AN ABSTRACT OF THE THESIS OF

Julie L. Maenhout for the degree of Master of Science in Forest Science presented on September 23, 2013.
Title: Beaver Ecology in Bridge Creek, a Tributary to the John Day River.

Abstract approved:

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Jimmy D. Taylor

The American beaver (*Castor canadensis*) was nearly extirpated by the late 1800's due to the fur trade. Due to reintroduction efforts, it now occupies much of its former range. Beavers are a keystone species and ecosystem engineers, greatly influencing riparian and instream habitats through selective harvesting of plant materials and dam building. Beaver dams can accelerate the recovery of stream and riparian habitats. These habitats are beneficial to a variety of wildlife, including some fish species. Relocating nuisance beavers to areas where their damming activity will benefit fish habitat by helping restore degraded streams is gaining interest as a restoration and management tool in Oregon. However, little is known about the extant beaver populations in Oregon, including in the areas of restoration interest.

We used genetic and radio telemetry approaches together to investigate the ecology of beavers in Bridge Creek; the site of a project partnering with beaver to aid in restoration efforts. Radio telemetry was used to estimate the home range size, habitat use, and survival rates for beavers in Bridge Creek and mitochondrial DNA

was used to investigate the genetic diversity of beavers in Bridge Creek. In order to put the genetic diversity of this watershed in the historical context of beaver management in Oregon, we used samples from the John Day River upstream of the Bridge Creek confluence and samples from another study being conducted in western Oregon. These samples together would represent a broader context of the western and eastern parts of Oregon, on both sides of the Cascade Range.

We tracked 24 radio tagged beavers in the summer of 2011 and 22 beavers in the spring of 2012 to estimate home ranges. The mean linear home range length was 1.56 ± 0.71 km. Home ranges did not differ by sex or age except for spring 2012; female home ranges were longer than males. Home ranges encompassed nearly the entire study area of Bridge Creek and in some cases overlapped. Habitat use showed that beavers used areas of grasses and herbaceous vegetation in greater proportion to its availability for spring 2012 but did not deviate from random in summer 2011. The survival rate was estimated to be 0.92 ± 0.05 for the entire 18 month study period.

While radio tagging captured beavers, a tissue sample was taken for mitochondrial DNA genetic analysis. Genetic diversity was very low for the samples from Bridge Creek beavers, and therefore we were unable to discern any genetic structuring. Eastern Oregon samples overall (Bridge Creek and John Day samples) had a low nucleotide and haplotype diversity (0.001 ± 0.001, 0.441 ± 0.056 respectively) while western Oregon samples had a higher nucleotide and haplotype diversity (0.003 ± 0.002, 0.546 ± 0.098 respectively). The two subpopulations were significantly differentiated from each other ($P < 0.001$, pairwise $F_{ST} = 0.499$).

The information gained on the survival, home range, habitat use, and genetic diversity of beavers in Bridge Creek is important in assisting managers; partnering with beaver to meet their stream restoration goals. Although beaver relocation is an attractive tool for alleviating nuisance beaver issues while potentially restoring fish habitat, our results indicate that Bridge Creek may not be able to support more beavers in its current condition. Additional research on the social structure, through the use of microsatellites, and continued year-round monitoring of beavers within Bridge Creek and the greater John Day basin will further inform managers on the feasibility of the use of beavers as a stream restoration tool.

Beaver Ecology in Bridge Creek, a Tributary to the John Day River

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Julie L. Maenhout, Author

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## CONTRIBUTING AUTHORS

Dr. Jimmy Taylor was involved in the overall conceptual design of this research and assisted with detailed editing of chapters one, two, three, and four. Dr. Antoinette Piaggio was involved in the conceptual design, statistical analysis, and detailed editing of chapter three.

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CHAPTER 1: INTRODUCTION

The American beaver (*Castor Canadensis*, hereafter beaver) is a large semi-aquatic rodent found in lakes and streams throughout much of North America. Beavers are a keystone species and ecosystem engineers, greatly influencing riparian and instream habitats through selective harvesting of plant materials and dam building (Wright et al. 2002, Baker and Hill 2003). Beavers create ponds on stream systems through dam building to suit their habitat needs. This created environment is beneficial to a variety of wildlife, including some fish species (Collen and Gibson 2001). Beaver dams also accelerate the recovery of stream and riparian habitats (Lautz et al. 2006, Pollock et al. 2007). The dams impound water, raise the water table, trap sediment, reduce channel erosion, and promote riparian vegetation establishment and production (Naiman et al. 1988, Collen and Gibson 2001, Pollock et al. 2007).

Beavers were nearly extirpated throughout the United States by the late 1800's due to the fur trade which moved west across the country (Baker and Hill 2003). The pre-European settlement beaver population of North America was estimated to be 60-400 million individuals (Seton 1929). By the 1900's, after over 200 years of intensive trapping, remnant populations remained (Baker and Hill 2003). Ranchers also moved west, allowing livestock to graze in newly beaver-free riparian areas. Although riparian areas may only represent 1% of the total land surface in dry regions, they provide wildlife and livestock with invaluable forage, cover, and a consistent water supply (Apple 1985). The removal of soil-binding vegetation from overgrazing, along with the dry climate, resulted in accelerated erosion (Munther 1981, Parker et al. 1985). The lack of beavers and overgrazing by cattle greatly contributed to channel incision and little to no riparian area, as seen on many western semi-arid area streams (Parker et al. 1985, Baker and Hill 2003). Through reintroduction efforts and trapping restrictions in the 1930's through the 1950's, beaver populations began to rebound and now occupy much of their former range. The current beaver population is estimated to be a fraction of pre-European settlement (Naiman et al. 1986) and the effects of their absence are still visible on many degraded western stream systems.

Millions of dollars are spent each year on efforts to restore degraded instream and riparian habitat in the western United States (Bernhardt et al. 2005, DeVries et al. 2012). The expense of these efforts, increased restrictions on lethal trapping methods in states such as Washington (West's RCWA 77.15.190 – 194), and the assumption that relocated nuisance beavers will build dams make nuisance beaver relocation an attractive option for stream restoration while reducing human-beaver conflict. However, little ecological research has been conducted on existing beaver populations in the western United States beyond damming activity (McComb et al. 1990, Leidholt-Bruner et al. 1992, Pollock et al. 2004, Demmer and Beschta 2008).

The Bridge Creek watershed is an eastern Oregon watershed that has experienced a history of beaver trapping and cattle grazing, common to western streams. The historic land use of the area, along with the semi-arid climate, has resulted in Bridge Creek's banks being steep and severely eroded with a limited riparian area and floodplain (Demmer and Beschta 2008, Pollock et al. 2007). Bridge Creek provides rearing and spawning habitat for an anadromous run of Middle Columbia River steelhead (*Oncorhynchus mykiss*) that is listed as threatened under the Endangered Species Act (ESA 71 FR 834). Due to Bridge Creek's current degraded status, its high potential for improving threatened steelhead populations, and its potential to support additional salmonid species; it has been identified as a restoration priority (CBMRC 2005). The Bridge Creek Intensively Monitored Watershed (IMW) project is a long-term study to restore stream and riparian habitat along the incised and degraded lower 32 km. One of the objectives of the IMW project was to partner with beaver to aid in stream restoration. This included anthropogenic activities to entice beaver occupancy and possible beaver relocation into the project area. However, there was no information on the existing beaver population beyond yearly dam numbers (Demmer and Beschta 2008; M. Pollock, NOAA Northwest Fisheries Science Center, unpublished data).

Research Objectives: My objectives were designed to investigate the ecology of the extant beaver population in Bridge Creek through radio telemetry and genetic approaches. The specific objectives were to:

1. quantify beaver home ranges within the Bridge Creek watershed
2. determine the relationship between beaver home ranges and restoration structures

3. determine vegetative habitat use of beavers in relation to season and water level
4. estimate survival rates and cause-specific mortality
5. investigate the genetic structuring of beavers in Bridge Creek
6. in order to put the genetic diversity of this Bridge Creek in the historical context of beaver management in Oregon, compare the genetic diversity of beavers observed in the eastern Oregon to beavers in western Oregon

The investigations from these set of objectives combined will help managers understand the ecology of stream dwelling beavers in the semi-arid west and the effects of past management activities. This information should be taken into account when further management actions are being considered, such as relocation.

# CHAPTER 2: SURVIVAL, HOME RANGE, AND HABITAT USE OF BEAVERS IN BRIDGE CREEK, A TRIBUTARY TO THE JOHN DAY RIVER

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# INTRODUCTION

Beavers are a keystone species and ecosystem engineers, greatly influencing riparian and instream habitats through selective harvesting of plant materials and dam building (Naiman et al. 1986, Wright et al. 2002, Baker and Hill 2003). Beavers create ponds on stream systems through dam building to provide security from predators, which in turn stimulates growth of woody and herbaceous food items utilized by beavers (Baker and Hill 2003). This created environment is beneficial to a variety of wildlife, including some fish species (Collen and Gibson 2001). Beaver dams also accelerate the recovery of stream and riparian habitats (Lautz et al. 2006, Pollock et al. 2007). The dams impound water, raise the water table, trap sediment, reduce channel erosion, and promote riparian vegetation establishment and production (Naiman et al. 1988, Collen and Gibson 2001, Pollock et al. 2003). Although still considered a nuisance species in many areas due to their ability to flood agricultural fields and roads, and depredate crops, beavers are gaining popularity in some western states (e.g. Wyoming, Washington, Oregon, Montana) as a possible inexpensive tool for riparian and fish habitat restoration (McKinstry and Anderson 1997, Bondi 2009, McColley et al. 2012, Baldwin 2013).

Beaver populations were decimated by fur trappers as settlers moved west across North America, and were largely extirpated by 1900 (Baker and Hill 2003). Ranchers also moved west, allowing livestock to graze in newly beaver-free riparian areas. Although riparian areas may only represent 1% of the total land surface in dry regions, they provide wildlife and livestock with invaluable forage, cover, and a consistent water supply (Apple 1985). The removal of soil-binding vegetation from overgrazing, along with the dry climate, resulted in accelerated erosion (Munther 1981, Parker et al. 1985). The lack of beavers and overgrazing by cattle greatly contributed to channel incision and little to no riparian area, as seen on many western semi-arid area streams (Parker et al. 1985, Baker and Hill 2003).

Millions of dollars are spent each year on efforts to restore degraded instream and riparian habitat in the western United States (Bernhardt et al. 2005, DeVries et al. 2012). The expense of these efforts along with increased restrictions on lethal trapping methods in states such as Washington (West's RCWA 77.15.190 – 194) make beaver relocation as a restoration tool an attractive option for stream restoration and alleviating nuisance beaver issues. However, little ecological research has been conducted on existing beaver populations in the western United States beyond damming activity (McComb et al. 1990, Leidholt-Bruner et al. 1992, Pollock et al. 2004, Demmer and Beschta 2008).

We investigated beaver habitat use on an incised stream that is the site of a restoration and monitoring project in eastern Oregon. Restoration structures were placed in the stream to aggrade sediment and encourage beaver damming. One of the objectives of the project was to partner with beaver to aid in the restoration efforts, but there is no information on the existing beaver population beyond yearly dam numbers. The objectives of this research were to 1) estimate home range size of the existing beavers 2) investigate habitat use and restoration structure associations and 3) estimate survival and cause-specific mortality.

## STUDY AREA

Bridge Creek drains a 710 km2 basin directly into the lower John Day River in the middle Columbia basin of Oregon (Figure 2.1). At higher elevations, near the headwaters, vegetation is mixed conifer forest; transitioning to a shrub-steppe environment with sagebrush (*Artemisia tridentate*) and juniper (*Juniperus occidentalis*) as the primary vegetation. The riparian vegetation is dominated by willow (*Salix* spp.), with infrequent black cottonwood (*Populus balsamifera*), thinleaf alder (*Alnus incana*), and a variety of shrubs. The stream elevation ranges from 499 to 2078 m.

The study was restricted to the 32 km stretch of stream just downstream from the town of Mitchell to just upstream of the confluence with the John Day River. The land is mostly managed by the Bureau of Land Management (BLM) with three segments of private ownership and one segment of National Park Service (NPS) land where Bridge Creek flows past the Painted Hills Unit of the John Day Fossil Beds National Monument. One of the private segments (approximately 5 km) was excluded due to lack of access permission. The stream gradient is between 0.5 and 3 percent within the study area.

BLM acquired much of the land surrounding the lower portion of Bridge Creek between 1988 and 1992. Previous to this acquisition, the land was heavily grazed by domestic cattle and sheep for over 100 years and beaver were extensively trapped throughout the basin. The land is now used for limited grazing and recreation, mostly hunting and camping, and beaver trapping is prohibited on public land. The historic land use of the area has resulted in Bridge Creek's banks being steep and severely eroded with a limited riparian area and floodplain.

Bridge Creek provides rearing and spawning habitat for an anadromous run of Middle Columbia River steelhead (*Oncorhynchus mykiss*) that is listed as threatened under the Endangered Species Act (ESA 71 FR 834). Due its current degraded status, high potential for improving threatened steelhead populations, and potential to support additional salmonid species; Bridge Creek has been identified as a restoration priority (CBMRC 2005). The Bridge Creek Intensively Monitored Watershed (IMW) project is a long-term study to restore stream and riparian habitat along the incised and degraded lower 32 km. The study is being conducted under the National Oceanic and Atmospheric Administration's (NOAA) Integrated Status and Effectiveness Monitoring Program (ISEMP), assessing change in salmonid habitat and populations.

Current and past research on Bridge Creek has focused on beavers and their restoration potential. Demmer and Beschta (2008) surveyed beaver dams on Bridge Creek from 1988 to 2004 and found the dams improved riparian and instream conditions. They also found a significant inverse relationship between annual peak flow of the John Day River and number of beaver dams (range 9-103), resulting in few dams (< 25%) lasting ≤ 2 years (Demmer and Beschta 2008). Beaver dam surveys continue to be conducted yearly on Bridge Creek (M. Pollock, NOAA Northwest Fisheries Science Center, unpublished data). In an attempt to increase the longevity and number of beaver dams on Bridge Creek, Pollock et al. (2012) placed Beaver Dam Support Structures (BDSS) in 4 restoration units of Bridge Creek. A total of 89 vertical wooden posts, in terraced rows perpendicular to stream flow, were driven into the stream bed (Pollock et al. 2012). The BDSS continue to be monitored for beaver activity (M. Pollock, NOAA Northwest Fisheries Science Center, unpublished data).

## METHODS

### Capture and Radiotelemetry

Beavers were captured using Hancock live traps (Hancock Trap Co., Custer, SD) from April to June, 2011 and in April 2012. Traps were baited with castor or food based lure and checked within an hour of sunrise to minimize the exposure time of a captured beaver. In 2011 traps were set along the entire study stretch of Bridge Creek, excluding the one restricted private segment. The second trapping event in April 2012 was conducted to increase low active radio tag numbers due to failed and dropped tags. Traps were only set in areas with fresh signs of beaver activity. Capture and handling procedures were approved by the National Wildlife Research

Center's Institutional Animal Care and Use Committee (QA 1719) and ODFW scientific taking permit (082-11).

We weighed captured beavers by hanging the beaver in the trap on a spring scale and subtracting the weight of the trap (12.7 kg). We then classified each individual into 1 of 4 age-classes based on their weight (Patric and Webb 1960, McNew and Wolf 2005): 0-12 month old kits (< 6.8 kg), 13-24 month old yearlings (6.8-10.8 kg), 25-36 month old subadults (10.9-16.0 kg), and > 36 month old adults (> 16kg). Beavers > 6.8 kg were immobilized with an intramuscular injection of ketamine (5mg/kg) and xylazine (0.1mg/kg). Sex was determined by external palpation for a baculum and signs of lactation (Osborn 1955), and later confirmed with molecular techniques (modified methods from Crawford et al. 2009).

Each immobilized beaver received 2 forms of identification. First, beavers were fitted with a modified cattle ear-tag, tail-mounted radio transmitter (Sirtrack Wildlife Solutions, Hawkes Bay, New Zealand), following the protocol in Arjo et al. (2008) (modified from Rothmeyer et al. 2002). A 5 mm hole was drilled through the tail no more than halfway down the tail and as close to the midline as possible, while avoiding the tail bones and major blood vessels. The transmitter was attached with a bolt, surrounded by a plastic sleeve, through the tail hole and a neoprene washer between the tail and transmitter to increase retention time (Arjo et al. 2008). Each 45 g transmitter was reported to have a 650 day battery life and a mortality sensor that was activated after 12 hours of inactivity. Before attaching the radio transmitter a small piece of tail tissue and hair was taken for later genetic analysis.

The second form of identification was a Passive Integrated Transponder (PIT) tag (Biomark, Boise, Idaho, USA) placed subcutaneously in the scruff between the shoulder blades. The PIT tag served as an identifier for any recaptured animals that may have dropped their radio transmitters. There were also 4 passive instream antennas placed along the study stretch of Bridge Creek for the purpose of tracking fish movement. This allowed us to track large movements and survival for animals with failed or dropped radio transmitters. After receiving both forms of identification, beavers were placed back into the trap or a plastic crate until fully recovered. Once recovered, they were released near the trap site.

During July through September 2011 and April through July 2012 radio tagged beavers were located ≥ 2 times/week using the triangulation method (White and Garrott 1990): these time periods represent the lowest and highest water discharge on Bridge Creek respectively. We attempted to relocate each radio tagged beaver once per sampling attempt. The order in which animals were located was randomly chosen for each sampling attempt to avoid animals being located at the same time of day for each attempt. Bearings were taken from at least 2 known locations using a receiver, hand held 4-element Yagi antenna, GPS unit (Garmin International Systems, Olathe, KS), and a compass. Usable bearings were restricted to ≥ 20 degrees apart and all bearings taken with 20 minutes of each other. Since beavers are primarily nocturnal, beavers were located within the period between sunset and sunrise. Radiotelemetry data were entered in the program Location of a Signal version 4.0.3.7 (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate beaver locations. Estimated locations were snapped to the closest location on a stream layer of Bridge Creek (derived from LiDAR data in 2005) in Geospatial Modeling Environment 0.7.1.0 software (Spatial Ecology LLC, http://www.spatialecology.com/gme) to better represent beaver locations within the severely restricted linear environment of Bridge Creek. These snapped points were then used for further analysis. Den locations were noted opportunistically during daylight hours during both field seasons using the homing method. Between field seasons, we attempted to locate all radio tagged beavers at least once a month for survival estimates and to document any large dispersal movements.

When a mortality signal was heard, we attempted to locate the transmitter as quickly as possible. If the transmitter was attached to a deceased animal, a field investigation was conducted to determine cause of death. Survival was estimated using the Known-fate model in program MARK (White and Burnham 1999). Animals with dropped or failed transmitters were right censored.

## Home Range Analysis

Beaver habitat was confined to the narrow band of riparian vegetation along the stream channel. This was due to deeply incised channels combined with undesirable sagebrush and juniper as the primary vegetation outside the riparian area. Commonly used home range estimators (e.g. minimum convex polygon and kernel density) were spatially inappropriate due to these ecological constraints. For example, they may inappropriately measure home range size by incorporating area unavailable or undesirable to the beaver or underestimate size by excluding sections of stream where there are large meanders between locations (Blundell et al. 2001, Knight et al. 2009). Measuring linear home ranges (LHR) and areas of ecologically relevant habitat within the LHR provided an accurate estimate of habitat used by beavers within this restricted environment (Blundell et al. 2001, Ahlers et al. 2010).

Core and home range areas were initially estimated using 50% and 95% density contours of the fixed kernel density estimator in Geospatial Modeling Environment 0.7.1.0 software (Spatial Ecology LLC, http://www.spatialecology.com/gme) to delineate the upstream and downstream boundaries of the linear core and home ranges. We selected the plug-in bandwidth, or smoothing parameter (Jones et al. 1996), due to its performance with triangulation-based telemetry data (Vokoun and Rabeni 2005, Gitzen et al. 2006). Home range areas were estimated for beavers with ≥ 20 fixes per field season. Although 20 is a relatively low number of fixes, the kernel method and bandwidth selected have been shown to have optimal performance under these conditions compared to other home range estimators (Blundell et al. 2001, Börger et al. 2006, Gitzen et al. 2006). The linear core (LC) and home range (LHR) lengths were estimated as the length of stream contained within the 50% and 95% density contours (Sauer et al. 1999, Havens et al. 2013). Beaver-built dams and Beaver Dam Support Structure (BDSS) associations were determined by overlaying existing dam and BDSS layers from the corresponding year's beaver dam survey (M. Pollock, NOAA Northwest Fisheries Science Center, unpublished data), and home range layers in ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA).

Non-parametric tests were used to test for core and home range length differences between age, sex, and season. A Kruskal-Wallis one-way analysis of variance (ANOVA) was used to test for differences between the three age classes. If significant differences were found, a Mann-Whitney U test was used for pairwise comparisons. A Mann-Whitney U test was also used to test for differences in home range size between sexes, and between seasons. Statistical analyses were performed using R version 2.15.1 (R Core Team, www.r-project.org, accessed 23 Aug 2012) at $\alpha = 0.05$.

Habitat Use Analysis

Study area length was restricted to the lower 30.5 km of Bridge Creek for habitat use analysis. The study area was delineated in ArcMap 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA) using orthorectified and georeferenced imagery from an unmanned aerial vehicle (UAV) drone flight conducted in October 2010, with a 0.1 meter pixel resolution (DeMeurichy et al. 2011, South Fork Research Inc., http://www.southforkresearch.org). The width of the study area was determined by digitizing a polygon over the 2010 imagery rastors in ArcMap to include the entire riparian area plus a small buffer (Josh Goldsmith, South Fork Research Inc., personal communication, April 30, 2013). The width of the polygon varied from approximately 12 m to 144 m due to the varying width of the riparian area. The study area was originally delineated to detect change in riparian vegetation from the installation of the BDSS but also encompassed the entire area available to beavers on the lower 30.5 km of Bridge Creek. An existing rastor layer, created by South Fork Research, Inc. using ERDAS IMAGINE (http://geospatial.intergraph.com) and ArcGIS (http://www.esri.com), classified the study area vegetation into 6 vegetation types: willow, sagebrush, grass/herbaceous, soil/grass, bare ground, and shadow. Willow corresponded to all woody species, grass/herbaceous corresponded to non-woody species, soil/grass was disturbed earth, gravel bars, and some bunch grasses, and bare ground corresponded to desert bare ground without sagebrush or grass. The shadow class was composed of pixels which could not be accurately categorized due to the angle of the sunlight, and generally were associated with an incised bank or mature woody vegetation. The shadow classification was eliminated from further analysis due to the inability to discern which vegetation type was present.

We analyzed habitat use at 2 spatial scales: the use of vegetation types within the home range compared to that available within the study area (second-order-selection, Johnson 1980) and the use of vegetation types within the core area compared to that available within the home range (third-order selection, Johnson 1980; Janke and Gates 2013). Beavers whose home ranges occupied the same stretch of stream were considered part of the same colony (Bradt 1938). A colony home range was used for habitat use analysis at the study area scale since their availability to resources at the home range level was statistically and biologically dependent on their other colony members (Alldredge and Ratti 1992, Millspaugh et al. 1998). All beavers were considered individually at the home range scale since colony members have been shown to act independently within a colony's home range and sometimes sleep in different dens (Bradt 1938, Busher and Jenkins 1985, Wheatley 1997, Baker and Hill 2003, Herr and Rosell 2004, personal observation). The home range and core areas were determined as the width of the study area (i.e., the area available to beavers) and the length of the linear home range or linear core as determined in the home range analysis. We analyzed beavers' vegetation type preference using log-ratio compositional analysis (Aebischer et al. 1993) with 2,000 permutations at an alpha level of 0.05 in R version 2.15.1, package adehabitat (Calenge 2006).

## RESULTS

During April-June 2011, we captured a total of 35 beavers (16 M, 18 F, 1 unknown) over 831 trap nights. Thirty-one beavers were captured in Bridge Creek while 3 were captured in smaller tributaries. The age distribution was 15 adults, 11 subadults, 8 yearlings, and 1 kit. Due to 3 capture related mortalities and 1 beaver being too young, 31 beavers were fitted with radio-tags. Five study animals were censored due to tag failure; they were confirmed to remain in the study area through PIT tag detections. We believe one animal dispersed upstream of the study area, its signal was lost shortly after being activated and was never detected passing over the downstream antennas. Two study animals were lost due to mortality 1 and 2 months after capture. During July-September, 1068 locations were collected for 25 animals. Of the 25 tracked animals, 24 had sufficient locations for home range analysis.

During April of the second year of the study, we captured an additional 14 beavers (10 M, 3 F, 1 unknown) over 153 trap nights. Eleven were captured in Bridge Creek and 3 were captured in smaller tributaries. The age distribution was 1 adult, 6 subadults, and 7 yearlings. Due to 1 capture related mortality and 1 yearling being too small, 12 beavers were fitted with radio-tags. Two of the beavers were recaptures from the previous year that had dropped their tags. Twelve tags were active from the previous year. During April-June, 876 locations were collected for 24 animals. Of the 24 tracked animals, 22 had sufficient locations for home range analysis.

Survival Analysis

The estimated survival rate for the 18 month study period of April 2011-September 2012 was $0.92 \pm 0.05$. There were only 2 documented non-capture related mortalities during the study period. The low number of mortality events did not allow us to investigate possible factors influencing survivorship. One adult male beaver died of unknown causes 1 month after being radio-tagged. He was found on the bank of Bridge Creek with no apparent injuries or signs of disease. Another adult male beaver's radio-tag signal was lost 2 months after capture but returned 3 weeks later. Upon homing in on the beaver's signal, it was apparent the animal had been trapped for its fur and the body was returned. Since the beaver was on public land, its death was considered poaching.

## Home Range Analysis

Linear home range and core lengths were estimated for 24 beavers in summer 2011 and 22 beavers in spring 2012. The distribution of beaver colonies on Bridge Creek and its tributaries is represented in Figure 2.2 for summer 2011 and Figure 2.3 for spring 2012. Mean lengths of core areas ($W = 343$, $P = 0.08$) did not differ seasonally nor did home ranges ($W = 334$, $P = 0.12$). The overall mean (SE) core and home range stream lengths were 0.72 (0.09) km and 1.56 (0.1) km respectively.

Home range and core lengths did not differ between sex ($W = 87$, $P = 0.39$; $W = 76$, $P = 0.82$; respectively) or age ($H_2 = 3.82$, $P = 0.15$; $H_2 = 5.27$, $P = 0.07$; respectively) for the summer of 2011. The mean number of active natural beaver dams within a home range was 4.8 (range 0-15) and 5 colonies were associated with BDSS (n=13 total beaver, tagged members of a colony grouped as 1 home range). The mean number of dens documented per individual beaver was 3.6 (range 1-6).

There was no difference in home range or core lengths between age for the spring of 2012 ($H_2$ = 0.96, P = 0.62; $H_2$ = 2.54, P = 0.28; respectively). However, home range and core lengths did differ by sex for the spring of 2012 (W = 98, P = 0.008; W = 89, P = 0.041; respectively). Female home range and core lengths were longer than male lengths (Table 2.1). The mean number of active natural beaver dams within a home range was 5.8 (range 0-20) and 5 colonies were associated with BDSS (n=15 total beaver, tagged members of a colony grouped as 1 home range). During the most recent beaver dam survey in winter of 2012, 32% of the BDSS had some amount of beaver added damming material. The mean number of dens documented per individual beaver was 3.1 (range 2-6).

Habitat Use Analysis

Habitat use was non-random at the study area scale (second-order selection) for the spring of 2012 ($\lambda$=0.182, P=0.005), with a ranking matrix (Table 2.2) ordering vegetation types as: grass/herbaceous > willow > bare ground > soil/grass > sagebrush. Grass/herbaceous vegetation type was used in the highest proportion relative to its availability over all other vegetation types for spring 2012 even though it was available in low abundance within the study area (11.1%). Willow was used in the second highest proportion relative to its availability and was the most abundant vegetation type within the study area (54.6%). For the summer of 2011, beavers did not use any vegetation type over another within the study area ($\lambda$=0.417, P=0.099).

Beavers did not use any vegetation type over another within their home ranges (third-order selection) for either year (2011 $\lambda$=0.655, P=0.176; 2012 $\lambda$=0.732, P=0.320).

## DISCUSSION

### Survivorship

Beaver survival on Bridge Creek was very high for the entire study period, much higher than the rate reported by the only other known study in the western United States involving resident beaver populations (67%) (Van Deelen and Pletscher 1996). The trapping restrictions on public lands may have contributed to the high survival rate because road access and narrow riparian buffers make it accessible to trapping, although there were no trapping related mortalities documented on private land where it was permissible. A study in an area with no harvesting reported high survival rates (76%) but they were still considerable lower than seen on Bridge Creek (Bloomquist and Nielsen 2010).

Predation by canids, felids, and bears are documented as an important source of mortalities in almost every study reporting cause-specific mortality (Van Deelen and Pletscher 1996, McKinstry and Anderson 2002, McNew and Woolf 2005, DeStefano et al. 2006, Bloomquist and Nielson 2010). We did not observe any incidences of predation during our study even though coyotes have been frequently seen and heard in the area and cougar prints have been seen along Bridge Creek. Beaver build dams and dig canals for protection from predators and to access forage

(Baker and Hill 2003). They become more selective of their forage in relation to increasing distance from the water's edge as a ways to maximize their energy gain while minimizing their predation risk (Basey and Jenkins 1995). Where beavers did not build dams and dig canals on Bridge Creek, the bank was steeply incised and the inset riparian area was narrow. This did not allow beavers to forage far from the water's edge. Although these conditions may not have been considered favorable, they may have contributed to the high survival rates.

## Home Range

The mean core length (0.72 km) and mean home range length (1.56 km) for beavers in the Bridge Creek watershed was considerably smaller than the other one other study reporting home range lengths in the western United States (Breck et al. 2001). Breck et al. (2001) reported mean home range lengths of 2.38 km and 2.19 km and core lengths of 1.01 km and 1.25 km on 2 northwestern Colorado rivers that were large enough that beavers could not build dams. Havens et al. (2013) found that in east-central Illinois home range and core lengths were longer in the main river than smaller streams. The core and home range lengths (0.7 km and 1.8 km respectively) of their study beaver in stream environments are much more comparable to what was documented in our study area than for their river dwelling beaver (1.2 km core and 3.6 km home range).

Several studies have found beaver home ranges smallest in the summer compared to other seasons (Bloomquist et al. 2012, Havens et al. 2013). We found a similar result, although the difference between spring and summer home range length was not significant. Havens et al. (2013) attributed the small summer home ranges partially to drought during the study period. Although no part of Bridge Creek became a dry streambed during our study period, the stream typically is no more than 0.1 m deep in places during the summer, due to the semiarid climate (DeMeurichy et al. 2011). The seasonal effect on home range may have been dampened by the unusually high water during summer 2011. The monthly mean flow rates for summer 2011 were consistently over twice that of the historical monthly means (2006-2012; http://waterdata.usgs.gov).

Most studies that compared home range sizes between sexes have found that females have a smaller home range compared to males during the summer (Boller 1991, Wheatley 1997, Herr and Rosell 2004, Havens et al. 2013). This is contributed to parturition in spring and subsequent rearing of kits during the summer by female beavers, keeping them closer to the den. Bloomquist et al. (2012) found no difference in home range size between sexes during the summer season. They credited a low breeding rate of females during their study, allowing the kitless female beaver to behave more like the males (Bloomquist and Nielsen 2010). We, unexpectedly, found the opposite result; female beaver core and home range lengths were longer than males in spring 2012. Pregnant adult females were documented in late April of 2011 and several lactating females were documented from late May through late June 2011, indicating our spring study season was the time of parturition and the beginning of kit rearing for females on Bridge Creek. Although we only trapped yearling and subadult females in our second trapping season in spring 2012, 4 adult females had working radio tags from the previous year which was 44% of our total female sample size for spring 2012. With almost half of the female samples being beavers of reproductive age, the larger female home ranges could indicate a low level of reproduction or kit survival in spring 2012.

Bloomquist et al. (2012) documented 1 to 2 active lodges in beaver core areas depending on season in a wetland environment in southern Illinois. We observed beavers using a mean of 3 dens for both seasons. Most dens were dug into an incised bank with or without sticks piled on top of the bank, and only approximately 8 standalone lodges for the entire study area. Beavers may have needed a higher number of dens due to the fluctuating water levels even within seasons. All stream segments containing BDSS were occupied by beavers, although not all had dams associated with BDSS. Unfortunately the structures were in place before our study began so we are unable to determine if beavers moved into those stretches of stream after the structures were put in or whether beavers already occupied the area.

## Habitat Use

Stream habitat is suitable for beavers if there is sufficient food, low gradient (i.e. < 15%) and adequate water (Williams 1965, Allen 1983). The lower 30 km of Bridge Creek has a gradient < 3%, flowing water year round, and a minimum of a narrow strip of willow along one bank. With the basic needs being met, beavers inhabited areas with greater proportions of grasses and herbaceous vegetation than the proportion present for the entire study area in the spring of 2012.

Jenkins (1981) found that beavers prefer herbaceous plants when available, which is typically during the spring season in semiarid regions. Beier and Barrett (1987), Hartman (1996), Suzuki and McComb (1998) and Cooke and Zack (2008) found herbaceous plants to have a strong association with beaver presence. Although Beier and Barrett (1987), Suzuki and McComb (1998), and Cook and Zack (2008) attributed the herbaceous plant abundance to beaver damming activity, Hartman (1996) found a similar result on an undammed river. Historic beaver damming and foraging, along with the installation of BDSS, has no doubt had an effect on the quantity and composition of riparian vegetation on Bridge Creek. There may be geomorphic attributes we did not investigate that initially attracted the beavers to those sections of stream beyond an adequately low gradient. For example, stream segments with less incision may have wider valley floors and active channel widths, which have been shown to be important to beavers in western Oregon (Suzuki and McComb 1998).

Using radio telemetry for beaver habitat use has its potential issues. Our study area scale analysis depended on our ability to capture and radio tag individuals and did not take into account untagged animals that may inhabit other sections of stream within the study area, as with studies that use signs of beaver activity as indicators of habitat use (John and Kostkan 2009). We believe we were able to capture at least one individual from each group of beavers within the study area. Young beavers that dispersed from their natal colonies during the study period were documented traveling throughout the study area and settling in previously unoccupied areas. Although running water is thought to be a cue for beavers to initiate building and maintaining dams (Baker and Hill 2003), we documented radio tagged beavers living in sections of stream without any evidence of damming activity. We were able to document the habitat use of non-damming and bank denning beavers which may be a section of the population that is overlooked in studies not using radio telemetry techniques. Radio telemetry does offer more detailed information on beaver space use and potential insights into beaver behavior that signs of beaver activity do not (John and Kostkan 2009).

Although my objectives did not include quantifying the biological carrying capacity of Bridge Creek, results suggest that the Bridge Creek beaver population may or may not be at biological carrying capacity. The discovery that beaver colony home ranges were in close proximity and sometimes overlapped within the study area, along with the high survival observed during the course of the study, indicated the beaver population may be at or nearing biological carrying capacity on Bridge Creek. The longer female home ranges for spring of 2012 also indicated reduced reproduction or kit survival for that year (Bloomquist and Nielsen 2010). This may have been a result of inter-colony aggression due to close proximity and overlapping of colony territories (Bloomquist et al. 2012).

Other results from our study suggested the population is not at carrying capacity. We estimated a density of approximately 0.44 colonies/km within the study area. This density is on the average to low end of the spectrum for studies on river or stream dwelling beavers, with a range from 0.2 to 1.14 colonies/km (Beier and Barrett 1989, Muller-Schwarze and Shulte 1999, Breck et al. 2001, Loates and Hvenegaard 2008). Bloomquist and Nielsen (2010) saw the highest ever reported the density for beaver at 3.27 colonies/km$^2$ in an area with trapping restrictions and high suitable habitat. Trapping has been restricted on Bridge Creek since 1991, so the result that beaver colonies inhabited areas with a greater proportion of grass and herbaceous vegetation than available in the study area may indicate those areas represent the highest suitable habitat within the study area.

Areas with high-density populations are expected to have a low number of short distance dispersing individuals and unsuccessful dispersal attempts (DeStefano et al. 2006). We documented the successful dispersal of 4 beavers and a relatively long mean dispersal distance of 16.17 ± 9.34 km. The 4 beavers that dispersed were even able to form 2 pairs and each pair settled in unoccupied habitat within the Bridge

Creek watershed. These successful dispersal attempts along with a relatively long mean dispersal distance may indicate a low population density. Future studies on the ecology of beavers in Bridge Creek should address whether or not the beaver population has reached biological carrying capacity. These studies also should quantify effective dispersal rates which would include measures of fitness.

## MANAGEMENT IMPLICATIONS

Few studies have described the ecology of a stream dwelling beavers in the semiarid west. The survival, home range, and habitat use information from our study can be useful for managers interested in partnering with an existing beaver population in efforts to restore a degraded stream. High survival rates and documented reproduction indicate that the relocation of additional beavers into Bridge Creek is not necessary to supplement the existing population. Home ranges were smaller than most other studies of beavers in linear habitats but colonies were close in proximity and with some instances of overlap. Beaver colonies in Bridge Creek inhabited areas with greater proportion of grasses and herbaceous vegetation than the proportion present for the entire study area during the spring which may represent areas of the highest suitable habitat. These findings indicate that restoration managers may need to continue to assist beavers in damming through the installation of additional Beaver Dam Support Structures (BDSS) to meet their restoration goals, because the current beaver population does not appear to be lacking and may not be a factor limiting damming activities. The installation of BDSS will also increase herbaceous vegetation growth through the diverting of water onto the inset floodplain and aggrading of sediment, increasing the habitat suitability for beavers in those areas.

Our study was limited to beavers in the Bridge Creek watershed, for only the spring and summer seasons. The information gained from this study could be expanded through further study of beavers in the greater John Day basin and beaver movements in Bridge Creek for all seasons. Investigating the geomorphic characteristics in beaver habitat use to accompany the vegetative results from this study will assist managers in further understanding how beavers use degraded stream systems. The investigation of beaver dam numbers, locations, and longevity, before and after the installation of the BDSS, may also give some insight into how the restoration structures may be affecting the beaver population in Bridge Creek.

Although beaver relocation is an attractive option to restore degrading streams while alleviating nuisance beaver issues, preliminary studies on the existing beaver population in an area of interest are necessary. Managers cannot assume the lack of damming activity is indicative of a lack of resident beavers. The seasonal use of herbaceous material may also need to be taken into consideration when investigating areas for possible beaver relocation.

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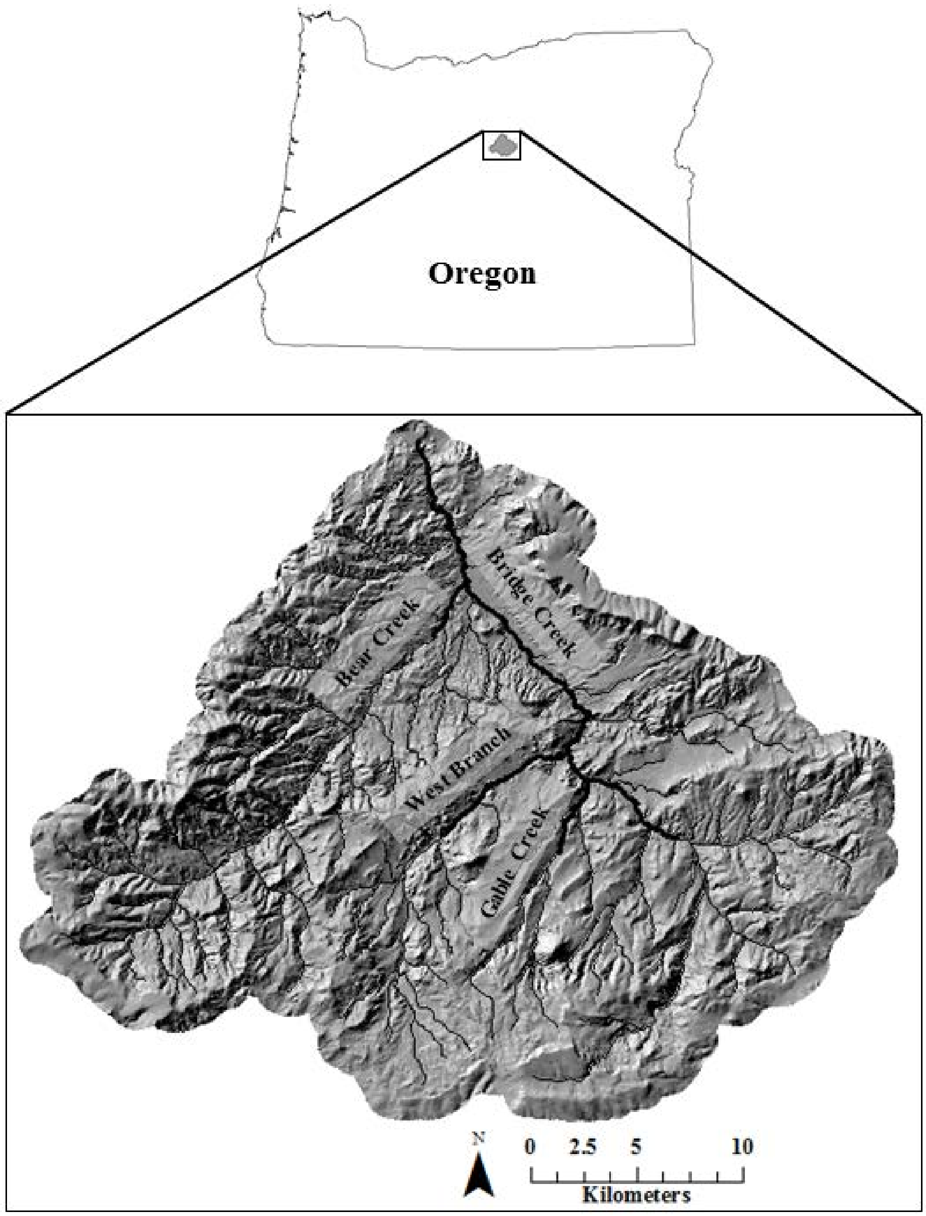


Figure 2.1. Bridge Creek drains a 710 km2 basin directly into the lower John Day River in the middle Columbia basin of Oregon. The incised and degraded lower 32 km is the site of an Intensively Monitored Watershed (IMW) project; a long-term study to restore stream and riparian habitat.

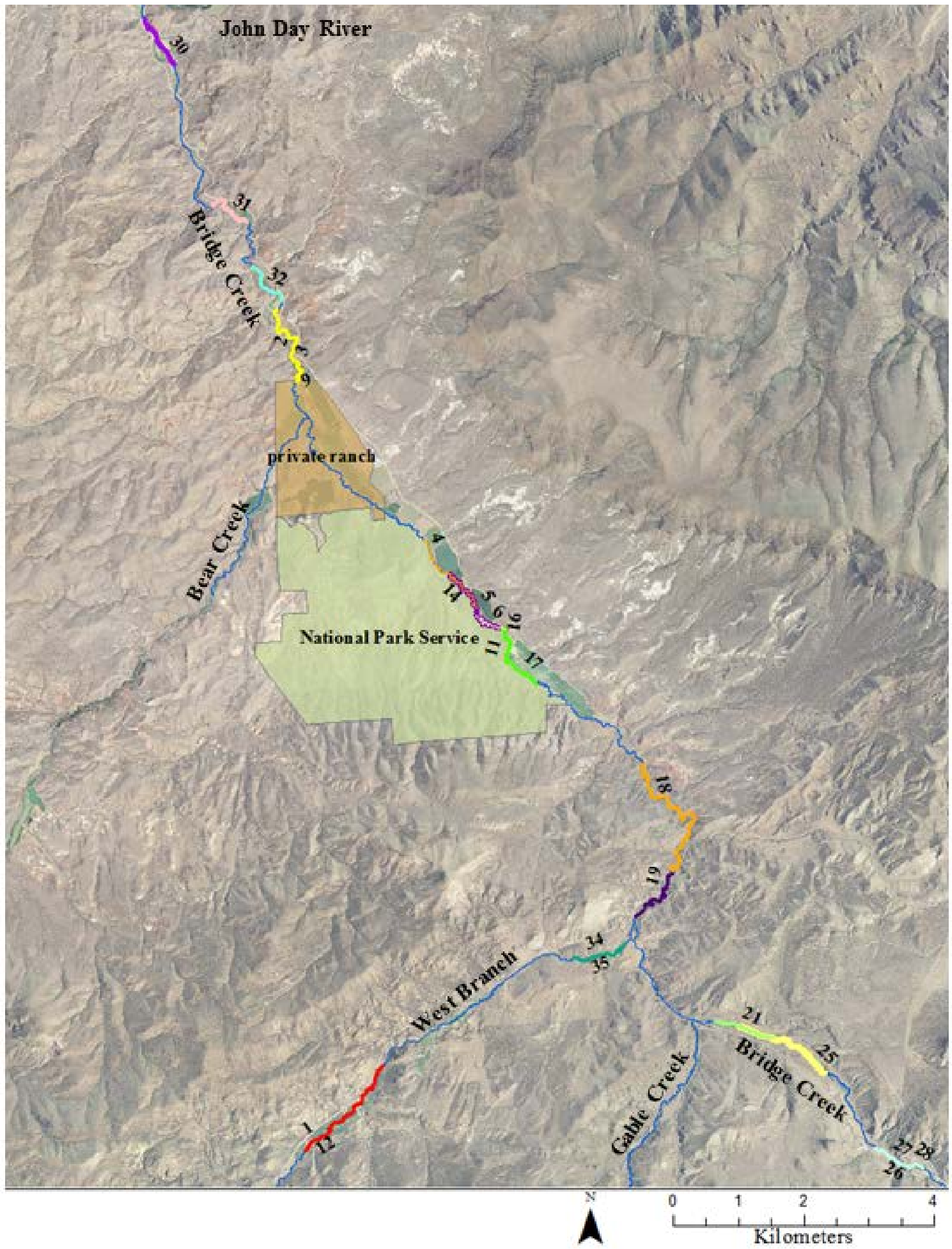


Figure 2.2. Distribution of beaver linear home ranges on Bridge Creek and its tributaries for summer 2011. Each color represents a colony home range and the numbers represent the beaver ID for each individual within a colony.

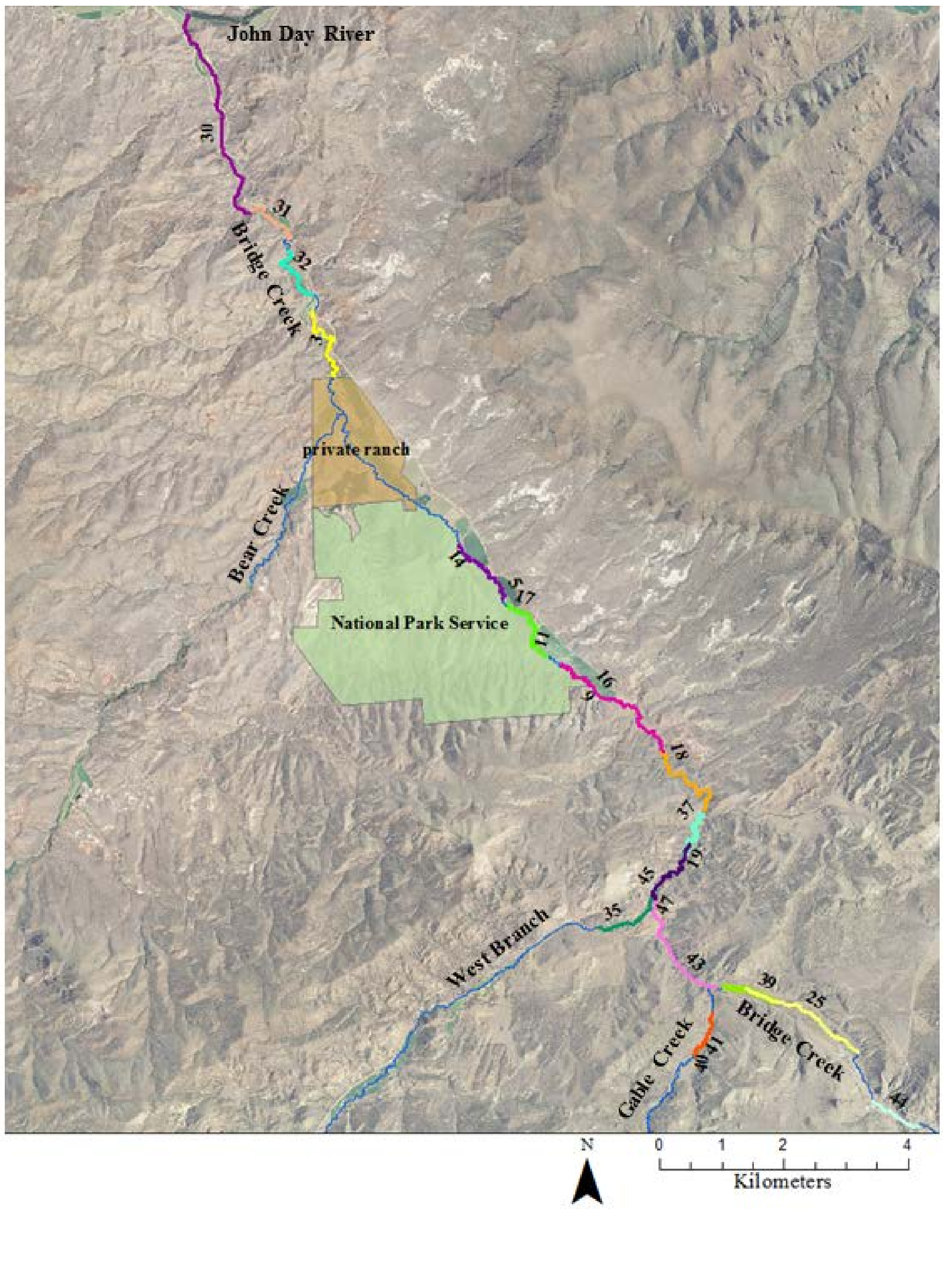


Figure 2.3. Distribution of beaver linear home ranges on Bridge Creek and its tributaries for spring 2012. Each color represents a colony home range and the numbers represent the beaver ID for each individual within a colony.

Table 2.1. Mean linear core (LC) and linear home range (LHR) lengths of beavers in the Bridge Creek watershed for summer: 8 July 2011-8 September 2011, and spring: 30 March 2012-10 July 2012.

| | | 50% LC (km) | | 95% LHR (km) | |
|---|---|---|---|---|---|
| Season and group | n | $\bar{x}$ | SE | $\bar{x}$ | SE |
| Summer | | | | | |
| Male | 12 | 0.58 | 0.12 | 1.29 | 0.15 |
| Female | 12 | 0.63 | 0.13 | 1.5 | 0.19 |
| Yearling | 6 | 0.92 | 0.23 | 1.66 | 0.14 |
| Subadult | 8 | 0.35 | 0.08 | 1.15 | 0.2 |
| Adult | 10 | 0.62 | 0.12 | 1.43 | 0.21 |
| Spring | | | | | |
| Male | 13 | 0.59 | 0.07 | 1.43 | 0.19 |
| Female | 9 | 1.21 | 0.35 | 2.18 | 0.26 |
| Yearling | 7 | 0.59 | 0.08 | 1.54 | 0.26 |
| Subadult | 7 | 1.04 | 0.46 | 1.91 | 0.44 |
| Adult | 8 | 0.89 | 0.17 | 1.76 | 0.17 |

Table 2.2. Ranking matrix based on comparing proportion of habitat used within home ranges to proportion of habitat available in the study area for beavers in Bridge Creek, Oregon for spring 2012 (GH-Grass/herbaceous, W-Willow, BG-Bare ground, SB-Sagebrush, SG-Soil/grass).

| | Vegetation type | | | | |
|---|---|---|---|---|---|
| Vegetation type[a] | GH | W | BG | SB | SG |
| Grass/herbaceous | 0 | + | + | + + + | + |
| Willow | - | 0 | + | + + + | + |
| Bare ground | - | - | 0 | + | + |
| Sagebrush | - - - | - - - | - | 0 | + |
| Soil/grass | - | - | - | - | 0 |

[a] (+) indicates the row vegetation type was used in greater proportion to its availability than the column vegetation type; (-) indicates the column vegetation type was used in greater proportion to its availability than the row vegetation type; sign is tripled (e.g., + + +) represents significant deviation from random use ($\alpha = 0.05$).

# CHAPTER 3: GENETIC DIVERSITY OF BEAVERS IN OREGON

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## INTRODUCTION

American beavers (*Castor canadensis*, hereafter beaver) were nearly extirpated throughout the United States by the late 1800's due to the fur trade which moved west across the country (Baker and Hill 2003). The pre-European settlement beaver population of North America was estimated to be 60-400 million individuals (Seton 1929). By the 1900's, after over 200 years of intensive trapping, remnant populations remained (Baker and Hill 2003). The Hudson's Bay Company, based out of England, wanted to make the Pacific Northwest a "fur desert" to dissuade American fur trappers and therefore American colonization of the region (Hammond 1993). Following incorporation into the United States and 40 years of shifting beaver management, in 1932, the state of Oregon recognized the beaver's near extermination and closed the entire state to trapping (Kebbe 1949). The Oregon State Game Commission then began live-trapping nuisance beavers from agricultural lands and reintroducing them into the then beaver-free mountain streams on National Forest lands; for the purpose of wildlife conservation and soil and water retention (Scheffer 1941, Meyers 1946, Kebbe 1949). Beaver populations quickly rebounded and the focus shifted from live-trapping to kill-trapping (Kebbe 1950). Today beavers in Oregon are managed as furbearers by the Oregon Department of Fish and Wildlife (ODFW) on public land (ODFW 2012b); however, beavers that cause damage on private lands are considered predators and can be taken lethally without reporting permits (Oregon Revised Statute 610.002).

More recently, beaver dams have been recognized for enhancing habitat for a variety of wildlife, especially threatened and endangered salmonid species (Collen and Gibson 2001). Dams impound water, raise the water table, trap sediment, reduce channel erosion, promote riparian vegetation establishment; helping to restore degraded streams (Naiman et al. 1988, Collen and Gibson 2001, Pollock et al. 2007). This has renewed interest in live-trapping nuisance beavers to relocate them to areas where their dams would be beneficial to other wildlife species without negatively impacting human activities. In response to this interest in Oregon, ODFW issued beaver relocation guidelines whereby agreeing landowners can relocate beavers from one property to another (ODFW 2012a).

Bridge Creek is a tributary to the John Day River in eastern Oregon. Like many streams in the western United States, it has a history of intense beaver trapping during the fur trade and subsequent overgrazing by cattle when ranchers settled in the west (Parker et al. 1985, Baker 2003). These factors, along with the semi-arid climate, have resulted in severe erosion, high incision, and limited riparian area and floodplain along Bridge Creek (Demmer and Beschta 2008, Pollock et al. 2007). However, Bridge Creek provides rearing and spawning habitat for an anadromous run of Middle Columbia River steelhead (*Oncorhynchus mykiss*) that is listed as threatened under the Endangered Species Act (ESA 71 FR 834). Due to its current degraded status, high potential for improving threatened steelhead populations, and potential to support additional salmonid species, Bridge Creek has been identified as a restoration priority

(CBMRC 2005). The Bridge Creek Intensively Monitored Watershed (IMW) project is a long-term study to restore stream and riparian habitat along the incised and degraded lower 32 km (Pollock et al. 2012). One of the objectives of the project is to use beaver as a resource for aiding restoration, with possible translocation to bring in beaver to accomplish these goals. However, little is known about the extant beaver population in Bridge Creek.

We used genetic and radio telemetry approaches as part of a larger study to investigate the ecology of beavers in Bridge Creek and to assess the need for additional beavers in the watershed to aid in steelhead habitat recovery efforts. Radio telemetry was used to estimate the home range size, habitat use, and survival rates for beavers in Bridge Creek (see Chapter 2). For this study, mitochondrial DNA was used to investigate the genetic diversity of beavers in Bridge Creek. Mitochondrial DNA has been shown as an effective way to investigate the genetic structure and history of a population (Avise 1998). In order to put the genetic diversity of this watershed in the historical context of beaver management in Oregon, we used samples from the John Day River upstream of the Bridge Creek watershed confluence and samples of beaver from another study conducted in western Oregon. These samples together represent a broader context of the western and eastern parts of Oregon, on both sides of the Cascade Range. Based on published historical accounts of beavers being trapped to near extinction, followed by remnant populations being redistributed throughout the state (Cliff 1936, Kebbe 1949, Meyers 1946), we hypothesized that genetic structure would be uniform and genetic diversity would be low across the entire state of Oregon.

## METHODS

### Sample Collection

We obtained a total of 87 tissue samples from 3 different 3rd level hydrological units (HUC6 basins). Thirty-four samples came from 2 different basins (Willamette and Northern Oregon Coastal, 10 HUC10 watersheds) in western Oregon and 53 samples from 1 basin (John Day, 3 HUC10 watersheds) in eastern Oregon (see Fig. 3.1 for sampling locations). We collected 44 beaver tissue samples from the Bridge Creek watershed, contained within the John Day basin, during trapping efforts for radio tagging (see chapter 2). Samples were also opportunistically obtained from the John Day River in eastern Oregon from a local trapper, for comparison of beaver genetic diversity from the greater John Day basin. The John Day River samples were dried castor gland tissue from lethally trapped beavers in 2011 and 2012. Seven samples were from around the town of Dayville, Oregon while the remaining 2 were from the Mount Vernon, Oregon area. These two locations are 79 and 116 road kilometers east of Bridge Creek respectively, on the mainstem of the John Day River. Western Oregon samples were collected from nuisance beaver colonies being relocated for research purposes (Petro 2013). Prior to analysis, all tissue samples were placed in 15 ml vials of lysis buffer. Capture and handling procedures to obtain the

Bridge Creek watershed samples were approved by the National Wildlife Research Center's Institutional Animal Care and Use Committee (QA 1719) and ODFW scientific taking permit (082-11).

DNA Extraction, Amplification, and Sequencing

DNA was extracted from each sample using a DNeasy extraction kit and the QIAcube automated purifier (Qiagen, Inc., Valencia, CA). The hypervariable domain I (HV I) (Saccone et al. 1987) of the mitochondrial DNA (mtDNA) control region (D-loop) was amplified using universal primers Thr-L15926 (5'-CAATTCCCCGGTCTTGTAAACC-3') and DL-H16340 (5'-CCTGAAGTAGGAACCAGATG-3') (Vila et al. 1999, Ducroz et al. 2005, Durka et al. 2005, Lizarralde et al. 2008, Fasanelle et al. 2010).

Polymerase chain reactions (PCR) were performed in 25 μl reaction volumes. Each 25 μl PCR mix consisted of 1 μl DNA, 0.7 μl of each primer (10 μM), and a illustra PuRe Taq Ready-To-Go PCR bead (GE Healthcare, Pittsburgh, PA) containing: 2.5 U Taq DNA polymerase in a reaction buffer of 200 μM deoxyribonucleotide triphosphates, 10 mM Tris-HCl, 50 mM KCl, and 1.5 mM MgCl2. The thermal profiles of all PCRs consisted of an initial denaturation cycle for 4 minutes at 96º C, followed by 35 cycles of 30 seconds at 96º C, 1 minute at 56º C, and 1 minute at 72º C, and a final extension cycle for 10 minutes at 72º C. Amplifications were performed in a Mastercycler EP Gradient programmable thermal cycler (Eppendorf, Hamburg, Germany). The amplified PCR product was purified with a combination of Exonuclease I and Shrimp Alkaline Phosphatase (ExoSAP; USB, Cleveland, OH).

The purified double-stranded PCR product was cycle sequenced using the BigDye Terminator Cycle Sequencing Kit (Life Technologies, Grand Island, NY). Dye terminators were removed using the PrepEase Sequencing Dye Clean-Up Kit (Affymetrix, Inc., Cleveland, OH). Sequencing for both strands was done on an Applied Biosystems 3130 automated sequencer (Life Technologies, Grand Island, NY). Sequences were visually edited and aligned in the program Sequencher version 4.10.1 (Gene Codes Corporation, Ann Arbor, MI). A median-joining network (Bandelt et al. 1999) was constructed using the program Network version 4.6.1.1 (Fluxus Technologies Ltd., 2012, Clare, Suffolk, England) to visualize the relationships among haplotypes.

Sequence Analysis

We grouped all samples from the John Day basin as an "eastern Oregon" subpopulation and samples from Willamette and Northern Oregon Coastal basins into a "western Oregon" subpopulation for analysis instead of treating them as multiple subpopulations. This approach allowed us to compare the genetic diversity of beavers on both sides of the Cascade Range. We used Arlequin version 3.5.1.3 (Excoffier and Lischer 2010) to calculate number of haplotypes, number of polymorphic sites, haplotype diversity (h), and nucleotide diversity (π) for these subpopulations. Haplotype diversity is the probability that two randomly chosen individuals will have different haplotypes while nucleotide diversity is the average number of nucleotide differences per site between any two sequences. We also estimated the differentiation between the two subpopulations using pairwise $F_{ST}$. This allowed us to see if these subpopulations experienced regular gene flow or were significantly genetically differentiated.

## RESULTS

We successfully sequenced a fragment of the mtDNA control region for 86 of the 87 samples obtained. The amplified fragment was 549 basepairs (bp) long. Overall 8 unique haplotypes were identified. Three haplotypes were found in eastern Oregon while 7 haplotypes found in western Oregon (Table 3.1, see Figure 3.3 for haplotype distribution); 2 haplotypes were shared between the subpopulations. There were 17 sites with polymorphisms, of which 16 were transitions and 1 was a transversion (Table 3.2). One of the haplotypes (OR2) represented in western and eastern Oregon has been previously reported in Serrano (2011) (GenBank Accession number JQ663962) from Alaska and Idaho.

The median-joining network clearly showed that haplotypes from eastern Oregon are closely related and recently derived based on short branch lengths; haplotypes from western Oregon are connected by longer branch lengths (Figure 3.2).

Three of the 8 haplotypes (OR1, OR2, OR3) were found in the eastern Oregon samples. All 3 haplotypes were found in the Bridge Creek samples while only OR1 and OR2 were sampled in the John Day River. The 3 haplotypes were derived from 2 polymorphic sites. The mean number ( ± SD) of pairwise differences was 0.467 ± 0.415. The nucleotide diversity ($\pi$) was correspondingly low, 0.001 ± 0.001. Haplotypic diversity (h ± SD) was 0.441 ± 0.056. Haplotype OR3 was only seen in one sample from Bridge Creek and was only one bp different from OR2. Seven of the 8 haplotypes (OR1, OR2, OR4, OR5, OR6, OR7, OR8) were found in the western Oregon samples. Seven of these haplotypes were derived from 16 polymorphic sites. The mean number of pairwise differences (1.769 ± 1.051) was higher than eastern Oregon, as was the nucleotide diversity (0.003 ± 0.002). The haplotype diversity was also higher (0.546 ± 0.098). The pairwise $F_{ST}$ estimate between the eastern and western Oregon subpopulations was 0.499, and the two subpopulations were significantly differentiated from each other ($P < 0.001$).

## DISCUSSION

A population bottleneck and relocation of remaining individuals will affect the genetic structure and diversity of a population (Höglund et al. 2013). The source, number, and genetic variability of individuals used as founders in reintroductions are key factors affecting the genetic diversity and persistence of resulting populations (Maudet et al. 2002). A small number of founding individuals can lead to a loss genetic diversity and evolutionary potential in the resulting population (Allendorf and Ryman 2002, Frankham et al. 2002).

Based on historical documentation of significantly reduced populations of beaver in Oregon followed by reintroduction, our hypothesis was that we would see uniform genetic structure and low genetic diversity across the state of Oregon. We found low genetic diversity among the eastern Oregon samples and relatively higher genetic diversity in western Oregon. We found 8 haplotypes that did not appear to be recently derived in our western Oregon samples. This was surprising as our sampling was limited across this broad geographical area and based on the historical accounts of the area. Although 2 of the 3 haplotypes from eastern Oregon were shared with western Oregon, the two subpopulations were significantly differentiated. Therefore our hypothesis was rejected. This suggests that the historical records of near extirpation were not accurate or that undocumented reintroductions have occurred.

Oregon's beaver management history allows for several possible scenarios to explain the higher than expected genetic diversity seen in our western Oregon samples and decreased diversity found in eastern versus western Oregon. A study investigating the success of the first beavers transplanted to National Forests in eastern Oregon one year after "liberation" reported the highest percentage of colonies had disappeared from the release location and their fate was unknown (Scheffer 1941). This is not unexpected considering relocation success depends on habitat quality and stream systems were already showing the effects from a lack of beaver presence (Finley 1937, Meyers 1946, Griffith et al. 1989). This indicates transplanted beavers may have had a low success rate in eastern Oregon and the lower number of survivors, or possibly even a remnant population that eluded trappers, repopulated the area. This low number of founder individuals would have produced the low genetic diversity seen in our samples. Haplotype OR3 was found in only 1 beaver sampled in Bridge Creek, was not found in western Oregon or the John Day samples, and was only 1 bp different from OR2. Based on these results and the time it would take for a change like this to occur in the mitochondrial DNA control region, OR3 could be locally derived and originating from a remnant population remaining after fur trappers went through the area. Although there is still the possibility that OR3 does occur in western Oregon and we did not sample it.

During the North American fur trade of 18th and 19th centuries, both eastern and western Oregon were the focus of extensive beaver trapping (Williams 1971, Mackie 1997). Although there is some evidence that the interior of the Coast Range was not heavily trapped due to the difficult terrain and abundance of fallen trees (Guthrie and Sedell 1988). The state was initially closed to beaver trapping in 1899, yet the number and location of remaining beaver populations was unknown. When reintroductions began in 1932, the Ochoco National Forest was the location for the first and greatest reintroduction efforts (Cliff 1936, Meyers 1946). The initial 17 source beavers originated from the agricultural lands near the Crooked River in Central Oregon and a total of 50 colonies were transplanted into the Ochoco National

Forest between 1932 to 1936 (Scheffer 1941, Meyers 1946). The Ochoco National Forest is the location of the headwaters of Bridge Creek and several other tributaries of the John Day River. Over the first 10 years of the reintroduction effort over 2,500 beavers were transplanted from agricultural lands into national forest, mostly east of the Cascade mountain range (Cliff 1936, Meyers 1946). Many beavers were reportedly live-trapped in the Willamette valley and relocated to eastern and southern Oregon (Larry D. Cooper, Oregon Department of Fish and Wildlife, personal communication, July 22, 2013).

Although the Willamette Valley was intensively trapped during the fur trade, western Oregon and the Willamette Valley in particular (28 out of the 34 western Oregon samples) shows a higher level of genetic diversity than eastern Oregon. This may be due to the reduced trapping pressure in the Coast Range. If a reservoir of beavers, and potential high genetic diversity, was in the Coast Range; the individuals on the east side of the Coast Range may have been able to easily repopulate the Willamette Valley. This is supported by the fact that we found haplotypes OR4, OR5, and OR6 on the west and east sides of the Coast Range.

The 2 main haplotypes seen in our eastern Oregon samples (OR1 and OR2) were also found in western Oregon, in the north Willamette River basin. This does not allow us to rule out the idea that these two haplotypes may be found throughout the lower Columbia River. Female beavers of haplotype OR1 and OR2 may have dispersed into the John Day River and been the founding reproductive members of beavers in the John Day River basin.

The low genetic diversity found in our eastern and western Oregon beaver subpopulations are only slightly higher than the sea otter (*Enhydra lutris*), another species that experienced a bottleneck and subsequent relocations due to the fur trade (Larson et al. 2002). The Eurasian beaver (*Castor fiber*) also experienced a similar history, with post fur trade populations not exceeding 30-300 individuals (Nolet and Rosell 1998). Ducroz et al. (2005) found one dominant haplotype and a low number (1-3) of additional haplotypes among *C. fiber* in single watersheds in Russia and Mongolia, which are similar to our results with *C. canadensis* in eastern Oregon. Their nucleotide and haplotype diversity also was comparably low. When Durka et al. (2005) expanded on the Ducroz et al. (2005) study and sampled *C. fiber* in Eastern and Western Europe, they saw an increase in haplotype and nucleotide diversity.

Translocation of a species can also result in low genetic variability when the number of founding individuals is small (Nei et al. 1975, Frankham et al. 2002). In 1946, 25 pairs of non-native American beavers (*C. canadensis*) were introduced into the Claro River on Isla Grande of Tierra del Fuego, Argentina as furbearers. The exotic species has now expanded to over 100,000 individuals, despite control efforts (Lizarralde et al. 2008, Fasanella et al. 2010). Lizarralde et al. (2008) sampled 30 beavers from 5 different watercourses in the Tierra del Fuego National Park. They detected 6 control region haplotypes with a nucleotide diversity of 0.323 and haplotype diversity of 0.87. Fasanella et al. (2010) reported lower genetic diversity in additional sample areas outside the Tierra del Fuego National Park and only 1 additional haplotype. Results were still higher than we saw in western and eastern Oregon, with a haplotype diversity of 0.57-0.59. Although the genetic diversity of the founding individuals in Tierra del Fuego and the size and genetic diversity of the remnant population of beavers in Oregon after the fur trade is unknown, it is surprising to find lower genetic diversity in our Oregon sampling area than in a population that was founded by just 50 individuals.

Serrano (2011) found high haplotype diversity (0.95) and moderate to low nucleotide diversity (0.015) when sampling beavers across the North America. We saw much lower haplotype and nucleotide diversity at our smaller scale of western and eastern Oregon. The management actions to increase beaver populations post fur trade in North America differed depending on the region. The original location, genetic diversity, and quantity of reintroduced beavers are factors that ultimately affect current beaver genetic diversity. For example, beavers from Ontario, Canada and Yellowstone National Park were released in the Adirondacks in New York in the early 1900's (Müller-Schwarze 2011). Reintroductions from multiple source populations would most likely result in higher genetic diversity than from a single source.

Our study had limitations such as the lack of random sampling throughout all of Oregon and historic samples representing the genetic diversity of beavers in Oregon before the fur trade drastically reduced populations. There are also no records on the beaver population size in Oregon after the fur trade. The loss in genetic diversity due to a bottleneck depends on the number of founding or remaining individuals and the rate of population growth (Nei et al. 1975). Beaver populations quickly rebounded in Oregon and the focus shifted from relocation to lethal trapping nuisance beavers by 1945 (Verts and Carraway 1998). Since both western and eastern Oregon population quickly rebounded, the loss of genetic diversity in eastern Oregon is either due to historically low diversity pre fur trade or the result of a low diversity founding population during reintroduction.

## MANAGEMENT IMPLICATIONS

Significant differences exist between the genetic diversity of western and eastern Oregon beaver populations, although the main haplotypes observed in eastern Oregon samples are also seen in the northern Willamette Valley of western Oregon. Any future translocation efforts of beavers in eastern Oregon should consider increasing the genetic diversity through translocations from the southern Willamette Valley. These translocations have the potential to increase the evolutionary potential of the beaver population in eastern Oregon by increasing the genetic diversity of beavers in the area, if they survive and reproduce. Although this may help the species itself, it may not help ecologically. The purpose of translocating nuisance beavers in Oregon is so their damming activities can help restore degraded stream and riparian habitat while reducing human-beaver conflict. As we saw in the previous chapter

(chapter 2), through radio telemetry, not all beavers build dams. Although we saw low genetic diversity in our Bridge Creek samples, it does not appear to be affecting the survival of the beaver population and relocating additional beavers into the watershed is not recommended due to lack of unoccupied habitat we observed through telemetry (see chapter 2).

We were unable to discern any genetic structure of beavers in Bridge Creek due to the low genetic diversity. We recommend additional genetic surveys of the beavers in Bridge Creek and the greater John Day basin that incorporates multilocus nuclear DNA markers, such as microsatellites. This would allow investigation of the mating system and social structure of beavers within Bridge Creek, and any gene flow into Bridge Creek through dispersing individuals from the John Day River.

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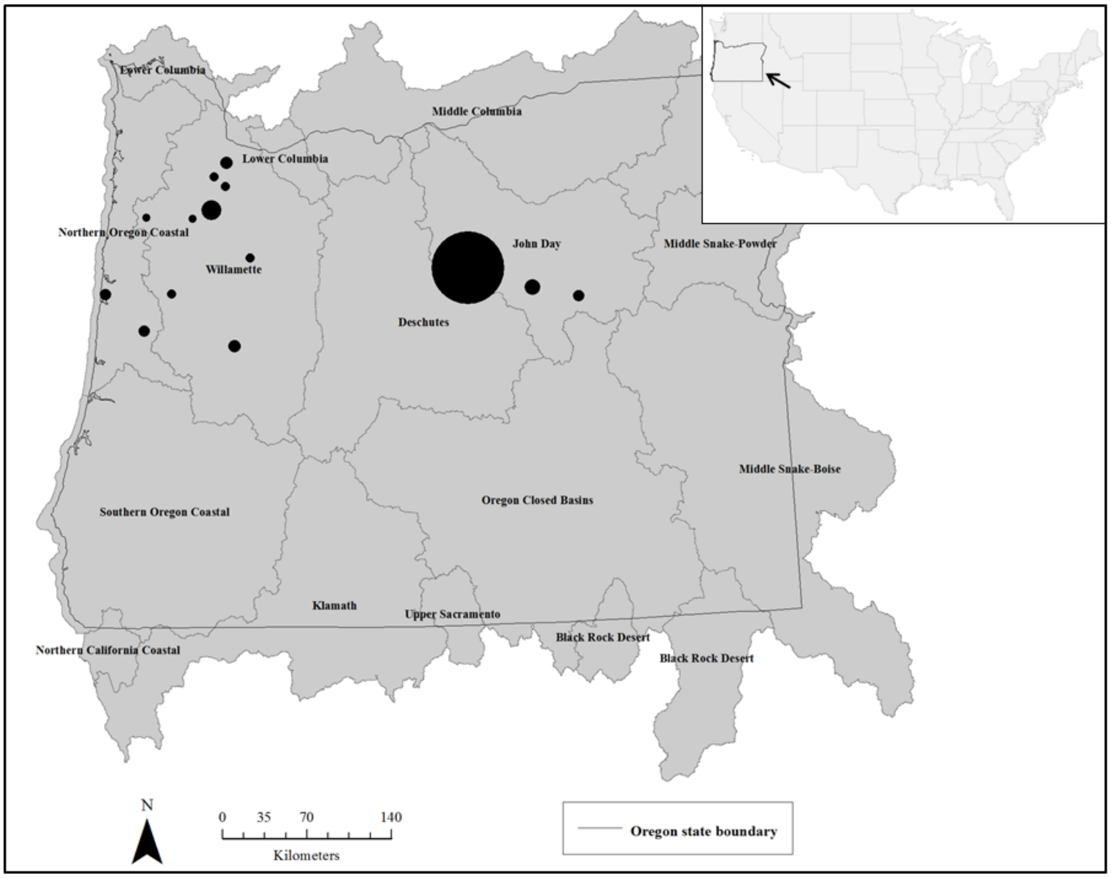


Figure 3.1. Map of Oregon indicating sampling locations. Circle sizes are proportional to sample size from the specific location. Eastern Oregon samples were all contained within the John Day River Basin while western Oregon samples were in the Willamette River and the Northern Oregon Coastal Basins.

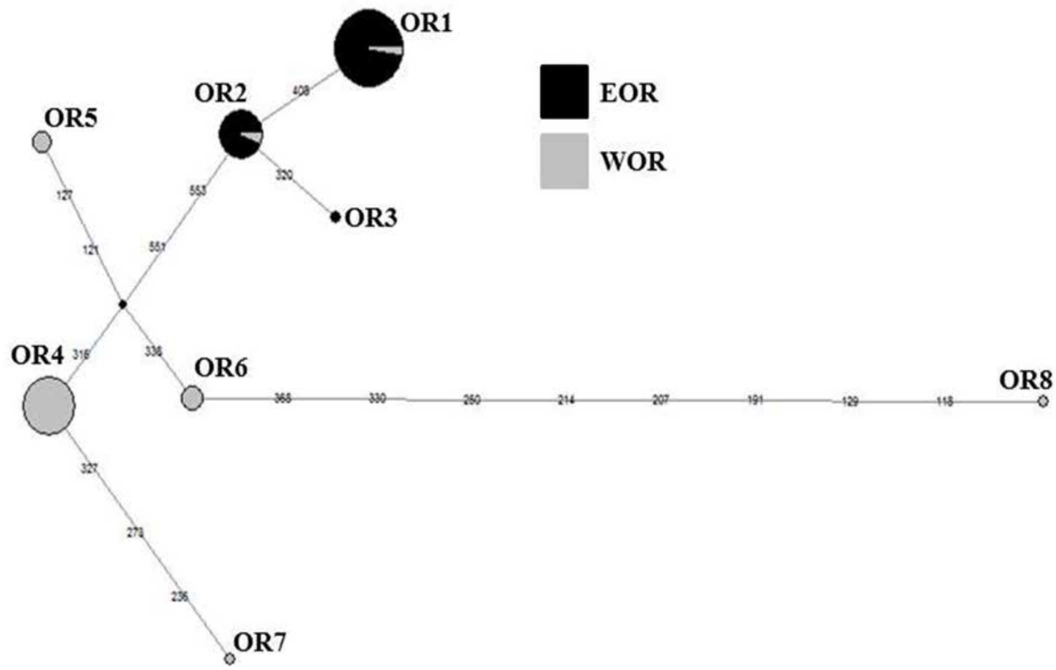


Figure 3.2. Median-joining network for haplotypes found among western Oregon (WOR) and eastern Oregon (EOR). Circles are proportional to haplotype frequency, and number on branches corresponds to mutation location.

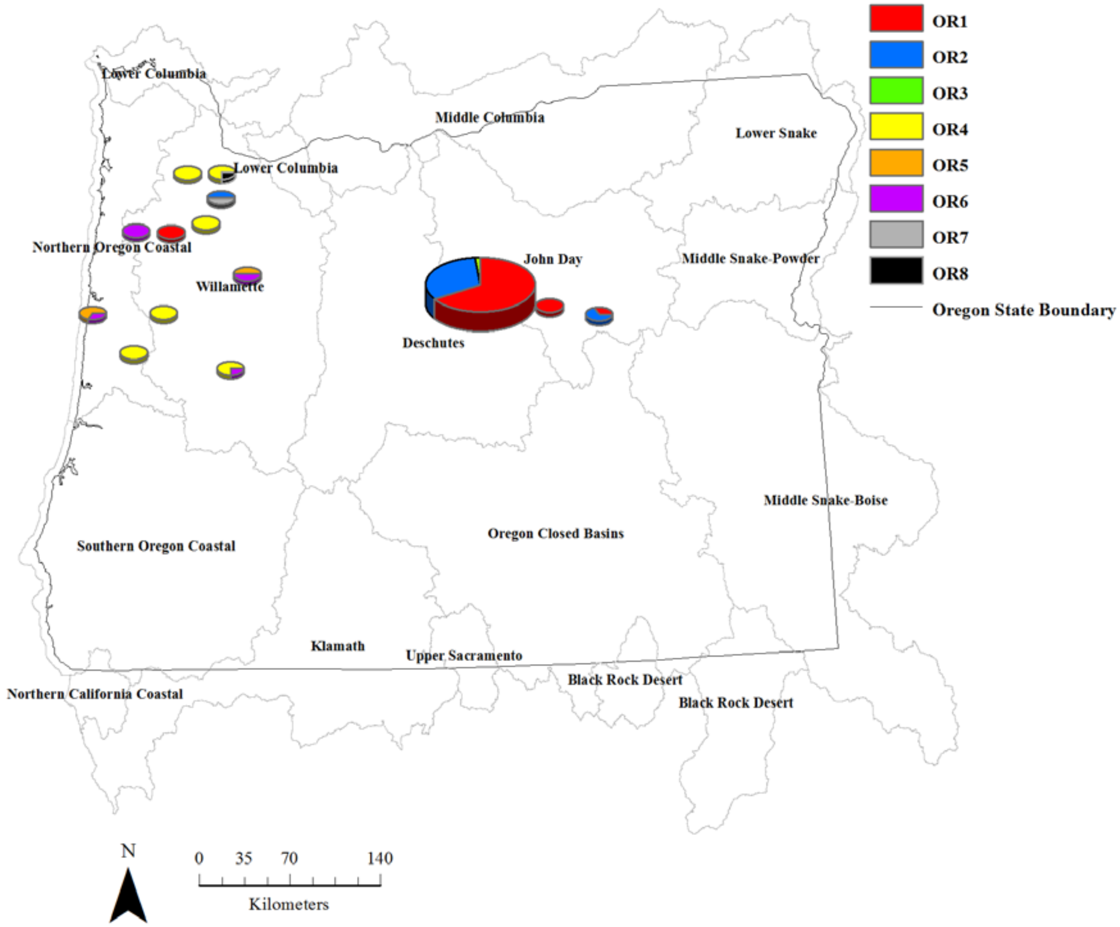


Figure 3.3. Haplotype distribution based on sampling location of beavers in Oregon. Circle sizes are proportional to sample size from the specific location and areas within the circles are proportional to haplotype frequencies.

Table 3.1. Frequency of beaver mtDNA control region sequence haplotypes by geographic sampling location.

| Haplotype | N | Sampling site locations | Frequencies |
|---|---|---|---|
| OR1 | 38 | WOR, EOR | 0.0303, 0.698 |
| OR2 | 16 | WOR, EOR | 0.0303, 0.283 |
| OR3 | 1 | EOR | 0.0189 |
| OR4 | 22 | WOR | 0.667 |
| OR5 | 3 | WOR | 0.0909 |
| OR6 | 4 | WOR | 0.121 |
| OR7 | 1 | WOR | 0.0303 |
| OR8 | 1 | WOR | 0.0303 |

WOR = western Oregon, EOR = eastern Oregon.

Table 3.2. Condensed matrix displaying polymorphic sites of the 549 bp aligned fragment of the mtDNA control region for 8 haplotypes found in *Castor canadensis* in Oregon, with number of samples of corresponding haplotype in western Oregon (WOR) and eastern Oregon (EOR). Vertical digits indicate nucleotide position relative to OR1.

| Haplotype | 120 | 123 | 129 | 131 | 193 | 209 | 216 | 238 | 252 | 275 | 318 | 322 | 329 | 332 | 340 | 370 | 410 | WOR | EOR | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| OR1 | T | A | G | A | G | T | G | A | G | T | T | A | T | G | A | G | C | 1 | 37 | 38 |
| OR2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | T | 1 | 15 | 16 |
| OR3 | . | . | . | . | . | . | . | . | . | . | . | G | . | . | . | . | T | 0 | 1 | 1 |
| OR4 | . | . | . | . | . | . | . | . | . | . | C | . | . | . | . | . | T | 22 | 0 | 22 |
| OR5 | . | . | . | . | . | . | . | G | . | C | C | . | A | . | . | . | T | 1 | 0 | 1 |
| OR6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | G | . | T | 4 | 0 | 4 |
| OR7 | . | G | A | . | . | . | . | . | . | . | . | . | . | . | . | . | T | 3 | 0 | 3 |
| OR8 | C | . | . | G | A | C | A | . | A | . | . | . | . | A | G | A | T | 1 | 0 | 1 |

# CHAPTER 4: CONCLUSION

The effects of beaver damming activity on salmonid species have interested scientists and managers in Oregon for decades. There is growing interest in partnering with beaver for fish habitat restoration but little is known about the ecology of beaver in Oregon. The preceding chapters contribute to the limited pool of knowledge on the ecology of beavers in Oregon, particularly the semi-arid east.

The lower 32 km of Bridge Creek's instream and riparian habitat is severely degraded. Due to its current degraded status, high potential for improving threatened steelhead populations, and potential to support additional salmonid species; Bridge Creek has been identified as a restoration priority (CBMRC 2005). Current restoration techniques were designed to partner with existing beaver populations (Pollock et al. 2012). Given the interest of managers and scientist on the project with the beaver population, we used radio telemetry to investigate the home ranges, habitat use, and survival of the extant beaver population on Bridge Creek.

In chapter 2, we found that beavers occupied nearly the entire study reach of Bridge Creek and had high survival rates for the study period. Home ranges were smaller than most other studies of beavers in linear habitats but colonies were close in proximity and with some instances of overlap. Even with the high occupancy of Bridge Creek, beaver colonies inhabited areas with greater proportion of grasses and herbaceous vegetation than the proportion present for the entire study area during the spring. These findings indicate that restoration managers may need to continue to assist beavers in damming through the installation of additional Beaver Dam Support Structures (BDSS) to meet their restoration goals, because the current beaver population does not appear to be lacking.

American beavers (*Castor canadensis*) in Oregon were trapped to near extirpation by the late 1800's due to the North American fur trade (Kebbe 1949). Remnant populations were relocated from agricultural areas to the mountain stream of National Forests, to allow populations to rebound and where their damming activities would be appreciated (Scheffer 1941). Relocation of nuisance beavers to areas in need of their habitat restoring damming activity has been a proposed tool for many restoration projects in Oregon, including the project on Bridge Creek. A low number of founding individuals and relocation can both have effects on the genetic diversity of a population. In chapter 3, we investigating the genetic structure and diversity of beavers on Bridge Creek to add to habitat and survival information in chapter 2 and to better inform managers if relocation into Bridge Creek continued to be a consideration. In order to put the genetic diversity of this watershed in the historical context of beaver management in Oregon, we also investigated the genetic diversity of western and eastern parts of Oregon.

We found very low genetic diversity within Bridge Creek which prompted us to sample the greater John Day basin for comparison. Due to the low diversity seen in both areas, we could not answer any questions on the genetic structuring at that scale. We then compared those results to beavers in western Oregon. We found significantly higher genetic diversity in western Oregon but it was still lower than what was seen in a study of beaver genetic diversity across North America (Serrano 2011). Although the genetic diversity of beavers in Oregon pre-fur trade is unknown, low diversity across the state could indicate a bottleneck affect from extensive historic trapping. The low genetic diversity seen in the Bridge Creek does not appear to be affecting the survival of beavers in the area.

The information gained on the survival, home range, habitat use, and genetic diversity of beavers in Bridge Creek is important in assisting managers on the feasibility of partnering with beaver to meet their stream restoration goals. Although beaver relocation is an attractive tool for alleviating nuisance beaver issues while potentially restoring fish habitat, our results indicate that Bridge Creek may not be able to support more beavers in its current state.

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