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RESEARCH ARTICLE

Livestock grazing limits beaver restoration in northern New Mexico

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The North American beaver (*Castor canadensis*) builds dams that pond water on streams, which provide crucial ecological services to aquatic and riparian ecosystems and enhance biodiversity. Consequently, there is increasing interest in restoring beavers to locations where they historically occurred, particularly in the arid western United States. However, despite often intensive efforts to reintroduce beavers into areas where they were severely reduced in numbers or eliminated due to overharvesting in the eighteenth and nineteenth centuries, beavers remain sparse or missing from many stream reaches. Reasons for this failure have not been well studied. Our goal was to evaluate certain biotic factors that may limit the occurrence of dam-building beavers in northern New Mexico, including competitors and availability of summer and winter forage. We compared these factors at primary active dams and at control sites located in stream reaches that were physically suitable for dam-building beavers but where none occurred. Beaver dams mostly occurred at sites that were not grazed or where there was some alternative grazing management, but were mostly absent at sites within Forest Service cattle allotments. Results indicated that cattle grazing influenced the relation between vegetation variables and beaver presence. The availability of willows (*Salix* spp.) was the most important plant variable for the presence of beaver dams. We conclude that grazing by cattle as currently practiced on Forest Service allotments disrupts the beaver-willow mutualism, rendering stream reaches unsuitable for dam-building beavers. We recommend that beaver restoration will require changes to current livestock management practices.

Key words: beaver dams, *Castor canadensis*, cattle, competition, habitat requirements, riparian, *Salix*, willow

Implications for Practice

- Dam-building beavers mostly occurred where no livestock grazing was allowed and were rare on Forest Service allotments grazed by cattle.
- Restoration of beavers will require managing livestock grazing in ways that will promote abundant willows.
- On severely degraded or entrenched streams, restoration of riparian habitats and beavers may require additional efforts, such as planting suitable vegetation and installing structures that can help reconnect streams with their floodplains.

Introduction

Riparian corridors serve as "keystone" habitats in arid and semiarid landscapes and they are one of the most productive habitat types in the western United States (Patten 1998; Stromberg et al. 2013). It is estimated that 90% of the original riparian habitat in New Mexico and Arizona has been destroyed or severely degraded (Ohmart & Anderson 1986). In addition, studies have predicted that increases in global temperatures will cause an increase in the intensity of winter flood events and increases in the duration and severity of drought conditions, particularly in the western United States (Seager et al. 2007; Dominguez et al. 2012). Consequently, there is heightened need for methods that will restore riparian habitats and associated aquatic environments, and that will contribute to the resilience of these systems in the face of a changing climate, particularly with respect to water conservation.

Castor canadensis (North American beaver; hereafter beaver) historically occurred in nearly all perennial streams throughout the American Southwest (Weber 1971; Findley et al. 1975). In small- to medium-sized streams beavers construct dams that pond water, which provides concealment cover from predators (Müller-Schwarze & Sun 2003). Beaver dams have far-reaching ecological effects due to factors such as storage of precipitation and seasonal runoff, decrease in stream flow velocity, which results in a decrease of bank erosion, and an increase in nutrient cycling rate (Gurnell 1998; Rosell et al. 2005; Andersen et al. 2011; Pollock et al. 2014). Beavers are also considered a keystone species because their dams cause

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an increase in biodiversity, particularly riparian and aquatic obligates (Naiman et al. 1993; Rosell et al. 2005; Stoffyn-Egli & Willison 2011).

During the eighteenth and nineteenth centuries, beavers were intensively harvested for their pelts, resulting in severely reduced populations and extirpation from many streams (Albert & Trimble 2000; Baker & Hill 2003; Fouty 2003; Carrillo et al. 2009). Although laws have since been enacted to protect beavers from overharvesting and there were intensive efforts to reintroduce populations during the mid 1900s, beaver populations remain low in many regions of the arid west and they have not reoccupied many smaller order streams where they historically occurred (Huey 1956; Baker & Hill 2003). For instance, though historical and current beaver populations are difficult to estimate, it has been estimated that the current beaver population in New Mexico is one sixth the size of the historical population with many stream reaches still unoccupied (Wild 2011; WildEarth Guardians 2013). Reasons why beavers have not recolonized historically occupied streams in the American West have not been well studied. Presumably, this relates to some aspect of habitat quality, given that successful beaver restorations supplemented vegetation or targeted areas with abundant vegetation (e.g. Apple et al. 1985; Albert & Trimble 2000; Pollock et al. 2015). Most studies on habitat requirements of beavers have been conducted in ecoregions with different habitat types than found in the arid west (Baker & Hill 2003). There is increasing interest in restoring populations of dam-building beavers in the western United States because of their positive effects on aquatic and riparian habitats (Keller 2014; Pollock et al. 2014, 2015) and as a means to mitigate impacts of climate change on stream systems and aquatic resources (Hood & Bayley 2008*a*; Bird et al. 2011; Wild 2011; Pollock et al. 2015).

The ability of beavers to build and maintain dams on a stream reach is limited by physical aspects of the reach. Stream flow must be great enough to allow for ponded deep water year-round, but also low enough that dams are not frequently or seriously breached by floods (Macfarlane et al. in press). Thus, prior studies have found that stream gradient, stream order, and bank or valley slope are related to occurrence of beaver dams (Slough & Sadleir 1977; Howard & Larson 1985; Suzuki & McComb 1988; McComb et al. 1990; Barnes & Mallik 1997). The thresholds for these variables are not expected to vary geographically and are difficult or impossible for managers to manipulate.

In contrast, biological factors such as vegetation that influence occurrence of beavers are more easily controlled by management. Beavers are central place foragers and "choosy generalist" herbivores that rely on a few key plant species (Allen 1983; Müller-Schwarze & Sun 2003). Thus, beavers require a suitable plant association in close proximity to the pond, which is used for both food and material to build dams. Herbaceous vegetation constitutes a major portion of beavers' summer diet whereas certain woody species constitute a major portion of their winter diet (Svendsen 1980; Müller-Schwarze & Sun 2003). If suitable herbaceous food plants are limited, then woody species also can become a significant portion of the summer diet (Müller-Schwarze & Sun 2003). Woody species most commonly browsed by beavers in western North America include willows (*Salix* spp.), cottonwoods (*Populus* spp.), quaking aspen (*Populus tremuloides*), and alders (*Alnus* spp.) (Jenkins 1975; Allen 1983; Barnes & Mallik 1996).

Another biological factor that may limit the presence of beaver is competition for shared forage species by other browsers (Brookshire et al. 2002; Hood & Bayley 2008*b*). Ungulate browsing can cause the loss of willows and subsequently beaver from a stream reach. This is true for both livestock and native ungulates such as elk (*Cervus elaphus*), especially when natural predators are missing from ecosystems (Baker et al. 2005; Ripple & Beschta 2012).

Our goal was to identify biotic factors that limit the occurrence of dam-building beavers in northern New Mexico in order to provide guidance to land managers on how they can establish or enhance riparian conditions that will support beavers. Our specific objectives were to determine vegetation required by beaver for summer forage (herbaceous vegetation) and winter forage (select woody species), and to determine the influence of livestock and native ungulates on riparian vegetation and beaver occurrence. We hypothesized that occurrence of dam-building beavers would be associated with certain herbaceous plants, deciduous shrubs and trees, and grazing by livestock and elk.

Methods

Study Site Selection

Our study area was located in north-central New Mexico on lands managed by Carson and Santa Fe National Forests. This region is in the Southern Rocky Mountains. Elevations range from 1,700 to 4,000 m elevation and the Köppen–Geiger climate classification is mostly temperate continental in the mountains and cold semiarid in the surrounding lowlands (Peel et al. 2007). This area was selected because it is public land, and it has the highest density of perennial streams and known active beaver dams in New Mexico (Fig. S1, Supporting Information). However, after we collected data at all known active beaver dams within the study area, we included additional dams on nearby lands managed by the Bureau of Land Management and private land owners in order to increase the sample size. Field data were collected 15 May to 15 August 2013.

We categorized sites as present (i.e. site had an actively maintained primary dam) or absent (i.e. stream reach had physical characteristics to support construction of a beaver dam but none currently occurred). We identified the primary dam by the presence of a lodge or bank den. We determined occupancy of a site by the presence of fresh plant cuttings, fresh mud on the dam, or fresh beaver slides entering and exiting the water. Because the home range of a beaver colony typically occupies 1.0 km or less of stream length (Aleksiuk 1968), we spaced sites no closer than 1.0 km from another site on the same stream, which prevented selection of multiple dams created by one colony as separate sites. Henceforth, we refer to active primary dams as beaver dams.

We used geographic information system (GIS) to identify stream reaches that were suitable for dam construction by beavers based on physical characteristics of the stream, including the presence of perennial water, stream order less than 5, and stream gradient less than 10% (Allen 1983; Beier & Barrett 1987; Suzuki & McComb 1988; McComb et al. 1990). Although beavers prefer lower stream gradients for building dams (e.g. ≤4%; Pollock et al. 2004), we sampled stream gradients of 0–10% to avoid excluding any potential habitat. These data were obtained from the National Hydrologic Dataset *Plus* v.2 database (http://www.horizon-systems.com/nhdplus/). We selected absence sites from within the same biotic community as presence sites, but regardless of grazing policy, based on the national land cover data (v. 2) from the National Gap Analysis Program (http://gapanalysis.usgs.gov/gaplandcover/). Within a stream reach with suitable physical characteristics for dam construction, we located the absence site at the downstream end of the lowest gradient region in order to maintain consistency and because beavers preferentially build dam on the lowest gradient reaches. We collected data at 29 beaver dams and at 28 sites where physical conditions were suitable for construction of beaver dams, but beaver dams were absent.

Field Data Collection

Plots. At each site we established a pair of 200 m primary transects that paralleled the stream (one on either side) and positioned 0.5 m inland from the greenline (i.e. the first vegetation growing next to the water). The dam (or absence site) was located midway along the primary transects. At 40 m increments along the primary transects, we established 80 m secondary transects that extended perpendicular from the primary transect into the uplands. We measured vegetation in 1.5 × 1.5 m–plots along these transects. Plots were located every 20 m along the primary transects to sample the shoreline vegetation. Prior studies have shown that most foraging by beavers occurs within 30 m of water's edge, with 100 m being a typical extreme distance (Allen 1983). Thus, we located plots on the secondary transects 5, 10, 20, and 80 m away from the primary transect. Each site had a total of 68 plots.

Availability of Summer Forage. We considered summer forage for beavers to consist primarily of herbaceous vegetation and leaves and twigs of riparian shrubs (Jenkins 1975, 1979). Beavers also utilize aquatic vegetation for food (Svendsen 1980), but we did not measure this aspect. To estimate the availability of summer forage, we established a 20 × 150 cm Daubenmire frame (Daubenmire 1959) within each plot to measure ground cover of plant groups. The Daubenmire frame was viewed from a 1 m height to estimate cover. Plant groups included sedge (*Carex* spp.), rush (*Juncus* spp.), forb, grass, cattail (*Typha* spp.), field horsetail (*Equisetum arvense*), rose (*Rosa* spp.), redosier dogwood (*Cornus sericea*), willow (*Salix* spp.), quaking aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), alder (*Alnus* spp.), juniper (*Juniperus* spp.), oak (*Quercus* spp.), bare ground, gravel/rock, and an "other" category consisting of ground cover such as woody debris, leaf litter, moss, and fecal piles. Cover classes were 0–5, 5–25, 25–50, 50–75, 75–95, and 95–100%. In addition, we measured two variables that might summarize summer forage availability, vertical cover, which is an estimate of the height of herbaceous vegetation (Robel et al. 1970) and soil moisture, which promotes growth of riparian plants. Vertical cover was measured with a Robel pole placed at the center of every frame and viewed from 1 m height and 4 m distance in two random directions (Robel et al. 1970). Soil moisture was measured within each frame using a soil moisture meter (Lincoln Irrigation Inc., Lincoln, NE, U.S.A.) inserted into the ground circa 115 cm, and ranged from 0 (dry) to 10 (saturated).

Availability of Winter Forage. We considered winter forage for beavers to consist primarily of small diameter (<5 cm) stems of woody plants that are selected by beavers disproportionately more than available (Barnes & Mallik 1996). We identified, counted, and measured the diameter of all woody plant stems (both cut and uncut by beaver) within each plot. We measured the diameter of stems 0.5 m aboveground level, which approximates the height of a foraging beaver (i.e. diameter-at-*beaver*-height; dbh), or at the tip of the ungnawed portion of the stump if it was less than 0.5 m in height.

Competitors. At our study sites, the potential herbivorous competitors of beavers included several species of native ungulates (deer [*Odocoileus* spp.], elk [*Cervus elaphus*]) and livestock (cattle, horse, sheep, American bison [*Bison bison*]; Lucas et al. 2004; Baker et al. 2005). We measured use of sites by ungulates using two methods. First, because livestock grazing is an anthropogenic factor that can occur independent of habitat characteristics, we categorized each site by livestock grazing policy: (1) grazing was not allowed (i.e. no grazing), (2) grazing by cattle was allowed and occurred via a permit within a Forest Service grazing allotment with no special provisions (i.e. Forest Service cattle allotment), or (3) grazing by livestock was allowed but was by species other than cattle (horse or bison), occurred on private land, or occurred on Forest Service land but under special treatment such as a riparian pasture or during short-term (i.e. 5 days) walk-through trailing (i.e. other grazing). Thus, we interpreted sites where grazing was allowed to reflect the potential for relatively long-term use of sites by livestock, regardless of recent unauthorized use by livestock or use by native ungulates. We obtained information on the grazing policy for each site from the land management agency or owner after all field data were collected. Second, we identified and counted all ungulate fecal piles within 1 m of secondary transects (Lancia et al. 2005) and interpreted these data as representative of the intensity of recent use by ungulates, regardless of livestock grazing policy. Fecal pile counts represent an index of relative use of an area by a given species, but counts are not directly comparable among species due to variation in detection, defecation and decomposition rates. Fecal pile counts can be influenced by observer, observation distance, vegetation characteristics, and other factors (Jenkins & Manly 2008). However, we considered our counts to have low observational bias because two observers made the counts and we only counted fecal piles in very close proximity (<1 m) to the transect line (Jenkins & Manly 2008).

Statistical Analysis

Analyses were performed using SAS 9.4 (SAS Institute, Cary, NC, U.S.A.) and Minitab 17 (Minitab Inc., State College, PA, U.S.A.). A change in field data collection methods resulted in missing data for four summer forage availability variables (percent cover of willow, alder, cottonwood, and aspen) at five sites; we imputed the missing data using linear regression. We calculated riparian width, which was tested as a potential confounder, by identifying the presence of hydrophilic species (e.g. sedge, rush, willow) in all plots on secondary transects; distances of these plots from the primary transect were averaged for the site. We used the midpoints of the cover classes to determine percent cover of plant groups for each plot. We averaged across all plots within each site to obtain site-level variables for analysis, except for fecal counts, which were averaged across all secondary transects, and livestock grazing policy, which was categorical. We tested data for normality with Kolmogorov–Smirnov tests. We tested variables for differences between presence and absence sites using two-tailed *t*-tests for normally distributed variables and Mann–Whitney *U*-tests for non-normally distributed variables (Table S1).

Grazing by livestock and native ungulates can have a strong influence on the composition and structure of riparian vegetation (Kauffman et al. 1983; Singer et al. 1994; Brookshire et al. 2002; Holland et al. 2005; Batchelor et al. 2014). Consequently, we explicitly considered competitor variables as potential confounders on the relations between plant variables and presence or absence of beaver dams. Confounding occurs when the relation between the plant variable and presence or absence of a beaver dam is distorted by a third variable (i.e. a competitor) that is associated with both the plant variable and the presence or absence of a beaver dam. We evaluated the extent of confounding by grazing policy on each vegetation variable by calculating the percent change in the odds ratio of the crude relation and the odds ratio of the adjusted relation when controlled for grazing policy (Rosner 2000); we considered a 10% change to indicate significant confounding (Greenland 1989).

We developed logistic regression models to predict presence or absence of beaver dams based on each of the biotic driver categories (i.e. competitors, summer forage availability, winter forage availability). For developing the competitor and summer forage availability models, the initial pool of variables included those that were significant at p less than or equal to 0.20 in the univariate tests. Because we had data on stems that were both cut and uncut by beavers, for the winter forage availability model, we used a different process to narrow the suite of variables to only species that were selected by beavers. Using data only from presence sites, we calculated diet selection using a standardized resource selection index B, which is a probability ranging from 0 to 1 that a food item will be selected if all types are equally available (Manly et al. 2002): for each of the 21 available woody plant species, $B = \left(\frac{u}{a}\right)/\Sigma\left(\frac{u}{a}\right)$, where u is the proportion of cut stems and a is the proportion of cut plus uncut stems. Selection for or against a plant is indicated by a value of B greater or less than 0.048 respectively (i.e. $1/n$ where $n = 21$, the number of available small diameter woody plant species; Manly et al. 2002).

Our modeling followed the "purposeful selection" approach of Bursac et al. (2008). Purposeful selection allows for variables known to be biologically important to be tested during model development, that otherwise would be removed from consideration due to statistical insignificance (Bursac et al. 2008). Although multimodel inference and information theory have become a favored approach in the analysis of ecological data (Burnham & Anderson 2002), we considered purposeful selection a superior method for these analyses because it allowed us to identify and incorporate variables that had a confounding effect on statistically significant variables. This permitted explicit inclusion of the most influential competitor variables as potential confounders within the vegetation models. First, a logistic regression model was created that used the initial pool of variables (plus potential competitor confounders) for each biotic driver category. The variable with the highest p was removed and a new model constructed based on the remaining variables. We evaluated significance at p greater than or equal to 0.10 due to small sample sizes and large variation inherent to natural communities. Thus, variables were removed in this way until no variables remained with p greater than or equal to 0.10. During this process of variable removal, we tested each removed variable to determine if it was a confounder on the remaining variables. Bursac et al. (2008) recommended identifying a variable as a confounder if, when the variable of interest was removed, the beta coefficient of any of the remaining variables in the model changed by more than 15–20%. We used a more stringent criterion, requiring a 25% or greater change in the beta coefficient; this assured we identified only the most strongly confounding variables. Variables found to be confounders were retained. Secondly, variables that did not make the initial pool of variables (i.e. p greater than or equal to 0.20 in univariate tests for the summer forage availability and competitors models; woody species unused or avoided by beaver for the winter food availability model) were included in the model one at a time in order to determine if the variable became significant ($p < 0.10$) in the presence of the other variables. Any variables identified as significant were retained and the iterative process was repeated for the variables added. Lastly, a final global model was created using the same iterative process of purposeful selection, but utilizing the final variables in each of the biotic driver models as the initial pool of variables. We tested select interactions with livestock grazing policy in the final global model including percent ground cover by grasses, forbs, and willows, and number of willow stems in the regeneration size class (dbh < 5 cm). Due to the potential for issues with multicollinearity, we required that all variables in final models have a variance inflation factor ≤ 2.5 (Allison 1999).

Results

The final model of competitors contained only livestock grazing policy (Table 1). Odds of an active beaver dam at sites with no grazing was 37.3 (90% CI [8.76, 159.11]) times the odds at

Table 1. Coefficients of determination, beta coefficients, odds ratios, and *p*-values for the biotic driver models and the final global models at sites with an active beaver dam present ($n = 29$) or absent ($n = 28$). [a]Non-significant variables in univariate testing: elk (*Cervus elaphus*), deer (*Odocoileus* spp.), American bison (*Bison bison*), horse (*Equus caballus*). [b]Significant variables removed during multivariable testing: bare ground/rock, percent rush (*Juncus* spp.), percent cattail (*Typha* spp.; non estimable), percent oak (*Quercus* spp.; non-estimable), percent cottonwood (*Populus* spp.), percent redosier dogwood (*Cornus sericea*; non-estimable), mean vertical cover, soil moisture, riparian width. [c]Non-significant variables in univariate testing: percent field horsetail (*Equisetum arvense*), percent juniper (*Juniperus*), percent sedge (*Carex* spp.), percent grass, percent forb, percent rose (*Rosa* spp.), percent alder (*Alnus* spp.), percent quaking aspen (*Populus tremuloides*). [d]Riparian width was tested as a potential confounder. [e]Significant variable removed during multivariable testing: redosier dogwood (non-estimable). [f]Canopy cover and riparian width were tested as potential confounders; juniper stems and oak stems were tested for significance in the final winter forage model. [g]NE indicates a non-estimable value (>999.99) due to the narrow range of sampling. [h]Retained as a confounder on other grazing policy.

Model	r^2	Beta Coefficient	Standardized Beta Coefficient	Odds Ratio	90% Confidence Interval	p Value
Competitor[a]	0.384					
Grazing policy						<0.001
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		2.86	—	17.50	4.29–71.41	0.001
No grazing		3.62	—	37.33	8.76–159.11	<0.001
Competitor (without livestock grazing policy)	0.173					
Cattle fecal piles		−0.25	−0.605	0.78	0.67–0.91	0.007
Summer forage[b,c,d]	0.421					
Percent willow (*Salix* spp.) ground cover		0.76	0.570	2.13	0.97–4.68	0.114
Grazing policy						0.004
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		2.53	—	12.62	2.95–53.94	0.004
No grazing		2.77	—	15.91	3.23–78.28	0.004
Winter forage[e,f] (=global model A)	0.614					
Willow stems		1.12	2.866	3.07	1.45–6.47	0.014
Alder (*Alnus* spp.) stems		3.02	0.951	20.43	2.20–190.11	0.026
Quaking aspen (*Populus tremuloides*) stems		8.78	1.365	NE[g]	12.77–NE	0.021
Cottonwood (*Populus* spp.) stems		5.64	1.460	282.27	3.20–NE	0.038
Boxelder (*Acer negundo*) stems		5.15	0.390	172.57	0.07–NE	0.277[h]
Grazing policy						0.032
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		5.67	—	291.18	8.23–NE	0.009
No grazing		1.13	—	3.10	0.16–59.79	0.530
Global model B	0.526					
Percent willow (*Salix* spp.) ground cover		1.07	0.810	2.93	1.19–7.22	0.050
Alder (*Alnus* spp.) stems		2.12	0.668	8.33	1.52–45.77	0.041
Quaking aspen (*Populus tremuloides*) stems		4.18	0.650	65.50	1.62–NE	0.063
Cottonwood (*Populus* spp.) stems		2.50	0.646	12.17	1.27–116.42	0.069
Grazing policy						0.011
Forest service cattle allotment		Referent	—	—	—	—
Other grazing		3.64	—	37.96	4.79–300.71	0.004
No grazing		3.69	—	39.89	3.78–421.34	0.010

sites in Forest Service cattle allotments and the odds of an active beaver dam at sites in other grazing was 17.5 (90% CI [4.29, 71.41]) times the odds at sites in Forest Service cattle allotments. In order to determine which species of competitors were most influential, we fit a second model that excluded livestock grazing policy. This model contained only cattle (Table 1). The odds of an active beaver dam decreased by 22% (odds ratio = 0.78, 90% CI [0.67, 0.91]) for each increase of 1 in the mean number of cattle fecal piles on transects. Thirteen of 27 variables were significantly different ($p \leq 0.1$) among sites that differed by livestock grazing policy (Table S2), such that sites where livestock grazing was allowed, particularly within Forest Service cattle allotments, often resembled upland communities (Fig. 1). In addition, livestock grazing policy had a confounding effect on 15 out of 23 estimable variables (Table S3). Consequently, livestock grazing policy was tested within the summer and winter forage availability models.

The summer forage availability model reduced to one that contained only livestock grazing policy. However, the penultimate model, which also contained percent ground cover by willow ($p = 0.114$) had a lower deviance (47.78 versus 61.41) and hence was selected as the final summer forage model (Table 1). The odds of an active beaver dam increased by 113% (odds ratio = 2.13, 90% CI [0.97, 4.68]) with every 1% increase in mean willow ground cover per plot (Table 1).

Beavers selectively cut stems from six species of woody plants, including willows, alders, quaking aspen, cottonwoods, boxelder, and redosier dogwood (Table 2). The final model for winter forage availability contained livestock grazing policy and all of these plants except redosier dogwood, which could not be modeled because it did not occur at Forest Service

Figure 1. Photo of a reach of the Rio de las Vacas (English translation: River of Cows), Sandoval County, NM, U.S.A., where livestock grazing is allowed and beaver dams are absent (top); photo of a reach of the Rio Grande del Rancho, Taos County, NM, U.S.A., where livestock grazing is not allowed and beaver dams are present (bottom).

cattle allotment sites (Table 1). The standardized beta coefficients indicate that willow was the strongest contributor to this model (Table 1). The odds of an active beaver dam increased 207% (odds ratio = 3.07, 90% CI [1.45, 6.47]) for every one stem increase in mean willow per 1.5 m^2 plot and increased 1,943% (odds ratio = 20.43, 90% CI [2.20, 190.11]) for every one stem increase in mean alder per 1.5 m^2 plot; odds ratios for quaking aspen, cottonwood, and boxelder were high but had non-estimable confidence intervals (Table 1).

Due to a strong correlation ($r_s = 0.846$) between willow stems and percent willow ground cover, we developed two separate global models that each deleted one of these variables from the final pool of variables derived from the final biotic driver models. When percent willow ground cover was deleted, the final global model (A) was the same as the winter forage model. When willow stems was deleted, the final global model (B) contained livestock grazing policy, percent willow ground cover, and stems of alder, quaking aspen, and cottonwood. The odds of an active beaver dam increased 193% (odds ratio = 2.93, 90% CI [1.19, 7.22]) for every 1% increase in mean willow ground cover per plot, increased 733% (odds ratio = 8.33, 90% CI [1.52, 45.77) for every one stem increase in mean alder per 1.5 m^2 plot, and increased 1,117% (odds ratio = 12.17, 90% CI [1.27, 116.42) for every one stem increase in mean cottonwood per 1.5 m^2 plot; the odds ratio for quaking aspen was high but the confidence interval was not estimable (Table 1). Willow was the strongest contributor to this model. However, the winter forage model ($r^2 = 0.614$) provided a stronger fit of the data compared to global model B ($r^2 = 0.526$) and hence was the overall best model.

Discussion

The sparse occurrence of beaver dams found during our study was in stark contrast to the widespread historical distribution and abundance of beavers along most perennial streams in New Mexico (Bailey 1931; Weber 1971; Findley et al. 1975). Our spatial model predicted 3,021 km (1,813 miles) of streams on federal public lands in New Mexico with potentially physically suitable characteristics for the construction of beaver dams. However, although we undoubtedly overlooked some beaver dams, we found only 38 active primary beaver dams occurring on public lands in the entire state of New Mexico. Given that on average a single beaver colony occupies 1 km of stream

Table 2. Availability (*a*), utilization (*u*), and standardized resource selection index (*B*) for small diameter (<5 cm) woody plant species used as winter forage at sites with an active beaver dam ($n = 29$). [a]Selection for or against a plant is indicated by a value of *B* greater or less than 0.048, respectively. [b]Species not used by beavers: juniper (*Juniperus* spp.), pine (*Pinus* spp.), spruce (*Picea* spp.), fir (*Abies* spp.), Rocky Mountain maple (*Acer glabrum*), mulefat (*Baccharis salicifolia*), snowberry (*Symphoricarpos oreophilus*), Russian olive (*Elaeagnus angustifolia*), New Mexico locust (*Robinia neomexicana*), chokecherry (*Prunus* spp.), rose (*Rosa* spp.), gooseberry (*Ribes* spp.), and elm (*Ulmus* spp.).

Plant Species	*Proportion Available (a)*	*Proportion Utilized (u)*	*Standardized Resource Selection Index (B)*[a]	*Selection Relative to All Species*[b]
Cottonwood (*Populus* spp.)	0.037	0.054	0.209	Positive
Alder (*Alnus* spp.)	0.069	0.085	0.179	Positive
Willow (*Salix* spp.)	0.711	0.820	0.166	Positive
Boxelder (*Acer negundo*)	0.006	0.006	0.132	Positive
Quaking aspen (*Populus tremuloides*)	0.013	0.012	0.131	Positive
Redosier dogwood (*Cornus sericea*)	0.019	0.015	0.114	Positive
Big sagebrush (*Artemisi tridentata*)	0.007	0.003	0.053	Neutral
Oak (*Quercus* spp.)	0.035	0.004	0.017	Avoid

(Aleksiuk 1968), the estimated colony density of dam-building beavers was 0.01 per km of physically suitable stream reaches on public lands in New Mexico. Another recent study also found beavers to be absent from many streams predicted to be suitable in New Mexico (WildEarth Guardians 2013). In contrast, reported colony densities on streams in other areas of North America range from 0.63 to 1.90 per km (Pollock et al. 2015). Our results suggest that the widespread absence of beaver in our study area was due to the widespread absence of adequate riparian vegetation and that the absence of adequate riparian vegetation was associated with livestock grazing, particularly as typically occurs on Forest Service cattle allotments.

In our study, beavers selected several species of deciduous woody plants, including alders, boxelder, cottonwoods, quaking aspen, willows, and redoiser dogwood. Other studies also have regarded these species, especially trees in the genus *Populus* (i.e. cottonwoods and quaking aspen), as preferred forage for beavers, and these are some of the few deciduous species that occur in the arid west (Pollock et al. 2015). However, we found willows to be the most important plant for occurrence of beaver dams in our study. In contrast, other studies often identify other species of deciduous shrubs and trees as more important to beavers than willows (e.g. Müller-Schwarze & Sun 2003). For instance, in eastern North America where there is relatively high diversity of deciduous trees and shrubs, beavers selectively forage on a wide range of other deciduous species, typically preferentially to willows (Fryxell & Doucet 1993; Doucet et al. 1994; Gallant et al. 2004). In those systems, high woody plant diversity may buffer competition between beavers and ungulates for overlapping resources (Hood & Bayley 2008*b*). In contrast, in the arid west there are fewer species of deciduous trees and shrubs, which places relatively greater pressure on the few species present. Although other species might be preferred more than willows, we attribute the overriding importance of willows in our study to the relative scarcity of other species in our study area. For instance, willows represented 71.1% of available woody stems found at dam sites, whereas alders, boxelder, cottonwoods, aspen, and dogwood accounted for less than 15% of available woody stems combined.

In western North America and other locations, beavers and willows exhibit a mutualism wherein beavers are benefitted via the food and building material provided by willows whereas willows benefit from beavers via the increase in wetland area created by dams, vigorous resprouting stimulated by beaver foraging, and reproduction of limbs cut by beavers (e.g. Kindschy 1989; Peinetti et al. 2009). However, browsing on willows by livestock or native ungulates can disrupt this mutualism by causing a decrease in willow biomass and thus a decrease in the suitability of an area for beavers (Kindschy 1989; Singer et al. 1994; Brookshire et al. 2002; Baker et al. 2005, 2012). Studies in national parks where livestock are not allowed found that elk are capable of disrupting the beaver-willow mutualism (Baker et al. 2005, 2012; Ripple & Beschta 2012). In contrast, in our study elk fecal piles were not an important predictor of beaver dam occurrence, and they were not highly correlated with any vegetation variable. In Yellowstone National Park, it was not until gray wolves (*Canis lupus*) were restored that woody species such as willow, aspen, and cottonwood showed an increase in growth rate and height (Ripple & Beschta 2012). Baker et al. (2012) found that in a simulated montane willow ecosystem within Rocky Mountain National Park, beavers persisted indefinitely when elk density was less than or equal to 20 elk per km^2 and persistence decreased exponentially as elk density increased beyond 30 elk per km^2. In contrast, the north-central elk herd in New Mexico has an estimated mean density of 2.2-2.3 elk per km^2 (N.A. Quintana 2015, New Mexico Department of Game and Fish, personal communication). Although density estimates are imprecise and locally higher densities occur in more favorable habitat and during certain seasons, the current estimated density of elk in most of our study area was well below the threshold found by Baker et al. (2012). Thus, we suggest that competition for willow by cattle and beaver is the likely mechanism that explains our statewide and regional patterns of beaver exclusion where grazing policies allow unrestricted access of cattle to riparian areas.

In conclusion, we found that beaver dams were exceptionally rare on public lands managed for cattle grazing. Large numbers of cattle and other livestock were first introduced to northern New Mexico by Spanish explorers and colonists during the late sixteenth century, predating even the establishment of the first English colony (Jamestown) along the eastern seaboard (Bowling 1941). In contrast, although cattle were introduced to some localized areas of southern Texas, Arizona, and California during the seventeenth and eighteenth centuries, cattle did not reach most parts of the West until the open range cattle boom, which followed the Civil War and expansion of the railroad system during the mid to late nineteenth century (Love 1916). Thus, livestock have been part of the landscape of northern New Mexico for circa 300 years prior to their introduction to many other regions of the West. Given the long period of time that livestock grazing has occurred in northern New Mexico, this region could serve as a harbinger for potential future conditions in other arid regions of the western United States, unless efforts are made to prevent and reverse any long-term detrimental effects of livestock grazing on riparian habitats.

Our results indicate that reestablishment of beavers in northern New Mexico, and likely elsewhere in many areas of the arid montane west where livestock management is similar, must involve the restoration of riparian woody plant communities, especially abundant willows. However, our results suggest that restoration of willows will often require changing grazing management. The net impact of cattle grazing on riparian habitat is a function of the number of cattle and timing of grazing. In our study area, most Forest Service cattle allotments have utilization rates for the uplands based on the conservative grazing intensity guidelines of Holecheck and Galt (2000) with use during the growing season (generally May or June depending on elevation through mid-October). Riparian zones within these allotments usually are not fenced and have no special grazing management other than a designated herbaceous utilization rates, typically 10 cm stubble height (F.E. Cortez 2016, Carson National Forest, personal communication). Rest may be used to offset adverse conditions or overutilization. However, in degraded habitats (such as found throughout most our study area) it may require more than a decade of nonuse to initiate recovery (Belsky et al. 1999). Consequently, complete removal of livestock from riparian zones, either via fenced exclosures or closing grazing allotments, is recommended to improve riparian habitats (Belsky et al. 1999). Indeed, the success of exclusion at restoring willows and other riparian vegetation is well-documented (e.g. Rickard & Cushing 1982; Schulz & Leininger 1990; Case & Kauffman 1997; Belsky et al. 1999; Brookshire et al. 2002; Hough-Snee et al. 2013).

The use of alternative controlled grazing strategies to benefit riparian habitats is generally less understood, more variable, and may not result in as much recovery as exclusion (e.g. Lucas et al. 2004). Cattle grazing during the mid- to late-growing season is particularly harmful to willows because grasses become less palatable than willows as they mature (Kovalchik & Elmore 1992; Pelster et al. 2004). Pelster et al. (2004) found that in willow-sedge habitats during fall, willows comprised greater than 20% of steer diets even at low utilization rates (15%; stubble height = 37 cm). They suggested that stubble height ≥ 20 cm may be necessary to minimize willow consumption by cattle in Rocky Mountain willow-sedge communities (Pelster et al. 2004). However, similar research has not been conducted in other riparian habitats. Consequently, cattle grazing restricted to the spring period, with close monitoring of utilization, may reduce browsing on willows, albeit less so than exclusion (Clary 1999; Pelster et al. 2004; Booth et al. 2012). More recently, Freitas et al. (2014) found that tightly controlled grazing based on riparian standards (herbaceous utilization < 35%, willow utilization < 20%, and streambank damage < 10%) resulted in similar response of riparian habitats in comparison to allotments not grazed for 10 years. However, controlled grazing strategies require more intensive management, such as use of smaller fenced riparian pastures and herding to improve livestock distribution and rotation, and adaptively variable timing of rest and grazing (Kovalchik & Elmore 1992; Freitas et al. 2014; Swanson et al. 2015). Furthermore, it remains largely unknown to what extent controlled grazing can reverse already degraded conditions over the long term, especially given that restoration of willows may lag behind other species even with exclusion (Hough-Snee et al. 2013). For streams that are highly degraded or incised, restoration also may require planting and protecting willows, in conjunction with other techniques to restore more natural hydrologies and floodplains, such as the use of beaver dam analogs and other instream structures (Dreesen et al. 2001; Hall et al. 2011; Hough-Snee et al. 2013; Pollock et al. 2015). Until livestock grazing is managed in a way that produces adequate amounts of willow growth, the restoration of dam-building beaver is not likely to be possible in many areas.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Data on variables at sites with an active beaver dam present ($n = 29$) or absent ($n = 28$).
Table S2. Data on variables at sites with different livestock grazing policy.
Table S3. Evaluation of grazing policy as a confounder on the relationship between vegetation variables and the presence or absence of an active beaver dam.
Figure S1. Locations of active primary dams created by the American beaver (*Castor canadensis*) on public lands in New Mexico during 2013 (green circles).

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