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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 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

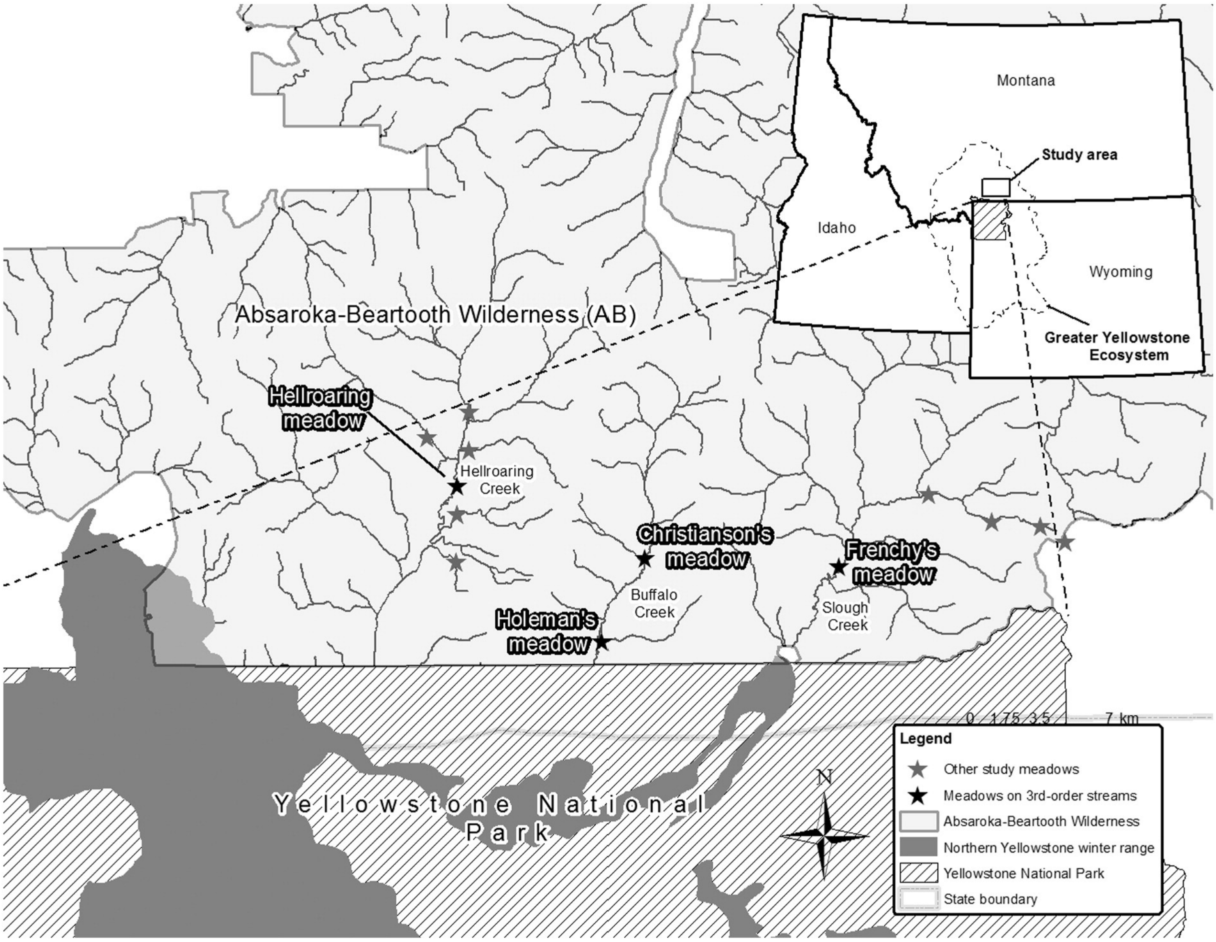

Figure 1. Study meadows (n = 13) within the Absaroka-Beartooth Wilderness located in southwest Montana adjacent and north of the northern Yellowstone winter range and Yellowstone National Park. We defined meadows as low-gradient sections of high-gradient mountain streams that have extensive stands of willow (*Salix spp.*) throughout the floodplain and along backwater sloughs. Hellroaring, Christenson's, Holeman's, and Frenchy's meadows are along 3rd-order streams. Other study meadows (n = 9) are along 1st- and 2nd-order streams.

not missed because of tall willow. Willow's height was measured with a meter stick at a willow that observers judged represented the average willow height along a transect.

Stream depth, stream width, and sandbar width were measured at the same position along the stream reach as the associated vegetative transect. Stream depth (m) was measured with a meter stick 1 m in from the edge of the stream. Stream width (m) was the stream surface distance perpendicular to the axis of the stream. Sandbar width (m) was the distance between the vegetation edge and the stream edge.

Beaver-colony Habitats

We linked the locations of beaver colonies with field measured transects to describe habitats at beaver colonies. The nearest transect to the beaver lodge was designated the center transect. Five transects up– and down–stream of the center transect, on both sides of the stream, were used to describe beaver habitats within colonies. We averaged values from all transects (n = 22) to produce a single value for each colony. If a stream reach was flooded from beaver activity at the time of field habitat sampling and it was part of a beaver colony identified through the structure inventory, we used transects from the closest non–inundated reach either up– or downstream to describe habitats within the beaver colony (Howard and Larson, 1985; Suzuki and McComb, 1998; Curtis and Jensen, 2004).

Several variables were measured relative to specific beaver-colony locations. Distance to secondary channel and stream sinuosity were measured in a Geographic Information System using orthocorrected aerial photographs from 2011 (1 m resolution) provided by the Remote Sensing Application Center in Salt Lake City, Utah. Distance to secondary channel was measured as the euclidean distance (m) from the beaver-colony center to nearest secondary channel. We define secondary channels as any channel other than the channel the colony was located upon (e.g., slough, second–order tributary). We used euclidean distance because of the beaver's ability to travel overland and through water. Sinuosity was measured as the stream distance 100 m above and below the beaver colony center divided by a euclidean distance between these two points.

A change in channel sinuosity since beaver introduction could equate to a change in habitats available to the beaver along that stream reach. Therefore, we compared sinuosity measurements at colony locations in 1981 and 2011 with aerial photographs. We excluded colonies with a change in sinuosity ≥ 0.50. This threshold removed colonies where substantive change occurred (river bed changed direction because of flooding) but kept colonies that had a small change in sinuosity owed to the seasonal changes in water levels when the aerial photographs were taken or differences in the resolution of the photos between years.

Habitat Modeling

We modeled beaver-colony longevity as a function of explanatory variables using negative-binomial regression. The response variable was the number of years a beaver colony was active. Beaver colonies were weighted by the number of years since the colony came into existence (2010 – year of colony establishment) which gave greater weight to colonies monitored for longer periods of time. Explanatory variables

Table 1

Models of beaver-colony longevity ($n = 29$) as a function of environmental variables in the Absaroka-Beartooth Wilderness, Montana. Beaver-colony longevity was modeled using negative-binomial regression with the number of years a colony was active as the response variable. Beaver colonies were weighted by the number of years they were in existence over the course of the inventory of beaver structures. For each model, we report K (number of model parameters), AIC_c ($[-2 \cdot \text{LogLikelihood} + 2k + 2k[k+1]/[n - k - 1]$), ΔAIC_c (change in AIC_c between each model and the top model with the lowest AIC_c weight), the AIC_c weight ($\exp[-0.5 \cdot \Delta AIC_c$ score for that model]), and the log likelihood. We report the top model as having the greatest AIC_c weight.

Model	Explanatory variables[a]	K	AIC_c	ΔAIC_c	AIC_c weight	Log likelihood
Null	Intercept only	1	2,212	262	0	−1,103.75
#1	Dist. to secondary channel + sinuosity + willow height	4	1,954	4	0.11	−970.73
#2	Dist. to secondary channel + sinuosity + sandbar width + willow height + willow cover	6	1,950	0	0.89	−965.24
#3	Stream depth + sandbar width + willow height + willow cover	5	2,198	248	0	−1,091.16
#4	Stream depth + sandbar width + stream width + willow height + willow cover	5	2,202	252	0	−1,091.00

included willow cover and height, stream depth and sinuosity, distance to secondary channel, stream width, and sandbar width. We predicted that beaver-colony longevity would be positively associated with willow cover and height because of their need for food and building materials (e.g., Small et al., 2016), positively associated with stream depth because deep streams are preferable habitats for foraging and building structures (e.g., Curtis and Jensen, 2004), and positively associated with sinuosity because deep water is often available on the outside bend of a sinuous stream reach (Boyce, 1981). We predicted that beaver-colony longevity would be negatively associated with distance to secondary channels because these channels provide shelter to beaver structures from spring floods, negatively associated with sandbar width because large sandbars might occlude beavers from reaching vegetation, and negatively associated with wide stream reaches because they are more difficult to dam. We created candidate models (Table 1) and used Akaike's information criterion corrected for small sample size (AIC_c) to assess model support. We report the log–likelihood, Akaike weight (w_i), K (including intercept and slope parameters), and ΔAIC_c (difference in AIC_c between top model and current model) for each model (Anderson and Burnham, 2002). We designated the top model as having the greatest weight. We report the 85% confidence interval of coefficient estimates from the top model (Arnold, 2010) and suggest high-variation in effect if the confidence interval crosses zero. All statistical analyses were conducted using R Version 3.2.5 (R Development Core Team, 2016).

We also used negative-binomial regression to determine the effect that years since colony establishment had on colony longevity. The response was the number of years a beaver colony was active since its establishment. The explanatory variable (years since colony establishment) was calculated by subtracting the year a colony was established from the first year beavers established within the associated meadow (the meadow where the beaver colony was located). We predicted that beaver colonies established earlier would have greater longevity (negative coefficient).

Results

The number of active-beaver colonies increased following reintroduction and their density appeared to level in 2000 (Fig. 2). The average-annual density of active-beaver colonies from 2000-2010, calculated using a bootstrap of density estimates (10,000 iterations, stratified by meadow), was 1.33 colonies/stream km (95th percentile = 1.23 − 1.44). The number of active-beaver dams also increased after reintroduction (Fig. 2). There were on average 2.37 active dams/stream km (2.04 − 2.71) from 2000-2010.

We identified 39 locations where beavers had established colonies on stream reaches within meadows along third-order streams. There were 33 colonies on the main stem of third–order streams and 6 on secondary channels. The average number of years active [calculated with a non-parametric bootstrap (10,000 iterations)] for all colonies was 8.8 years (7.1 − 10.7) and inactive was 4.0 years (2.9 − 5.1). Beaver colonies on secondary channels were more successful than those on the main stem. Beaver colonies on the main stem of third-order streams were active 8.0 years (6.2 − 10.0) and inactive 4.4 years (3.2 − 5.6). Beaver colonies on secondary channels were active 12.9 years (9.4 − 16.6) and inactive 2.3 years (0.9 − 4.3).

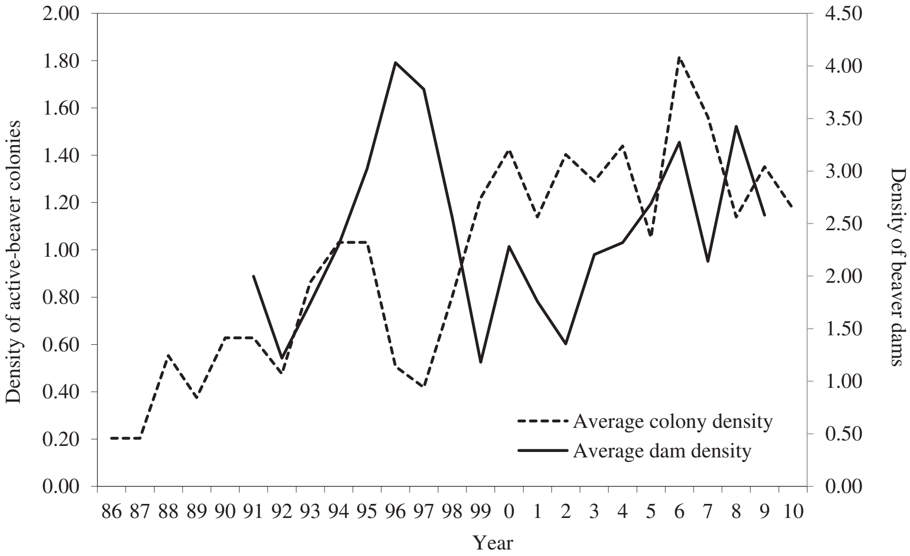

Figure 2. Annual density of active beaver colonies and dams since beaver reintroduction to the Absaroka-Beartooth Wilderness, Montana. Annual beaver colony density was calculated per year as the number of active colonies divided by the total number of stream kilometers within a meadow. An "R" indicates the years when beavers were reintroduced. Dam density was calculated as the number of dams surveyed in a meadow divided by the total number of stream kilometers within a meadow.

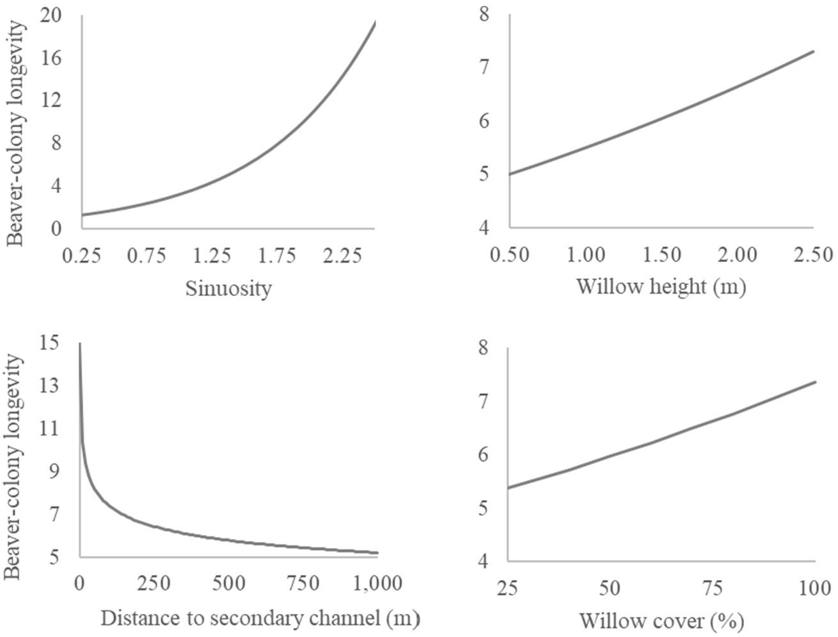

Figure 3. Predicted longevity of beaver colonies (n = 29) as a function of environmental variables. Coefficient estimates were from the best-performing model. For prediction purposes, all other variables within the best-performing model were held at their median value in the dataset.

Meadows increased in willow cover from 1981 to 2011. The average willow cover in 1981 was 32% and cover increased to 48% by 2011. Willow cover in Hellroaring meadow in 1981 was 36.5% and cover increased to 54% in 2011. Willow cover in Holeman's meadow in 1981 was 30% and cover increased to 51% in 2011. Willow cover in Christianson's meadow was 33% in 1981 and cover increased to 52% in 2011. Willow cover in Frenchy's meadow was 27% in 1981 and increased to 37% in 2011.

Of the 39 beaver colonies we identified, our analysis of environmental variables influencing beaver colony longevity included 29 locations from the main stem of third–order streams. We did not include colony locations on secondary channels (n = 6) because entire channels were flooded by beaver dams when stream data were collected which did not allow for measuring stream characteristics. We also excluded four colonies that had changes in channel sinuosity ≥ 0.50.

The most supported model of beaver colony longevity was model #2 and included as explanatory variables distance to secondary channel, sinuosity, sandbar width, willow cover, and willow height (AIC$_c$ weight = 1.00). Model #3 was the next best model but it had minimal support from the data (AIC$_c$ weight = 0.13, Table 1). Beaver colony longevity increased near to secondary channels and increased with greater stream sinuosity, sandbar width, willow cover, and willow height (Fig. 3). The confidence intervals of all explanatory variables did not cross zero (Table 2).

We used all beaver colonies identified with the inventory of beaver structures (n = 39) in the analysis of colony longevity as a function of years since the first establishment of beaver colonies within an associated meadow. We found that beaver colonies established early after reintroduction were more successful over the course of the inventory (β = -0.053, SE = 0.015, p–value = 0.0003, Fig. 4).

Discussion

We assessed the growth, environment effects, and habitat selection of beavers reintroduced in 1986 to drainages in the Absaroka-Beartooth Wilderness immediately north of Yellowstone National Park. Although trapping likely played a significant role in reducing beaver populations in the study area by the 1950s, beavers also were suspected to decline because moose populations reduced the quality of willow stands (Smith and Tyers, 2012). Moose populations were reduced thereafter because of habitat loss from the Yellowstone wildfires, hunting, and wolf reintroduction to Yellowstone (Bangs and Fritts, 1996; Tyers, 2003). The establishment of reintroduced beavers in 1986 and their subsequent expansion demonstrated that the riparian environment recovered enough as the moose population declined to provide adequate habitats for the expansion of beaver populations. Moreover, as beaver numbers increased and moose numbers decreased, willow canopy cover increased - an increase that was sustained even with the beaver population at carrying capacity.

Beaver population expansion after reintroduction resulted in meadows being at carrying capacity approximately 14-years after reintroduction (2000). From 2000–2010, the density of active colonies was

Table 2
Coefficient estimates, standard errors, and 85% confidence intervals for the top model (model no. 2) of beaver-colony longevity (*n* = 29) in the Absaroka-Beartooth Wilderness, Montana. We modeled beaver-colony longevity using negative-binomial regression with the number of years a colony was active as the response variable. Colonies were weight by the number of years they were in existence over the course of the inventory. An explanatory variable is considered to have a strong effect on beaver-colony longevity if the confidence interval of the coefficient estimate does not cross zero.

Explanatory variable	Coefficient estimate	Standard error	Lower confidence bound	Upper confidence bound
Intercept	0.465	0.203	0.172	0.758
Distance to secondary channel	−0.159	0.012	−0.177	−0.142
Sinuosity	0.988	0.055	0.910	1.067
Sandbar width	0.017	0.007	0.008	0.027
Willow cover	0.004	0.002	0.001	0.007
Willow height	0.189	0.092	0.056	0.322

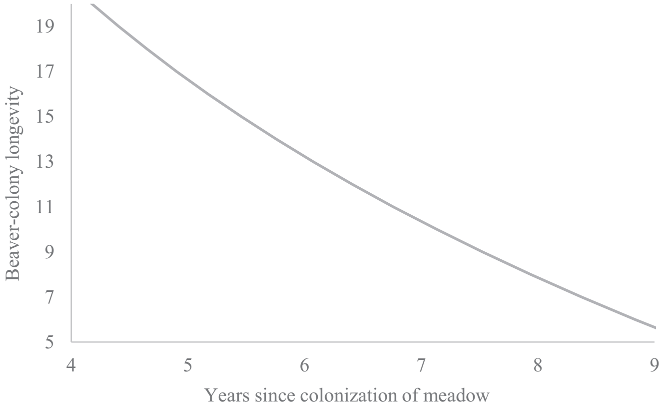

Figure 4. Predicted longevity of beaver colonies ($n = 39$) as a function of years since the first beaver colony established within the meadow. We used negative-binomial regression to model beaver-colony longevity.

1.33/stream km (95th percentile $= 1.23 - 1.44$) which aligns with estimates by other researchers (Nordstrom, 1972; Boyce, 1981; Collins, 1976; Hill, 1976; Howard and Larson, 1985). The spread of beavers did not appear to negatively affect willow cover but may have improved it. Five years before beavers were reintroduced (1981) the average cover of willow in meadows was 32% but by 2011 willow cover had increased to 48%. An increase in willow cover also was found at a fine scale outside of exclosures in Frenchy's meadow between 1986 and 1997 (36% in 1986 to 84% in 1997; Tyers, 2003). The increase in willow cover could be a result of reduced ungulate browsing commensurate with the decline of ungulate populations (e.g., Hough-Snee et al., 2013; Booth et al., 2012; Beschta et al., 2013; Batchelor et al., 2015). However, beavers also might have increased the cover of willow through their activities. For example, we found willow cover and height were positively associated with the longevity of beaver colonies. This is logical considering that long-term use of a location by beavers might only have occurred if willow was abundant (e.g. Howard and Larson, 1985; Hall, 2005; Harrison, 2011). However, the results also could indicate that beavers have increased the cover and height of willow by promoting vegetation growth with raised water tables from dams (Gurnell, 1998) or through mutualism when cutting vegetation (e.g., Kindschy, 1989; Hood and Bayley, 2009). Beavers have been implicated in the expansion of riparian vegetation in other environments as well [Gordon and Meentemeyer, 2006 (17-year period); McColley et al., 2012 (15-year period)].

We also found an increase in the density of dams as beavers expanded. Our average estimate since 2000 was 2.37 active dams/stream km ($2.04 - 2.71$), which is close to that reported in Minnesota (2.5 dams/km; Naiman et al., 1988), less than reported in Quebec (10.6 dams/km; Nainman et al., 1986) and Utah (8.8 dams/km; Macfarlane et al., 2017), and more than reported in Oregon (0.14/km; McComb et al., 1990). Beaver dams have likely provided ecosystem benefits including sediment retention (Naiman et al., 1988) and habitat for fish (Kemp et al., 2012) and waterfowl (McKinstry et al., 2001). The difference in dam density across environments is likely related to a range of conditions including vegetation availability and stream-flow characteristics (Macfarlane et al., 2017). For example, spring floods might reduce the number of dams on streams with destructive spring flooding (Collins, 1976). Future research should investigate variables that influence dam density so that the effects of dams on the environment can be better predicted.

Beavers would not have expanded after reintroduction if other habitat features besides willow were not available. We found that beaver colonies settled soon after reintroduction had greater longevity than colonies settled later. We suggest this longevity is associated with beavers first colonizing high-quality habitats (Frantisek et al., 2010) that provide safe access to forage and sites for building beaver structures. For example, we found that long-lived beaver colonies were more likely to be located on or near secondary channels. The affinity of beavers to secondary channels, such as sloughs, has been noted by other researchers (Billman et al., 2012). Sloughs might be attractive to reintroduced beavers because they are slow moving and deep-water bodies that require minimal effort to dam relative to fast-moving water on the main stem of third-order streams. Beaver colonies also might be long-lived on sloughs and other secondary channels because they provide a refugia from spring floods that can destroy beaver colonies on the main stem (Townsend, 1953; Rutherford, 1964; Butler and Malanson, 2005; Andersen and Shafroth, 2010).

Sinuous stream reaches also were associated with long-lived beaver colonies. Sinuous reaches often have enhanced stream depth, especially on the outside of stream bends under cutbanks, that is available without beaver dams and serve as suitable building sites for beaver lodges and caches (Beier and Barrett, 1987; Howard and Larson, 1985; Hartman, 1996). These deep pools might be especially important for colonies after spring floods destroy dams. Moreover, sinuous stream reaches often have abundant willow (Mortenson et al., 2008) and reduced stream velocity (as suggested by Howard and Larson, 1985; Davis et al., 2016), making them suitable sites for building beaver structures compared to straight stream sections. Pools associated with sinuous stream reaches, in addition to deep water on secondary channels (e.g., slough), might be important to the survival of reintroduced beavers before they can build dams (McKinstry and Anderson, 2002). Sinuosity and secondary channels can be identified using a geographic information system (Macfarlane et al., 2017) which reduces the need for extensive field surveys.

Implications

We have shown that beavers can successfully be reintroduced into environments with sub-optimal biological condition but promising site-potential. We hypothesize that beaver activities contribute to improving the quality of the habitats they occupy through their foraging and building activities and can thus be used for the restoration of riparian areas (e.g., Gibson and Olden, 2014; Pollock et al., 2015). The circumstances that lead to successful recovery of riparian vegetation is multifaceted, likely depending on local climates and hydrology, competition with ungulates, and the availability of vegetation. Beavers that exist or are reintroduced into environments where suitable conditions are not available could cause the decline of local vegetation (e.g., McColley et al., 2012). In contrast, we found that willow stands thrived with beaver reintroduction and speculate that low-ungulate populations combined with adequate growing conditions contributed to the recovery of willow stands and their robustness to continued use by beavers. Managers should be aware of these dynamics in watersheds that are targeted for beaver reintroduction.

There are some tools available to managers to reduce the negative effects of overabundant ungulates on riparian areas before beaver reintroduction. In landscapes managed for livestock grazing, managers can exclude livestock from riparian areas before beaver reintroduction to facilitate regrowth of vegetation (Apple, 1985; McKinstry et al., 2001; Small et al., 2016). In Yellowstone National Park, wolf eradication in the 1900's contributed to an increase in ungulate populations that heavily browsed riparian vegetation and contributed to beaver population decline. In response, managers reintroduced wolves in 1995 and 1996 which had positive cascading effects on riparian vegetation and beaver populations (Ripple and Beschta, 2016). In the Absaroka-Beartooth Wilderness, wolf reintroduction to Yellowstone likely suppressed ungulate populations and their effects on riparian environments, but so did the increase in hunting quotas of moose allotted by managers (Tyers, 2003; Smith and Tyers, 2012).

The U.S. Forest Service focused their reintroduction efforts in four meadows along third-order streams where multiple beaver colonies could establish both on the main stem and secondary channels on the floodplain. Beavers expanded from these meadows to 10 additional meadows within 9 years. Because of this process of expansion, managers could save resources by focusing reintroduction efforts in select meadows that can accommodate multiple beaver colonies and which have high-habitat quality (e.g., riparian vegetation, sinuosity, secondary channels). From these locations, beaver populations will likely naturally expand to additional meadows and not require additional reintroductions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2017.12.001.

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