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Beaver Habitat Selection for 24 Yr Since Reintroduction North of Yellowstone National Park

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ABSTRACT

Beavers *(Castor canadensis)* disappeared from drainages north of Yellowstone National Park in the mid-1900s because of trapping, a potential tularemia outbreak, and willow (*Salix* spp.) stand degradation by ungulates. Beavers were reintroduced in 1986 after a 40–yr absence with inventories of active-beaver structures completed each fall after reintroduction for 24 consecutive yr. We used this inventory to evaluate the expansion of beaver populations in a riparian environment recovering from past overuse by ungulates. Specifically, we investigated the density of active-beaver colonies and dams, the change in willow cover, and habitats associated with beaver expansion since reintroduction. Successful establishment and expansion of beavers indicate that sufficient resources were available to the population despite the suboptimal condition of riparian vegetation. Carrying capacity on third-order streams was reached approximately 14 yr after reintroduction (2000) with an average annual density of 1.33 (95th percentile = 1.23 − 1.44 active colonies/stream km) between 2000 and 2010. The average annual density of beaver dams during this time was 2.37 (2.04 − 2.71 active dams/stream km). Despite the beaver population being at carrying capacity in meadows since 2000, willow cover increased by 16% between 1981 and 2011. We speculate that beaver activities, together with reduced ungulate browsing from predation and habitat loss, combined to increase willow cover. Willow cover and height were positively associated with colony longevity, but numerous other influencing variables included secondary channels, sinuosity, stream depth, and sandbar width. Our results provide evidence that beaver reintroduction can be successful in riparian areas where willow stand condition is less than optimal and that beavers might ultimately improve willow condition. We suggest that reducing ungulate use of overgrazed riparian environments will facilitate the reestablishment of beaver populations. We also provide managers with habitats that should be identified in an environment targeted for reintroduction.

Introduction

Beavers are considered ecosystem engineers because they alter riparian areas to suit their needs (Jones et al., 1994). These alterations can have positive effects on stream and riparian habitats and the species that use them. Beaver dams can raise the water table for local vegetation (Gurnell, 1998), create open-water habitats (Hood and Bayley, 2008; Johnston and Windels, 2015; Morrison et al., 2015) used by waterfowl (McKinstry et al., 2001), maintain stream flows when water levels are low (Westbrook et al., 2006), aggrade stream channels through sediment retention (Pollock et al., 2007; Levine and Meyer, 2014), and create pond habitat for fish (Kemp et al., 2012). Beaver foraging can increase plant species richness (Wright et al., 2002), promote the growth and spread of riparian vegetation (Hood and Bayley, 2009; McColley et al., 2012), and expand wetland perimeters (Hood and Larson, 2014). Because of these effects, beavers have been used for stream and riparian restoration (Pollock et al., 2015).

Beavers were extirpated from much of North America by the early 1900s because of trapping and habitat loss (Nainman et al., 1986; Baker and Hill, 2003). Wildlife agencies began beaver reintroductions into former habitats in the mid-1900's (Apple, 1985; Albert and Trimble, 2000; McKinstry et al., 2001; Cunningham et al., 2006; Carrillo et al., 2009; Pollock et al., 2015). However, efforts to increase beaver

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populations in the western United States have been hampered by overgrazing and erosion of riparian areas by livestock, reducing woody vegetation for beavers to eat and use for the building of beaver structures (Belvsky et al., 1999; Albert and Trimble, 2000; Baker and Hill, 2003; DeVries et al., 2012; Small et al., 2016). Native ungulates also have hampered beaver recovery in some regions. Beavers were suspected to decline on the Northern Yellowstone Winter Range in Yellowstone National Park because expanding elk *(Cervus elaphus)* populations reduced aspen *(Populus tremuloides)* and willow (*Salix* spp.) in riparian areas after wolf *(Canis lupus)* extirpation in the early 1900s (Warren, 1926; Jonas, 1955; Weaver, 1978; Ripple and Beschta, 2016). Beaver decline in Rocky Mountain National Park also was suspected to be a result of competition for forage with increasing elk populations (Peinetti et al., 2002; Baker and Hill, 2003).

Many factors contributed to the disappearance of beavers from drainages in the Absaroka-Beartooth Wilderness north of Yellowstone Park in the mid-1950s. Trappers harvested beavers, and there also were reports of tularemia outbreaks. Moreover, growing moose *(Alces alces)* populations after wolf extirpation in the early 1900s likely reduced the suitability of willow stands to beavers (Tyers, 2003; Smith and Tyers, 2012). Elk also browsed willow stands in these high-elevation drainages but less consistently and generally only in mild winters. Willow was able to slowly recover with moose population declines following the commencement of annual harvests in 1945, the destruction of mature conifer forests important to moose (critical winter habitat) after the 1988 Yellowstone fires, and wolf reintroduction to Yellowstone Park in 1995 and 1996 (Bangs and Fritts, 1996; Tyers, 2003). In 1986 beavers were reintroduced by the US Forest Service to mountain meadows in the Absaroka-Beartooth Wilderness north of Yellowstone Park with the aim of restoring populations and riparian environments. The restoration of beavers was aided by a moratorium on trapping put in place by Montana Fish, Wildlife, and Parks. The location of active-beaver structures was recorded annually after reintroduction (1986 − 2010) to monitor the expansion of beaver populations (Smith and Tyers, 2012). We used this inventory to evaluate the success of the reintroduction effort and ability of a recovering-riparian vegetation community to support a population of reintroduced beaver.

Our research took place in four low-gradient mountain meadows with extensive willow floodplains that were the focus of the reintroduction effort. Our general knowledge of beaver ecology in these semiarid mountain streams is lacking relative to temperate environments. This is surprising considering arid and semiarid environments comprise much of the land area in western North America and that riparian areas are critical to livestock and wildlife in these regions (Gibson and Olden, 2014). Specifically, we assessed 1) the growth of beaver populations and dams post reintroduction, 2) the change in willow canopy since reintroduction, and 3) riparian habitat variables associated with the longevity of beaver colonies. We suggest these data can be used to assess the ability of recovering-riparian environments to support beaver populations, the suitability of reintroduction locations, and potential effects of beavers on the environments in these areas.

Study Area

Three drainages within the Absaroka-Beartooth Wilderness portion of the Custer-Gallatin National Forest comprised our study area: Hellroaring, Buffalo Fork, and Slough. These drainages are all on the north boundary of Yellowstone National Park (Fig. 1). Four meadows were studied on three third-order streams within these drainages. These included Hellroaring, Christenson's, Holeman's, and Frenchy's meadow. Meadows were defined as the willow floodplains that surround low-gradient sections of third-order streams. Stream gradient within meadows ranged from 0.3% to 2.4% with a median of 0.38%. Stream gradient was measured as change in elevation (m) from one end of a meadow to the other divided by stream distance. We judged the end of a meadow to be where the meadow transitioned to forest.

Woody riparian vegetation was primarily willow, including Geyer's *(Salix geyeriana)*, Wolf's *(Salix wolf)*, Drummond's *(Salix drummondiana)*, Barclay's *(Salix barclayi)*, Eastwood's *(Salix eastwoodi)*, Booth's *(Salix bothii)*, and Farr's *(Salix farriae)* (Tyers, 2003). Using climate data from the weather station in Cooke City, Montana (2 520-m elevation, 45°01′N, 109° 56′W), mean annual precipitation was 65.5 cm with peak precipitation occurring in May and June. Mean minimum temperature in January was −15.4°C and mean maximum temperature in July was 23.2°C (Western Regional Climate Center, 2009).

The US Forest Service released 46 beavers into the study area between 1986 and 1999 (Tables S1 and S2; available online at https://doi.org/10.1016/j.rama.2017.12.001). Most beaver releases occurred in the Buffalo and Hellroaring drainages ($n = 38$ beavers). Beavers were reintroduced to Hellroaring meadow in 1988. After the release of beavers in 1986 in Christenson's meadow, beavers traveled 6 km downstream to colonize Holeman's meadow in 1988. Frenchy's meadow was colonized by beavers in 1996. These beavers likely dispersed 12.1 km downstream from reintroduction locations in the Stillwater and Lake Abundance area in the early 1990s. A number of other meadows were also colonized by beavers dispersing from reintroduction locations (see Fig. 1, Table S1).

Methods

Inventory of Beaver Structures

Observers inventoried streams for active-beaver structures each fall, including lodges, caches, dams, and bank dens. Beaver activity was determined from recently cut vegetation and fresh mud comprising beaver structures, along with recently traveled paths to and from beaver structures (Jonas, 1955; Fryxell, 2001; Pinto et al., 2009). We used this inventory to calculate the annual activity of colony locations (active lodge and associated structures) from their establishment through 2010. We calculated the annual density of active-beaver colonies to estimate population growth. Colony density was calculated per year as the number of active colonies in a meadow divided by the total number of stream kilometers. We calculated the density of active-beaver dams using these same methods.

Change in Willow Cover Since Beaver Reintroduction

We quantified change in willow canopy cover (%) since beaver reintroduction using aerial photographs taken in 1981 (acquired from the US Department of Agriculture [USDA] National Agriculture Imagery Program at a 1-m resolution) and 2011 (acquired from the USDA Farm Service Agency Aerial Photography Field Office at a 0.5-m resolution). Meadows were delineated as a polygon within a Geographic Information System. A systematic grid of random points (spaced every 25m) were created throughout meadow polygons using the U.S. Forest Service Digital Mylar Image Sampler. Each point was then assessed for whether it represented willow. The number of points classified as willow divided by the total number of points within a meadow were used to calculate willow cover (%) for each year (USDA–Remote Sensing Application Center 2011).

Field-data Collection

Observers conducted stream and vegetation measurements in the summer and fall of 2009 and 2010. Measurements were taken at 34 m transects placed perpendicular to the stream axis at 10 m intervals along streams. Transects were located on both sides of the stream from one end of a study meadow to the other. Vegetation was sampled beginning at the high–water mark. We initially measured willow cover using line-intercept transects. This method required extensive effort and provided similar estimates to visually estimating willow cover (%) along transects. Therefore, we estimated willow cover visually and verified these estimates by walking transects to ensure gaps in cover were