (U) for beaver pond #2, and the unimpounded reach just above pond #2 on four dates. b) Calculated uptake lengths (Sw) for the beaver pond and the unimpounded reach on each date.

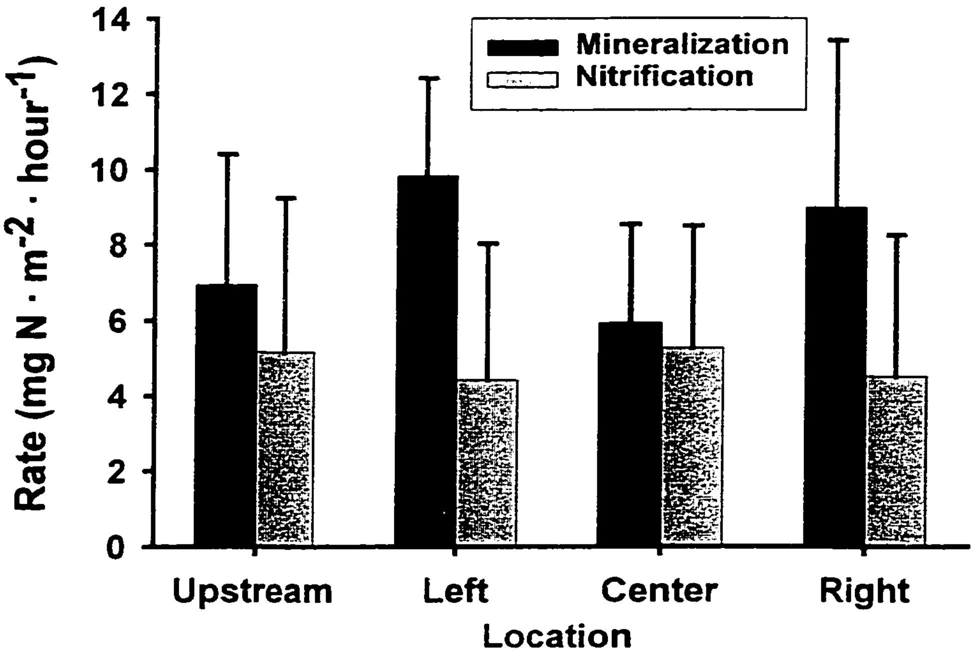

Figure 7. Results of laboratory estimates of net mineralization of organic matter and net nitrification for sediments collected upstream of beaver ponds and within different portions of the pond. Bars are equal to the standard error of the mean.

CHAPTER 4

CONCLUSIONS

Along Meadow Valley Wash in southern Nevada, beaver ponds are quite common, occurring along almost 8% of the streams length. This work has shown that in arid regions such as the Southwest, beavers and beaver ponds may alter riparian community structure and species abundances through selective foraging. Future studies need to address the temporal cycles of beaver pond construction and abandonment in this and other regions in order to investigate how sparse upland vegetation may limit the carrying capacity of the ecosystem for beaver.

Management practices utilizing beaver to restore riparian corridors and critical wetland habitats have become increasingly common (Brayton 1984). However, this work suggests that management officials should consider factors such as the presence of invasive species before re-introducing beavers. It appears that in the Southwest, beavers are foraging on the invasive *Tamarix*, and as such, may be impacting the rate at which the *Tamarix* is invading streams.

Ecosystem-level processes are also affected by the presence of beavers in Meadow Valley Wash. The impoundment of water and the concomitant effects on particulate organic matter retention and inorganic nitrogen retention alter the availability of nitrogen to sustain primary and secondary production in these nitrogen-limited systems. I have shown that beaver ponds increase the amount of nitrogen retained

relative to reaches without beaver present; thus, the impact of beavers on desert stream ecosystems may be even greater than would be expected based on research conducted in wetter climates. Although unimpounded reaches often have higher nitrogen uptake rates, the linear "metrics" of nitrogen retention that do not account for the overall surface area and velocity of beaver ponds underestimate the ecological importance of these animals year-round.

Beaver ponds are not static features of the landscape, but rather represent dynamic patches within the landscape. As beavers colonize a stream reach, riparian soils are flooded and riparian species composition is altered. Species selectively foraged by beaver may be eradicated from a given reach where beavers are present. In desert regions, the sparse vegetation to support beavers beyond the riparian corridor likely leads to a more rapid abandonment cycle of ponds as food supplies become scarce. During the course of my investigations I watched the construction and abandonment of a pond occur over a course of 17 months. After abandonment, the pond drains and riparian species eventually return; however, the characteristics of soils from former beaver ponds are altered for prolonged periods following abandonment (Naiman et al. 1994), and so the impact of a given pond remains long after beavers leave a reach. Streams with beaver present are subjected to patch disturbances that may occur with a higher frequency in desert streams than in other biomes and that may alter the trajectory of community succession.

Interactions among factors such as climate, geomorphology, hydrology, and the species composition of streams make it difficult to understand the fundamental, system level characteristics of streams (Naiman et al. 2000). The traditional view of streams as

top-down structures governed primarily by their geomorphology and hydrologic regimes is accurate. However, as Naiman et al. (2000) point out, the biotic feed-backs on top-down regulation of ecosystem processes should not be overlooked. Beavers exert a strong biotic feedback on the physical structure of streams, and so the role of beavers as keystone species potentially reaches far beyond the impact of beavers on community structure.

The ecological role of beavers in stream ecosystems cannot be overlooked. In the early 1900s, when the field of stream ecology was young, beaver were absent from many streams throughout the world. The river continuum concept (Vannote et al. 1980), which views streams as continual gradients of physical conditions from their headwaters to the mouth, may not be valid in streams where organisms such as beavers can dramatically modify the physical characteristics of a stream reach. The serial discontinuity concept of riverine systems put forth by Ward and Stanford (1983) that views streams as alternating sequences of lotic and lentic environments is perhaps a better starting model for describing the ecology of streams with beaver present. In their description of what occurs in a discontinuous flow regime, Ward and Stanford (1983) suggested that maximum nutrient spiraling is maintained throughout the stream continuum by biotic adjustments to continually changing physical conditions. This hypothesis is supported by the data presented here, which show similar inorganic nitrogen uptake lengths for impounded and unimpounded reaches, despite dramatically different uptake rates.

Future studies should take a comparative approach and look at specific ecological effects of beavers across habitat types. In each type of environment the impact of beavers differs in some instances (e.g., organic matter mineralization, foraging preference), and

yet remains the same for others (e.g., nutrient and organic matter retention), so future research should take a comparative approach to understanding how beavers impact the ecology of streams and rivers. I make no attempt to claim generality of my results to streams in other regions of the world, yet I believe generalities exist and that understanding those generalities is the key to understanding the complete ecological role of beavers in riverine ecosystems.

Beavers are present in streams worldwide, and so the global ecological impact of beavers is immense. Currently, an estimated 6-12 million beavers inhabit streams worldwide (Naiman et al. 1988) and the range of beavers continues to expand. As beaver populations continue to grow, the impact of beavers on the ecology of flowing waters will no doubt increase. This thesis provides a more thorough understanding of the role of beavers in stream ecosystems and provides novel information on the role of beavers in arid regions of the United States. Data presented here show that beavers may play a key role in the successional pattern of riparian species and that beavers may impact the invasion of certain exotic species such as *Tamarix*. This research provides specific data on nitrogen retention in a nitrogen-limited Mojave Desert stream that will lead to a better understanding of the nutrient dynamics of streams in the Mojave Desert. The nutrient dynamics of Meadow Valley Wash will help to form a more general view of how stream ecosystems function in the Southwest, as well as worldwide. These data provide information on the applicability of models designed to explain the structure and function of streams in wetter climates to streams in more arid regions. In addition, this research will assist wildlife managers and land management officials in making informed

decisions on how to regulate beaver populations and to understand the factors that need to be considered when deciding to use beavers to restore wetlands, streams and rivers.

LITERATURE CITED

Anderson, S. 1964. Return of the beaver. Natural History **73**:38-43.

Barnes, W. J. and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Canadian Journal of Botany **66**:40-44.

Barnes, D. M. and A. U. Mallik. 1996. Use of woody plants in construction of beaver dams in northern Ontario. Canadian Journal of Zoology **74**:1781-1786.

Barnes, D. M. and A. U. Mallik. 1997. Habitat factors influencing beaver dam establishment in a northern Ontario watershed. Journal of Wildlife Management **61**:1371-1377.

Beier, P. and R. H. Barrett. 1987. Beaver habitat use and impact in Truckee river basin, California. Journal of Wildlife Management **51**:794-799.

Bilby, R. E., 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology **62**:1234-1243.

Bilby, R. E. and G. E. Likens. 1980. Importance of debris dams in the structure and function of stream ecosystems. Ecology **61**:1107-1113.

Brayton, D. S. 1984. The beaver and the stream. Journal of Soil and Water Conservation. **39**:18-109.

Bridgham, S. D., Updegraff, K. and J. Pastor 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology **79**:1545-1561.

Busch, D. E. and S. G. Fisher. 1981. Metabolism of a desert stream. Freshwater Biology **11**:301-307.

Busher, P. E. 1987. Population parameters and family composition of beaver in California. Journal of Mammalogy **68**:860-864.

Busher, P. E., R. J. Warner and S. H. Jenkins. 1983. Population density, colony composition, and local movements in two Sierra Nevadan beaver populations. Journal of Mammalogy **64**:314-318.

Butler, D. R. 1995. The geomorphic influence of beavers. Pages 148-183 *in* D. R. Butler (ed.) Zoogeomorphology: Animals as Geomorphic Agents. Cambridge University Press, New York, NY, USA.

Butler, D. R. and G. P. Malanson 1994. Canadian landform examples – Beaver landforms. Canadian Geographer **38**:76-79.

Cirmo, C. P. and C. T. Driscoll. 1993. Beaver pond biogeochemistry: Acid neutralizing capacity generation in a headwater wetland. Wetlands **13**:277-292.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **lll**:1119-1144.

Correll, D. S., T. E. Jordan and D. E. Weller. 2000. Beaver pond biogeochemical effects in the Maryland Coastal Plain. Biogeochemistry **49**:217-239.

Devito, K. J., R. J. Dillon, and B. D. Lazerte. 1989. Phosphorus and nitrogen retention in five Precambrian shield wetlands. Biogeochemistry **8**:185-204.

DiTomasso, J. M. 1998. Impact, biology, and ecology of saltcedar (*Tamarix* spp.) in the southwestern United States. Weed Technology **12**:326-336.

Donkor, N. T and J. M. Fryxell. 1998. Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. Forest Ecology and Management **118**:83-92.

Elwood, J. W., J. D. Newbold, R. V. O'Neill and W. VanWinkle. 1983. Resource spiraling: an operational paradigm for analyzing lotic ecosystems. *In* Fontaine, T. D. and S. M. Bartell (ed.) The dynamics of lotic ecosystems. Ann Arbor Science Publishers Inc., Ann Arbor, MI, USA.

Fisher, S. G. 1986. Structure and dynamics of desert streams. Pages 119-139. *in* Whitford, W. G. (ed.) Pattern and Process in Desert Ecosystems. University of New Mexico Press, Albuquerque, NM, USA.

Ford, T. E. and R. J. Naiman. 1988. Alteration of carbon cycling by beaver: methane evasion rates from boreal forest streams and rivers. Canadian Journal of Zoology **66**:529-533.

Francis, M. M., R. J. Naiman and J. M. Melillo. 1985. Nitrogen fixation in subarctic streams influenced by beaver (*Castor canadensis*). Hydrobiologia **121**:193-202.

French, R. H. 1983. A preliminary analysis of precipitation in southern Nevada. Water Resources Center, Desert Research Institute, Reno, NV, USA. Publication Number 45031.

Grimm, N. B. and S. G. Fisher. 1986a. Nitrogen limitation in a Sonoran Desert stream. Journal of the North American Benthological Society **5**:2-15.

Grimm, N. B. and S. G. Fisher. 1986b. Nitrogen limitation potential of Arizona streams and rivers. Journal of the Arizona Nevada Academy of Sciences **21**:31-43.

Gurney, W. S. C. and J. H. Lawton. 1996. The population dynamics of ecosystem engineers. Oikos **76**:273-283.

Hedin, L. O. 1990. Factors controlling sediment community respiration in woodland stream ecosystems. Oikos **57**:94-105.

Holmes, R. M., S. G. Fisher and N. B. Grimm. 1994. Parafluvial nitrogen dynamics in a desert stream ecosystem. Journal of the North American Benthological Society **13**:468-478.

Holmes, R. M., S. G. Fisher, N. B. Grimm and B. J. Harper. 1998. The impact of flash floods on microbial distribution and biogeochemistry in the parafluvial zone of a desert stream. Freshwater Biology **40**:641-654.

Howard, R. J and J. S. Larson. 1985. A stream habitat classification system for beaver. Journal of Wildlife Management **49**:19-25.

Jacobs, J. 1974. Quantitative measurement of food selection: a modification of forage ratio and Ivlev's electivity index. Oecologia **14**:413-417.

Johnston, C. A., G. Pinay, C. Arens and R. J. Naiman. Influence of soil properties on the biogeochemistry of a beaver meadow hydrosequence. Soil Society of America Journal **59**:1789-1799.

Johnston, C. A. and R. J. Naiman. 1987. Boundary dynamics at the terrestrial aquatic interface: The influence of beaver and geomorphology. Landscape Ecology **1**:47-57.

Johnston, C. A. and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. Ecology **71**:1617-1621.

Jones, C. G., J. H. Lawton and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.

Jones, J. B., S. G. Fisher and N. B. Grimm. 1995. Vertical hydraulic exchange and ecosystem metabolism in a Sonoran Desert stream. Ecology **76**:942-952.

Kent, M and P. Coker. 1992. The description of vegetation in the field. Pages 28-76 *in* Vegetation Description and Analysis: A Practical Aproach. Belhaven Press, London, UK.

Kindschy, R. R. 1985. Response of Red willow to beaver use in southeastern Oregon. Journal of Wildlife Management **49**:26-28.

King, S. L., B. D. Keeland and J. L. Moore. 1998. Beaver lodge distributions and damage assessments in a forested wetland ecosystem in the southern United States. Forest Ecology and Management **108**:1-7.

Klotz, R. L. 1998. Influence of beaver ponds on the phosphorus concentration of stream water. Canadian Journal of Fisheries and Aquatic Sciences **55**:1228-1235.

Leidholt-Bruner, K., D. E. Hibbs, and W. C. McComb. 1992. Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two coastal Oregon streams. Northwest Science **66**:218-223.

Marti, E. and F. Sabater. 1996. High variability in temporal and spatial nutrient retention in Mediterranean streams. Ecology **77**:854-869.

McComb, W. C., J. R. Sedell, and T. D. Buchholz. 1990. Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist **50**:273-281.

McDowell, D. M. and R. J. Naiman. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). Oecologia **68**:481-489.

McGinley, M. A. and T. G. Whitham. 1985. Central place foraging by beavers (*Castor candensis*): test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia 66:558-562.

Mulholland, P. J., A. D. Steinman and J. W. Elwood. 1990. Measurement of phosphorus uptake length in streams: comparison of radiotracer and stable PO_4 releases. Canadian Journal of Fisheries and Aquatic Sciences **47**:2351-2357.

Nadelhoffer, K. J. 1990. Microlysimeter for measuring nitrogen mineralization and microbial respiration in aerobic soil incubations. Soil Science Society of America Journal **54**:411-415.

Naiman, R. J., C. A. Johnston, and J. C. Kelly. 1988. Alteration of North American streams by beaver. Bioscience **38**:753-762.

Naiman, R. J. and J. M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia **62**:150-155.

Naiman, R. J., J. M. Melillo and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology **67**:1254-1269.

Naiman, R. J., G. Pinay, C. A. Johnston and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology **75**:905-921.

Naiman, R. J., T. Manning, and C. A. Johnston. 1991. Beaver pond fluctuations and tropospheric methane emissions in boreal wetlands. Biogeochemistry **12**:1-15.

Nolet, B. A. and F. Rosell. 1998. Comeback of the beaver *Castor fiber*: An overview of old and new conservation problems. Biological Conservation **83**:165-173.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist **103**:91-93.

Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston,. J. Pastor and G. Pinay. 1995. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pages 117-126 *in* C. G. Jones and J. H. Lawton (eds.) Linking Species and Ecosystems. Chapman and Hall, New York, NY, USA.

Rosenfeld, J. S. and J. J. Hudson. 1997. Primary production, bacterial production, and invertebrate biomass in pools and riffles in southern Ontario streams. Archive für Hydrobiologia **139**:301-316.

Smith, M. E., C. T. Driscoll, B. J. Wyskowski, C. M. Brooks and C. C. Cosentini. 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. Canadian Journal of Zoology **69**:55-61.

Smith, S. D., D. A. Devitt, A. Sala, J. R. Cleverly, and D. E. Busch. 1998. Water relations of riparian plants from warm desert regions. Wetlands **18**:687-696.

Snodgrass, J. W. 1997. Temporal and spatial dynamics of beaver created patches as influenced by management practices in a south-eastern North American landscape. Journal of Applied Ecology **34**:1043-1056.

Snodgrass, J. W. and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology **79**:928-942.

Songster-Alpin, M. S. and R. L. Klotz. 1995. A comparison of electron transport system activity in stream and beaver pond sediments. Canadian Journal of Fisheries and Aquatic Sciences **52**:1318-1326.

Stream Solute Workshop. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. Journal of the North American Benthological Society **9**:95-119.

Suzuki, N. and W. C. McComb. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon coast range. Northwest Science **72**:102-110.

Swenson, J. E., S. J. Knapp, P. R. Martin and T. C. Hinz. 1983. Reliability of aerial cache surveys to monitor beaver population trends on prairie rivers in Montana. Journal of Wildlife Management **47**:697-703.

Tiedje, J. M., S. Simkins, and P. M. Groffman. 1989. Perspectives on measurement of denitrification in the field including recommended protocols for acetylene based methods. Pages 217-240 *in* M. Clarholm and L. Bergstrom (eds.) Ecology of arable land perspectives and challanges. Kluwer Academic Publishers, Dordrecht.

Updegraff, K., J. Pastor, S. D. Bridgham and C. A. Johnston. 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecological Applications **5**:151-163.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Ward, J. V. and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29-42 *in* T. D. Fontaine and S. M. Bartell (ed.), Dynamics of lotic ecosystems. Ann Arbor Science Publishers Inc., Ann Arbor, MI, USA.

APPENDIX

Raw data for individual plots used to calculate the percent cover and proportion of individual species foraged upon by beaver. Cover and forage scores are Braun-Blanquet scores as described in Table 1 and Kent and Coker (1992).

Pond	Plot	Genus	Cover Score	Foraged Score
Cliff Pond	1	*Artemisia*	1	+
		Baccharis	2	3
		Chilopsis		
		Chrysothamnus	1	+
		Fraxinus	2	5
		Gutierrezia		
		Populus		
		Salix		
		Tamarix	2	3
	2	*Artemisia*	1	+
		Baccharis		
		Chilopsis		
		Chrysothamnus	2	1
		Fraxinus		
		Gutierrezia		
		Populus		
		Salix		
		Tamarix	3	4
	3	*Artemisia*		
		Baccharis	1	3
		Chilopsis		
		Chrysothamnus		
		Fraxinus	2	+
		Gutierrezia		
		Populus		
		Salix	2	5
		Tamarix	3	5
	4	*Artemisia*		
		Baccharis	3	3
		Chilopsis		
		Chrysothamnus	1	
		Fraxinus		
		Gutierrezia		
		Populus		
		Salix	1	+
		Tamarix	2	2

Pond	Plot	Genus	Cover Score	Foraged Score
Cliff Pond	5	*Artemisia*		
		Baccharis	3	3
		Chilopsis		
		Chrysothamnus	1	2
		Fraxinus	1	5
		Gutierrezia		
		Populus	1	5
		Salix		
		Tamarix	2	2
	6	*Artemisia*		
		Baccharis	1	3
		Chilopsis		
		Chrysothamnus		
		Fraxinus		
		Gutierrezia		
		Populus	1	5
		Salix	3	5
		Tamarix	1	1
Last Pond	1	*Artemisia*		
		Baccharis	2	2
		Chilopsis		
		Chrysothamnus	1	+
		Fraxinus		
		Gutierrezia		
		Populus	2	N/A
		Salix		
		Tamarix		
	2	*Artemisia*		
		Baccharis		
		Chilopsis		
		Chrysothamnus	1	+
		Fraxinus		
		Gutierrezia	1	+
		Populus	3	5
		Salix		
		Tamarix		
	3	*Artemisia*		
		Baccharis	2	1
		Chilopsis		
		Chrysothamnus	1	+
		Fraxinus		
		Gutierrezia	1	+
		Populus	2	5
		Salix		
		Tamarix		

Pond	Plot	Genus	Cover Score	Foraged Score
Last Pond	4	*Artemisia*		
		Baccharis	3	1
		Chilopsis	1	+
		Chrysothamnus		
		Fraxinus		
		Gutierrezia		
		Populus	1	N/A
		Salix		
		Tamarix		
	5	*Artemisia*		
		Baccharis	2	+
		Chilopsis		
		Chrysothamnus	1	3
		Fraxinus		
		Gutierrezia		
		Populus	+	5
		Salix		
		Tamarix		
	6	*Artemisia*	1	+
		Baccharis	2	+
		Chilopsis		
		Chrysothamnus	1	1
		Fraxinus	1	3
		Gutierrezia		
		Populus	2	N/A
		Salix		
		Tamarix		
PC Pond	1	*Artemisia*	2	3
		Baccharis		
		Chilopsis		
		Chrysothamnus		
		Fraxinus	3	1
		Gutierrezia		
		Populus	2	+
		Salix		
		Tamarix	1	+
PC Pond	2	*Artemisia*		
		Baccharis	1	+
		Chilopsis		
		Chrysothamnus		
		Fraxinus	5	1
		Gutierrezia		
		Populus		
		Salix		

Pond	Plot	Genus	Cover Score	Foraged Score
PC Pond	2 (Cont.)	*Tamarix*	1	+
	3	*Artemisia*		
		Baccharis	2	+
		Chilopsis		
		Chrysothamnus		
		Fraxinus		
		Gutierrezia		
		Populus	3	3
		Salix		
		Tamarix	1	+
	4	*Artemisia*	1	+
		Baccharis	1	+
		Chilopsis		
		Chrysothamnus		
		Fraxinus		
		Gutierrezia	1	+
		Populus	4	5
		Salix		
		Tamarix	2	3
	5	*Artemisia*	2	+
		Baccharis		
		Chilopsis		
		Chrysothamnus	2	+
		Fraxinus		
		Gutierrezia		
		Populus		
		Salix		
		Tamarix	1	2
Rainbow Pond	1	*Artemisia*	1	+
		Baccharis	2	5
		Chilopsis	1	+
		Chrysothamnus		
		Fraxinus	5	2
		Gutierrezia		
		Populus	1	5
		Salix		
		Tamarix		
	2	*Artemisia*		
		Baccharis		
		Chilopsis	2	+
		Chrysothamnus	2	+
		Fraxinus		
		Gutierrezia	1	+
		Populus	1	5

Pond	Plot	Genus	Cover Score	Foraged Score
Rainbow Pond	2 (Cont.)	*Salix*		
		Tamarix		
	3	*Artemisia*	2	+
		Baccharis	1	+
		Chilopsis		
		Chrysothamnus	2	+
		Fraxinus		
		Gutierrezia		
		Populus		
		Salix		
		Tamarix	2	1
	4	*Artemisia*		
		Baccharis	2	1
		Chilopsis		
		Chrysothamnus		
		Fraxinus		
		Gutierrezia		
		Populus	2	4
		Salix		
		Tamarix	2	+
Rainbow Pond	5	*Artemisia*		
		Baccharis	2	1
		Chilopsis	1	+
		Chrysothamnus		
		Fraxinus		
		Gutierrezia		
		Populus	3	5
		Salix	2	4
		Tamarix	1	2
	6	*Artemisia*	1	+
		Baccharis	1	+
		Chilopsis	1	+
		Chrysothamnus		
		Fraxinus		
		Gutierrezia		
		Populus	2	5
		Salix		
		Tamarix		

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