

Effects of Wolf Reintroduction on Plant Communities in the American West

Roy Moger-Reischer

Abstract

Gray wolves (Canis lupus) have been reintroduced in Yellowstone National Park after a seven-decade period of extirpation. Elk (Cervus canadensis) populations have declined in response, but the extent of cascading effects to plants are more recondite. This literature review finds that while eventual recovery of aspen (Populus tremuloides) is a probable consequence of wolf reintroduction, the recovery patterns of three other categories—willow (Salix spp.), cottonwood (Populus spp.), and berry-producing shrubs—are more complicated. The latter three groups are limited by various factors in addition to elk herbivory, from stream hydrology to browsing by bison (Bison bison). Less-obvious, additional factors such as these should be a consideration in any long-term plant management undertakings in future.

1. Introduction

Wherever they settle, humans have long been altering native animal populations, in turn changing food webs and species interactions. Historically, the largest fauna have been hit hardest by human activity, and more recently top predators in particular have been targeted for persecution (Sandom et al. 2014; Ripple et al. 2012). Loss of top predators from ecosystems has resulted in degradation thereof in numerous instances and across many biomes (Estes et al. 2011). Predators influence prey behavior and density, in turn affecting herbivores' top-down control of plant communities (Fortin et al. 2005; Carpenter et al. 2008). Horizontal interactions among apex predators can be complex, ranging from shared niches to niche exclusion (Bartnick et al. 2013). Large predators can limit densities of smaller predators; loss of mid-level predators can lead to mesopredator irruptions (Ritchie and Johnson 2009). Yet the strength of top-down control by large terrestrial mammalian predators is a subject of ongoing debate (Ripple and Beschta 2007; Tveraa et al. 2007). Extirpation (local extinction) of wolves in Yellowstone National Park in early 20th century and wolves' subsequent reintroduction seven decades later in 1995-1996 provides an excellent natural experiment to help understand just how heavily an ecosystem is shaped by its top predator, and whether restoration of a top predator can effectively restore an entire ecosystem to its historical state.

Yellowstone National Park (YNP) lies in the American West, where the Greater Yellowstone Ecosystem is one of the largest remaining nearly intact northern temperate ecosystems in America (Schullery 2006). It comprises nearly sixty mammal species and more than 1,700 vascular plant species (“Yellowstone Fact Sheet”). It was clear that the extirpation of wolves altered interactions among these denizens. Ungulate populations, especially elk (*Cervus canadensis*), irrupted. Herbivory on willows, aspen, and cottonwoods increased in turn (Singer, Mark, and Cates 1994; Mech and Peterson 2003; Beschta 2005; Ripple and Beschta 2012). Beaver (*Castor canadensis*) were outcompeted for willow resources, and many dams were abandoned (Wolf et al. 2007). Coyote populations irrupted and some populations of their leporid (rabbits and hares) prey dropped dramatically (Ripple et al. 2013; Berger 2008). Cougars were released from competition, and their predatory niche expanded (Bartnick et al. 2013). Data on the cascading effects of wolf extirpation are abundant and well-documented.

Scientific controversy arises more readily when the efficacy of wolf *reintroduction* questioned. Mech (2012) is especially critical of people—scientific, popular media, and lay communities alike—who lionize the wolf as the alpha and omega of ecosystem restoration in the American West. Mech argues that ecosystem recovery is far more complex than advocates of reintroduction believe. There are many climate change processes at play, and wolf extirpation may be a hysteretic one, such that its changes are not reversible by the same pathway along which they occurred. Taking the historical pre-extirpation Greater Yellowstone Ecosystem to be a stable state, we can investigate whether, during the lengthy extirpation period, alternative *stable* states took hold.

Wolf reintroduction is an obvious and necessary step toward restoration of an historical ecosystem state. The efficacy of reintroduced wolves to decrease elk population densities is well supported by population surveys. Elk population in YNP decreased from > 15,000 individuals before wolf reintroduction to around 5,000 individuals by 2010 (White et al. 2012). Plants, however, are a full trophic level further removed from wolves—evidence for plant recovery from the potentially stable alternative state is more controversial. During the wolf extirpation period, riparian willow, aspen, and cottonwood communities declined by an estimated 50% in Yellowstone National Park (Chadde & Kay 1991). Restoring the

historical ecosystem in YNP will require restoration of these three types of trees. I assess the effectiveness of wolf reintroduction on each of these three in the following sections of this paper. I also investigate the effects on berry-producing shrubs, a less well-studied plant group.

The primary objectives of this paper, then, are to 1) assess the effects of wolf reintroduction on several plant categories and 2) for cases in which wolf reintroduction appears insufficient, examine further management steps. In this paper I show that wolf reintroduction alone is rarely sufficient, because there are various additional factors which contributed to establishment of hysteretic alternative stable states.

2. Wolf Effects on Willow (*Salix spp.*)

Riparian willow communities were depleted by ungulate irruption. There is a definitive threshold height willows must achieve if they are to recover: 2 meters, above which the stems are out of reach of browsing elk (Marshall et al. 2013). This ensures willow establishment in the following year (Keigley, Frisina, and Fager 2002). The threshold height has significance for beaver populations, which need willows for forage and for dam-building material (Wolf et al. 2007). The 2 m threshold is important because dam construction requires tall trees (Baker et al. 2005). During the wolf extirpation period, beaver were outcompeted by ungulates for willow resources, and many dams were abandoned (Wolf et al. 2007).

Wolf et al. (2007) investigated the possibility of an alternative stable state whereby loss of beavers might hamper the ability of willow stands to reach the threshold height. As the authors explain, riparian willows are inextricably dependent on hydrology and streamflow. Beaver dams, or lack of them, alter hydrologic regimes. A beaver dam forms a pond. Beavers maintain the dam until they deplete the local environment of tall willows, then move on. The pond drains, leaving behind fine wet sediment—perfect willow establishment conditions. When the new stand of willows grows beyond 2 m, it can again support beavers. The dam is rebuilt, and the dynamic of pond formation and drainage continues, maintaining both species in a sustainable way. Wolf et al. described this mutualistic historic state as beaver-willow state. The alternative state is designated elk-grassland state, wherein riparian willow stands have become de-

pleted and isolated, and beavers are absent. They proposed that elk-grassland state could be stable and resilient to wolf reintroduction because of a “Catch-22” whereby willows do not reestablish without the favorable conditions created by beaver dams, and beavers do not rebuild dams because adequate materials are not available. The Catch-22 hinges on channel incision. When a beaver dam is abandoned, it takes ~30 years for the released stream to cut into a new bed and lower its elevation. At this point upland plants invade, displace willow, establish the elk-grassland state, and render conditions unfavorable for either beavers or willows to return. Hence, it is proposed that the elk-grassland state is hysteretic: a return to the beaver-willow state could not be achieved simply by reversing the pathway (i. e. reintroducing wolves). Even if some willows grew taller than the 2 m threshold they would be too sparse to support reestablishing beavers.

Wolf et al. tested which climate factors were most closely associated with decline and establishment of willows, and explored whether ecosystem recovery is possible. They studied four streams that had historically (until the early 20th century) been dammed by beavers in Yellowstone National Park’s northern range. 78 willow individuals were included in their analyses.

Analysis of timing of willow establishment found recently-established willows to be vastly underrepresented. Wolf et al. measured the ages of the 78 sample willows and compared their age distribution to a model generated for a stable population containing one 86-year-old individual, the age of the oldest tree in the sample. For all years after 1940, willows established much less frequently than for a predicted stable population. What is in my opinion most telling with regard to wolves is that the underrepresentation of willow individuals was greatest in the most recent years—including the decade since reintroduction of wolves. The authors found that at least one willow tree established in all years 1935 – 1956 except for one four-year period (1931 – 1934) and one five-year period (1984 – 1988) of particularly dry conditions. In addition, two of the climate-derived hydrologic variables in their nonlinear Poisson regression model had significant predictive ability for willow establishment. These were i) precipitation in the year following establishment (positive correlation) and ii) mean annual Yellowstone River discharge in the establishment year plus the previous four years’ discharge (negative correlation). The authors pro-

posed that predictive ability comes from describing willow establishment at the end of a drought followed by a wet year. This makes sense—there would be low establishment during a roughly four-year drought (small discharge); when a high precipitation year finally arrived, willows having established the year prior could grow quickly when intraspecific competition was lower. Still, the best model explained only 11% of variation in willow establishment, so climate hydrology was probably not the main limiting factor for willow establishment.

Thus climate factors can influence willow establishment, but only marginally. Still, the strength of beaver hydrology effects has yet to be examined. To investigate how willow establishment correlated with damming by beavers, the scientists measured sediments. They created artificial beaver dams, and analyzed the sediment signature in the resulting ponds and in one natural beaver. Willows established in sediments with fineness signature \geq the pond sediment were denoted pond willows ($n = 38$); those established in coarser sediments where water flowed reliably were denoted alluvial willows ($n = 32$). Only one of the alluvial willows established prior to 1943. Either i) only a tiny proportion of establishing willows did so in alluvial sediment in those years or ii) alluvial willows are shorter-lived than pond willows—either way, pond willows were more successful at long-term establishment. Significant trends through time were found for alluvial willows: In later years, establishment elevation and distance with respect to stream decreased.

The trends make sense in light of wolf extirpation. Historically, beaver dams would have created wide valleys of accumulated fine-grained sediment (“beaver meadows”) highly suitable for willows. The removal of wolves and ensuing trophic cascade in the 1920s led to abandonment of beaver dams. The dams began to degrade and within a few decades stream incision would occur. What had once been areas with fine sediment were now high-energy streams. Floodplains with shallow historical water tables now had deep water tables. The high-elevation willow establishments in the 1940s and 1950s imply that stream channels were higher at that point, and the declining elevation of alluvial willows supports this. Moreover, the scientists found *no* willows established on pond-like sediment subsequent to 1989—these most-optimal establishment sites are disappearing, and only physiologically stressful ones remain availa-

ble. And as Wolf et al. have observed, upland plants are now invading the formerly riparian floodplains, bringing about the elk-grassland state. Thus it appears that stream incision, which removes the pond-like sediments, is the point of no return for shifting ecosystem state.

Marshall et al. (2013), too, investigated a potentially stable alternate hydrologic state for willow and beaver. Specifically, they asked if wolf reintroduction alone was enabling willows to reach the threshold height of 2 m, or whether presence of beavers was also a necessary condition. They measured changes in willow height over a span of ten years (2001 – 2010) on YNP’s northern range. They used a factorial design with four treatment combinations. For herbivory intensity, willows were either “browsed” (control) or “unbrowsed” (2.4 meter-high fencing erected to exclude ungulates). For the water table depth variable, plots were either “undammed” (control) or “dammed” (artificial dams constructed)—water table levels were a mean 33 cm deeper in undammed plots. Marshall et al. gathered height and biomass data for an additional 164 naturally established willows in their study area as a control. The probability distribution of on-plot control treatment willow height closely matched that for the 164 trees growing at other locations, indicating that the study results were an accurate representation of height outcomes.

Only willows in the dammed, unbrowsed treatment plot reached the 2 m threshold height within the duration of the study. Neither the dammed nor the unbrowsed condition alone allowed sufficient growth. The effects of the treatments were additive (no interaction effect). Willow biomass did not respond to browsing treatment, but was significantly different between dammed and undammed treatments—with browsing treatment held constant, biomass was 90% greater for dammed plots. Dammed vs. undammed condition had a large effect on height, too, with dammed trees being about 40% taller than undammed when browsing treatment was held constant.

The situation may not be as dire as the authors present it to be. While the effect of browsing treatment on undammed willows was small, unbrowsed willows *were* taller. Unbrowsed, undammed willows had mean height 160 cm (95% prediction interval: [138, 185]), while browsed, undammed reached 117 cm (95% prediction interval: [105, 131])—43 cm shorter. Significantly, the prediction intervals do not overlap. Moreover, the height-through-time trends give me cautious optimism for undammed, un-

browsed willow. Only dammed, unbrowsed willows reached a mean height of 2 m. Yet, mean heights for all treatment types increased over the study decade. Dammed, browsed trees improved from ~100 cm to ~170 cm on average; for undammed, unbrowsed plots the increase was from ~85 cm to ~155 cm. Height increase through time was roughly linear, and if the pace continues, then the average height of undammed, unbrowsed willows will reach the 2 m threshold within the next decade. However, Marshall et al. do note that height distribution of the 164 offplot trees had not changed substantially since a census taken in 1990. This probably reflects the fact that even with wolves present, elk are not 100% excluded from browsing willows. Only time will tell if the subsequent decade does bring veritable improvement.

The two above studies imply that damage to willow populations has so far been resilient to reintroduction of wolves. The altered hydrology regime in the elk-grassland state is not reversible by reduction in browsing alone. Willows are not establishing at historical rates. While the Marshall et al.'s height trendline through time gives hope for willows eventually reaching threshold height, willow density may still not be sufficient for beaver recovery (Wolf et al. 2007). Other management options should be considered. The most auspicious option would be construction of artificial dams in strategically chosen streams with historical beaver activity, coarse sediment, and where water table is ≥ 1 meter deeper than the historical level. In synergy with wolf reintroduction, this would improve willow establishment opportunities. Wolf et al. also suggest fencing of riparian zones, but I argue that this would be imprudent. We have seen that reduced browsing is an insufficient condition for willow recovery at substantial density or within a 10-year timeframe. Moreover, whereas artificial dams could serve as a starting point for beavers to build natural ones, fencing would be more liable to *inhibit* beaver activity, in addition to generally disrupting natural dispersion of wildlife.

There is another potential top-down culprit for lack of willow recovery in response to wolf reintroduction: Painter and Ripple (2012) investigated whether a separate trophic cascade was occurring in the Lamar Valley in the Greater Yellowstone Ecosystem's northern range. Here, reintroduced wolves have suppressed elk, which in turn releases bison (*Bison bison*) from competition. Since 2005, the decrease in elk has coincided with an increase in bison density (Beschta and Ripple 2014). More abundant

bison could then browse more heavily, hindering willow recovery. The scientists sampled i) in the Lamar Valley, and ii) on Oxbow Creek where few bison are active as a comparison. A high rate of summer browsing indicates bison use, because elk are largely absent from the area in summer. Under 1 m height, 84% of willows were browsed in summer 2010 for Lamar Valley. Percent browsing at 1.5 – 2 m height was only 28%. These numbers were significantly smaller at Oxbow Creek, 26% and 10% respectively. The distinction between heights is important because only elk can browse the 1.5 – 2 m height. If elk were the primary browse species, browsing would be equal at all heights. Thus the findings indicate that browsing by bison may have been a substantial factor at the Lamar Valley. Growth since browsing was large and positive for 1.5 – 2 m height class at both locations (+36 cm at Lamar Valley; +71 cm at Oxbow Creek), but was -3 cm (i. e. height *decreased*) for willows below 1 m at Lamar Valley (+21 cm for < 1 m at Oxbow Creek). Scat were not found at Oxbow Creek, but fecal piles collected at the Lamar Valley plots corroborated heavy presence of bison. Of 1,326 fecal piles collected, 1,302 were from bison. The only evidence of elk presence in the summer was a single fecal pile in the 12,620 m² sampling area. From all this evidence, it appears that a secondary trophic cascade is occurring in which elk reduction releases bison to browse more heavily than they did historically. Despite being an historical YNP resident, bison are now problematic because their behaviors have been anthropogenically altered for fear of bovine brucellosis, introduced through domestic cattle. This provides further motivation for willow management that goes beyond reliance on wolves.

Other studies have found non-hydrologic bottom-up factors to be as important as wolf effects. Tercek, Stottlemeyer, and Renkin (2010) hypothesized that willow stands with low growth since wolf reintroduction were limited by abiotic factors. Prior to wolf reintroduction, all willow stands in their study area were < 250 cm maximum height, so any differences in height would have to have accumulated in the 15 subsequent years. They contrasted abiotic conditions for newly “tall” (> 250 cm maximum height) willow stands with stands that were still “short” (≤ 250 cm) post-reintroduction. Except during the spring, when runoff is high, short willow stands had significantly deeper water tables. Tall-willow subplots had significantly higher moisture than short-willow-subplots. Short willow sites had significantly warmer soil

temperature in summer, and colder (though not significantly) soil temperature in winter. Correlated with warmer soil, taller sites had significantly deeper snow and greater snow water equivalent than short willow sites. Net NO_3^- mineralization rates for tall willow sites were more than double that for short willow sites.

This study confirms that there are numerous bottom-up factors, from water table depth (as previously seen in association with beavers) to nitrogen availability that limit the recovery of willows. Although these abiotic factors are completely unrelated to wolf presence or absence, it is worth reiterating that prior to wolf reintroduction, there were *zero* “tall” willow stands. While the study demonstrates that wolves cannot be completely relied upon for willow recovery, wolf reintroduction is implicated as a necessary initial stipulation for recovery of willows experiencing favorable abiotic conditions.

3. Effects on Cottonwoods (*Populus spp.*)

Cottonwoods represent another group of browse species for ungulates in Yellowstone National Park. Like willows, riparian cottonwood populations in YNP declined during the 70 years of wolf absence. Beschta and Ripple (2003) investigated whether cottonwoods were recovering, and by what mechanism. They hypothesized that, in addition to ungulate density mediated reductions in browsing, reintroduction of wolves could bring about a *behaviorally* mediated trophic cascade (BMTC). In such a case, elk would preferentially forage in areas where perceived risk of predation is lower, such as those without visual impediments or escape impediments. The implication for browse plant recovery is that effects of wolf reintroduction could prove patchy.

Beschta and Ripple conducted their study in valley bottoms in northeastern YNP, along Soda Butte Creek and Lamar River. They surveyed young cottonwood stands, censusing individuals with a 2×30 m transect, recording the height of the tallest leader between each meter mark and the next (i. e., $n = 30$ per stand). For stands larger than 2×30 m, they placed the transect where cottonwood stem density was the greatest. This is worrisome. If locations with the highest stem density included e. g. the best nutrients and therefore the healthiest cottonwood individuals, it could have produced a biased result if the

same nutrients also contributed to growth in height. Too, they always selected the tallest—and possibly healthiest—individual in each 1 m segment.

Comparison of photographs taken during the study period to photos of the study sites taken prior to 1998 confirmed that height had increased for 6 of the 8 study sites. Both of the sites that did not exhibit increased height were located on straight reaches on the Lamar River. In the pre-1998 photographs, all 8 sites' tallest height class of was < 1 meter tall, implying suppression. Thus, the finding that there were any stands at all with trees 2 – 4 m is auspicious.

The scientists compared cottonwood growth between areas with low and high perceived predation risk factors. The risk factors they tested included 1) inhibitions to detection of predators and 2) inhibitions to escape. High risk sites usually experienced lower percent of cottonwood stems browsed, although in half of the sampling years high risk sites experienced > 80% browsing at Soda Butte Creek. The difference in cottonwood *growth* between high and low risk sites was more consistent. Stands with low perceived predation risk barely grew at all over the four years of the study. At high risk sites, however, leader height doubled (Lamar River) or tripled (Soda Butte Creek). At another site, adjacent gully depth, a proxy for perceived inhibition of escape, correlated linearly with cottonwood leader height ($r^2 = 0.76$).

Thus Ripple and Beschta (2003) found evidence that cottonwoods were rejuvenating. Moreover, the proposed behaviorally mediated mechanism of top-down control was substantiated, helping to explain why cottonwood growth was observed to be patchy. Although this study, as I have said, may have been skewed by the authors' sampling method, Ripple and Beschta (2011) continued their cottonwood research. For the Soda Butte and Lamar Valleys, they found an increase in recruitment since 2003 of 156 new cottonwoods.

However, almost all of the observed cottonwood recruitment had occurred along Soda Butte Creek or the upper Lamar, upstream of their confluence. With the aim of comparing upstream recovery patterns to downstream ones, Beschta and Ripple (2014) divided the Lamar Valley into two study ranges, upper and lower Lamar. The study ranges were chosen based on discrepancies in their cottonwood populations. The sampling methods were sound (an improvement from 2003). There were 370 and 199 over-

story individuals in the upper and lower ranges, respectively, corresponding to model-predicted and vastly low recruitment rates, respectively. In the upper Lamar, the youngest age class of trees ≥ 5 cm diameter at breast height (DBH) had been underrepresented compared to model distribution ($p < 0.05$) for the seven decades during the wolf extirpation period, but had now rebounded in the 2000-2009 decade to meet the model expectations. Yet for the lower Lamar, wolf reintroduction had not brought an increase in recruitment of trees ≥ 5 cm DBH. For the 2000-2009 decade, only 7 cottonwoods were recruited (vs. > 60 predicted by the model). Based on aerial photos, Beschta and Ripple estimated counts of 41,700 and 75,700 young cottonwoods in the 28 and 78 ha of active channels in the upper and lower Lamar ranges, respectively. In the upper Lamar, 4,660 were estimated to exceed 2 m in height (the upper browse limit for elk); the estimated number for the lower Lamar was only 22 cottonwoods. Compared to data from a decade earlier, the upper Lamar cottonwoods were vastly improving: median height of the tallest three cottonwoods was 5.1 m, nearly five times taller, and instead of zero cottonwoods ≥ 5 cm DBH there were now an estimated 1,210 such individuals, matching that predicted by the regression model. Yet the situation in the lower Lamar remained woeful. There was no increase in median height, and there were a pitiful 11 cottonwoods ≥ 5 cm DBH.

Ungulate use was investigated as a possible cause of difference between the upper and lower regions. Interestingly, elk scat was absent (< 0.01 fecal piles per 100 m^2) from the lower Lamar, so browsing by elk was not the cause for poor cottonwood performance. However, bison appeared to be more abundant in the lower Lamar. There were significantly more bison scats in the lower Lamar (10.0 fecal piles per 100 m^2) than upper Lamar (5.6 fecal piles per 100 m^2); overstory scarring was visible on 32% and 12% of cottonwoods in the two ranges, respectively. In their 2012 bison study (discussed above regarding willows), Painter and Ripple investigated bison browsing on cottonwood in the Lamar Valley. Across 7 study sites, mean percent summer browsing (indicative of bison activity, as for willows above) was 54% (range: 13% - 100%). For all sites, mean cottonwood height was < 1 m; at only 2 sites did even a single plant exceed 1 m height. Height was significantly correlated with summer browsing ($r^2 = 0.69$, $p < 0.02$). Clearly, bison browsing was a factor suppressing cottonwood recovery.

Thus, while wolf reintroduction has coincided with cottonwood recovery in some areas of YNP, the effect is not generalizable across all areas and terrains. Cottonwood recovery was not nearly as impressive in areas with low perceived risk of predation—elk may have modified their behavior and continued to suppress recovery in such places. Moreover, wolves have little effect on habits and density of bison (Beschta and Ripple 2014). Wolf predation on elk could actually hinder cottonwood recovery in heavily bison-browsed areas when bison are released from competition with elk. In summary, cottonwood recovery is not a foregone consequence of wolf reintroduction.

4. Effects on Aspen (*Populus tremuloides*)

While aspen represent only 1.4% of forest cover in the Greater Yellowstone Ecosystem (Brown et al. 2006), Winnie (2012) recognized their contributions to biodiversity: “aspen groves account for a disproportionately high percentage of plant (Stohlgren et al. 1997, 1999, Chong et al. 2001), bird (Salt 1957), and insect (Chong et al. 2001) biodiversity, with species richness 3–30 times higher than nearby conifer forests, sage, and meadowlands.” Like the other tree species considered above, aspen populations declined during the wolf extirpation decades (Ripple and Beschta 2007).

Winnie investigated aspen recovery and assessed the behaviorally mediated trophic cascade hypothesis for this species. He surveyed 65 aspen stands in the Daly Creek drainage. He characterized four different perceived predation risk factors (ones similar to Ripple and Beschta). Two aspen enclosures (at Porcupine and Crown Butte) were utilized as a paired control. Aspens within enclosures were immune to browsing. The enclosure fences also created a visual impediment, so aspens in immediate vicinity of an enclosure would serve as a behaviorally mediated treatment group subject to the same environmental conditions as protected aspens. If the two groups both experienced very little similar browsing, then a behaviorally mediated trophic cascade hypothesis would be supported. Of note, Winnie also controlled for stand size, since large stands could have either attracted (more forage) or repelled (visual impediment) elk: He found no correlation between stand size and browsing.

He did, however, find a *positive* correlation between the number of risk factors and proportion of aspen suckers browsed. Also contrary to the BMTC hypothesis, there was a strong negative correlation between the number of risk factors and the number of juveniles in aspen stands. Too, when visual impediments were present, there were fewer juvenile aspens on average. Overall, the BMTC hypothesis was not substantiated. Out of the 65 aspen stands censused, 44 had ≥ 3 risk factors yet, 96% of aspen suckers were browsed. The most telling data come from the aspen enclosure pseudoexperiment. Within both enclosures, as expected, there was no browsing. Adjacent to the Porcupine and Crown Butte enclosures, 99.82% and 100% of aspen suckers were browsed, respectively. Recruitment of juveniles was 0 at both sites. At these sites, the risk factors were obviously not lessening elk browsing. Winnie assessed the effects of physical barriers to elk similarly to risk factors. Significant positive & negative correlations were found between physical barriers and number of juvenile aspen & proportion browsing, respectively. Winnie's findings show that physical inhibitions, not behavioral ones, were influencing patterns of elk browsing and aspen recruitment. This is not a good sign for wolf reintroduction, for wolves do not modify the physical environment. Moreover, with 96% of aspens browsed, it is not clear that wolves were causing a density-mediated trophic cascade in Daly Creek, either. While it is possible that wolf populations can, given time, grow to the point at which they provide effective top-down control, additional reintroductions may be necessitated to ensure it.

An earlier study by Ripple and Beschta (2007) in the Lamar Valley in YNP's northern range did find significant effects of wolf reintroduction on aspen recovery. In riparian areas, average aspen height was $214 \text{ cm} \pm 48 \text{ cm}$. In uplands, average height was only $105 \text{ cm} \pm 16 \text{ cm}$, which still represents impressive recovery, considering that average height in both ecosystem types was below 50 cm prior to wolf reintroduction. Ripple and Beschta also found some evidence for behavioral mediation: Aspens at sites with fallen logs (an escape impediment and perceived predation risk factor) were on average 62 cm taller than those at sites without downed logs.

Ripple and Beschta optimistically reported a highly auspicious prognosis for aspen recovery, but some qualifications were in order. While browsing did decrease from near 100% prior to wolf reintroduc-

tion, the decrease was not uniform. Riparian sites were experiencing < 50% browsing, and this number was even lower (< 20%) for riparian sites with escape impediments. But browsing was > 60% for uplands with downed logs and > 80% for uplands without logs, which is concerning. For one thing, the northern range is primarily uplands, so the extent of aspen recovery could be highly limited. Secondly, before wolf reintroduction, browsing levels were similar between upland and riparian locations. Thus, while part of elk behavior modification is predilection for sites without escape impediments, it appears that another facet of it is to preferentially browse upland aspens. If so, wolf populations—at their current densities—will not prove sufficient for plant community recovery at more than a patchy scale, especially because the majority of the northern range is upland terrain. We have already seen that the alternate state of riparian willows and some cottonwoods may be resilient to wolf reintroduction; if upland plant populations, too, are resilient to wolf reintroduction, further steps may be necessary. Here at least the situation may not be hysteretic: higher densities of wolves could be sufficient to create a density mediated trophic cascade that would benefit both ecosystem types.

In part to allay these worries, Ripple and Beschta (2011) surveyed the same 98 aspen stands four years later. Percentage aspen leaders browsed decreased from 2006 to 2010 for both upland and riparian patches with and without perceived predation risk factors. Importantly, browsing in uplands decreased from 67% to 20% and from 84% to 24% at sites with and without escape impediments, respectively. Aspen mean height increased from 154 cm to 265 cm across those same years. When Beschta and Ripple (2012) conducted an even more recent survey of aspen stands, they found that browsing of aspens 1 – 2 m height was only 12% (averaged across both ecosystem types), down from as much as 63%. Too, they found that > 60% of aspen stands, averaged across both ecosystem types, featured aspen leaders taller than 2 m, at which height they are essentially immune to browsing by elk. This provides a healthy dose of evidence that wolf reintroduction successfully instigates aspen recovery in some parts of YNP. Combined with Winnie's findings, I conclude that reintroduced wolves, through a *density mediated* trophic cascade, can aid recovery of aspens. Winnie's finding of 96% aspen browsing may indicate that wolf and/or elk populations have not yet reached the requisite densities for cascading effects to be felt by aspen.

5. Effects on Berry-producing Shrubs

Trees were not the only woody plants suppressed by elk herbivory in the absence of wolves. Willow, aspen, and cottonwood stands are often characterized by a diverse understory including berry-producing shrubs (Ripple et al. 2014). Suppression of these stands can then suppress shrubs; understory shrubs are browsed directly by elk, too. Berry-producing shrubs are critical to historical YNP ecosystems, supporting animals from insects to hummingbirds to bears by providing shelter or forage.

Prior to wolf reintroduction, Kay (1995) showed that ungulate browsing was a likely cause of diminished berry-producing shrub productivity. The study utilized ungulate exclosures. Berry-producing shrubs within exclosures were 2 – 6 times taller on average and produced ~1,000 times more berries than shrubs outside exclosures.

Subsequent to wolf reintroduction, Beschta and Ripple (2012) conducted a study investigating characteristics of berry-producing shrubs growing in stands of aspen. They observed that aspen stands were recovering, and wanted to assess whether the status of berry-producing shrubs was improving as well. They obtained mixed results. At least one species of berry-producing shrub was present in each of 97 aspen stands sampled. The number of stands in which a particular berry-producing shrub species was found varied broadly, from $n = 3$ stands for raspberry to $n = 90$ for rose *spp.* Only 3 berry-producing shrub genera were present in > 30% of aspen stands (rose *spp.*, snowberry *spp.* ($n = 60$ stands), and gooseberry *spp.* ($n = 28$)). For these genera, and twinberry and serviceberry as well, shrub height was significantly associated (linear regression) with aspen leader height in the stand. For these five types of berry-producing shrub and for chokecherry, shrub height was significantly associated (logistic regression) with percent of individual shrubs bearing fruit. The average number of berry-producing shrub species present was greater when understory aspens were taller, and less when understory aspens were shorter.

The meanings of the data are not immediately clear. For five types of berry-producing shrub, recovery was correlated to aspen recovery. This implies that shrub recovery is, like aspen recovery, attributable to herbivory reductions, corroborating Kay's 1995 findings. Yet, as we saw in Winnie's 2012 study,

the progress of aspen recovery is not full-throttle, and we cannot assume that progress for berry-producing shrubs is more ubiquitous. Even if we interpret the findings as a good sign, it still represents improved status for only half of the shrub categories tested. Furthermore, berry-producing shrub heights were substantially shorter than expected for mature shrubs (Beschta and Ripple).

Ripple et al. (2014) continued to pursue the relationship between wolves and berry-producing shrubs in Yellowstone National Park, this time including data on grizzly bear (*Ursus arctos*) habits. The scientists hypothesized that increased recruitment of berry-producing shrubs following a trophic cascade from wolf reintroduction could aid grizzly bears as a source of forage in the summer as the bears build their energy reserves for hibernation. The study revealed (via scat analysis) that proportion fruit in grizzly bear diet had been very low prior to reintroduction, averaging 0.3% in July and 7.8% of diet in August. After wolf reintroduction, fruit consumption was as high as 39% (for female bears in the month of August 2008), but the increase was not consistent for all three post-reintroduction years examined. The authors found an inverse correlation between elk population density and fruit consumption by grizzly bears.

The scientists collected data on serviceberry plants, a species carefully chosen based on prior experience as representative of the berry-producing shrub community at large. They found that age structure of serviceberry within ungulate exclosures (control group) closely matched the expected exponential distribution. For serviceberries outside exclosures, by contrast, all 240 of the sample plants had established subsequent to wolf reintroduction. The age structure was thus strongly skewed toward younger plants, indicative of a wolf effect. Mean serviceberry stem height in stands was inversely correlated with mean percent browsing—herbivory directly stunts shrub height. A trend through time was also observed. Mean height increased from 38 cm to 65 cm from 2008 to 2012; mean percent ungulate browsing decreased from 81% to 12% across the same years. This correlates well with the documented (by Yellowstone National Park) decline in elk density for the study area during those years. Too, the scientists controlled for site NPP, which was found to have no significant correlation ($r^2 = 0.03$, $P = 0.61$) with shrub height, providing further evidence for cascading wolf control for berry-producing shrub communities.

With elk populations declining, bear fruit consumption increasing, and serviceberry establishing once again, is the ecosystem returning to its historical state? It appears to me that it is in the process of return, but historical fidelity with elk-bear-berry coexistence is still far from being achieved. While the findings of the studies show promise, they aren't at all conclusive. The latter study only surveyed serviceberry; it is possible that other species are not rebounding. The authors specifically acknowledge that serviceberry occurred at lower-than-historical densities. It may take another decade or two for berry-producing shrubs to fully recover. For grizzly bears, energy from berries is more important than ever, because other food sources are disappearing. The whitebark pine, whose seeds boost energy reserves for hibernation similarly to berries, is experiencing increased mortality due to climate change-induced mountain pine beetle irruptions (Jewett et al. 2011). Cutthroat trout, a favored bear prey species, has seen its numbers decline drastically since humans introduced lake trout to the Yellowstone region. As a consequence of lake trout predation on cutthroat trout, bears shift habits and increase predation on elk (Middleton et al. 2013). This brings bears and wolves into more direct competition than in the historical setting.

The salient implication of the intricate web of wolf-bear-elk-shrub-trout-tree interactions is that reintroduction of one species, even the top predator, is liable to produce multiple, diffuse, and sometimes conflicting effects. Reintroduction represents an attempt by humans to restore the historical state, and given time, it can perhaps restore berry-producing shrubs. Yet for this food web, reintroduction may prove ineffectual in the face of the other hysteretic human-mediated changes, i. e. climate change and lake trout. As these changes continue to limit bears' foraging options, the bears, like elk before them, could overexploit berry-producing shrubs and once again unbalance the ecosystem.

6. Conclusions

The impacts of wolf reintroduction cannot be ignored. Elk populations have declined across Yellowstone National Park. Numerous studies find evidence for recovery of plant communities within particular study sites. Recovery, however, is not uniform across the American west. For each study that shows promising ecosystem restoration, another study finds a location or a species for which the outlook is less

propitious. In the research presented here, it is hard to find a plant species with a consistently positive prognosis. Aspen studies are the most auspicious. Each iteration of Beschta and Ripple's studies found a progressively healthier aspen community. At the same time, Winnie found that 96% of physically available aspen were browsed. Still, the aspen studies are more promising than those for willow or cottonwood: even Winnie found no evidence of an hysteretic alternative stable state. This means that, given time and eventual increased wolf density, wolf effects alone could prove sufficient to restore historical fidelity for this community member.

However, based on what I have presented, wolf reintroduction alone is probably not sufficient to restore historical fidelity for the other plant groups examined. There exist several reasons for these hysteretic changes.

1) Stream hydrology and other abiotic factors limit willow recovery. Willows need fine sediment and high water tables if they are to thrive. Beavers require high density of tall willows if they are to build successful dams. Once beavers abandon dams and stream incision occurs, an elk-grassland state takes hold. Without induced hydrology reversions, willows do not reach the necessary density and height to break this alternative state. Unfortunately, wolves are not known to build dams. Instead, management options could include: i) construction of artificial dams to simulate historical hydrological conditions. These dams might provide the activation energy, so to speak, required to boost willow establishment and growth, and shift the ecosystem back to its original state. Too, dams could attract beavers directly by creating enticing ponds. ii) Supplementing locations at which beaver dams were historically present with long logs and other dam-building material for beavers. While this might prove less effective than creating dams directly, it has benefits. For one thing, it removes the possibility of creating further disturbances through introduction of foreign artificial materials into the wild. Secondly, it would be less expensive.

2) Bison continue to browse at the same or elevated levels in the presence of wolves. Reduction in elk population density can release bison from competition, increasing their plant-destroying potential. In addition, bison lifestyle is different from historical patterns. Under the Interagency Bison Management Plan, bison are prevented from roaming beyond a specified range in YNP, for fear of bovine brucellosis

spreading (introduced to bison populations by cattle in the 1910s) (White et al. 2011). Concentrated within a smaller area than is historically natural, bison suppress woody browse species, limiting the efficacy of wolf reintroduction. Nor has reintroduction of wolves increased predation on bison (Painter and Ripple 2012). Bison are experiencing historically low predation pressure (from either wolves or humans). Without the ability to travel freely, bison overexploit local plant communities, and the effects of such browsing are too strong to be controlled by wolves. A change in bison management practices would be a better method to augment recovery of cottonwoods and willows in parts of YNP where bison are abundant.

3) Behaviorally mediated trophic cascades are not consistently effective. A BMTC appears to work for cottonwoods, evidenced by Ripple and Beschta's findings (2003). Of course, this leaves large "safe" patches of cottonwoods browsed as heavily as before. For other species, e. g. aspen, foraging behavior does not appear to be influenced, as shown by Winnie (2012). This implies that for some species, plant restoration requires substantial elk density mediation. At first, Beschta and Ripple (2007) found aspen recovering only in riparian areas. The good news was that given enough time (Beschta and Ripple 2011; 2012), wolves did cause a density mediated trophic cascade which allowed regrowth of aspen at broad scale.

4) The case study of berry-producing shrubs highlights the vast inadequacy of wolf reintroduction in the face of other anthropogenic impacts, namely climate change and introduced species. Even if wolf reintroductions do restore historical fidelity for berry-producing shrubs, the restoration is occurring in an altered ecological context. Bison dispersion is constrained. Whitebark pine mortality spikes as climate change takes hold. Predation by introduced lake trout reduces biomass of cutthroat trout available to terrestrial predators by upwards of 90% (Middleton et al. 2013). Together, these can more than cancel out effects of berry-producing shrub recovery when grizzly bear diets shift heavily toward berries as a result.

This brings us back to Mech's argument that the scientific community cannot afford to "sanctify the wolf." More than questioning whether wolf reintroduction can directly reverse effects of extirpation, Mech (2012) emphasizes that wolf reintroduction represents a mere drop in the bucket compared to the necessary steps humanity must undertake to diminish and reverse its collective crushing impact on the

world's biota. Mech is correct, for there is a danger incurred by “sanctifying the wolf” if in so doing the scientific community blinds itself to the complexity of the ecosystems being studied and the many other processes—especially anthropogenic processes—that influence outcomes. We cannot rely on wolves to solve the myriad problems we are creating. Nor, as I have shown in this paper, can we rely on wolves to solve the very specific and seemingly reversible problem of wolf extirpation. This anthropogenic change has instead proved hysteretic, which is worrisome. There are *many* anthropogenic alterations at work in the American west—if many or all of them are hysteretic, the outlook for ecosystem restorations is very bleak. Moreover, when alternative states are directly reversible—as we have seen with willows, aspens, and berry-producing shrubs—a long time, in this case more than two decades, is required before a full return to historical state. It is critical, therefore, to implement management strategies as soon as possible, before even more disruptions are incited. Based on the literature examined in this review, it is clear that management efforts in Yellowstone National Park must include, *but cannot end with*, wolf reintroduction.

LITERATURE CITED

- Baker, B.W., H. C. Ducharme, D. C. S. Mitchell, T. R. Stanley, and H. R. Peinetti. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecol. Appl.* 15: 110–118
- Bartnick, T.D., T. R. Van Deelen, H. B. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. *Canadian Journal of Zoology* 91: 82–93.
- Berger, J. 2008. Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem, USA. *Oryx* 42: 139–142.
- Beschta, R.L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. *Ecology* 86: 391–403.
- Beschta, R.L. and W. J. Ripple. 2012. Restoring berry-producing shrubs with wolves in Yellowstone National Park. *Forest Ecology and Management* 276: 132–138.
- Beschta, R. L. and W. J. Ripple. 2014. Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone, USA. *Ecohydrol.* doi: 10.1002/eco.1487
- Brown, K., A. J. Hansen, R. E. Keane, and L. J. Graumlich. 2006. Complex interactions shaping aspen dynamics in the greater Yellowstone ecosystem. *Landscape Ecology* 21: 933–951.
- Carpenter, S. R., W. A. Brock, J. J. Cole, J. F. Kitchell, M. L. Pace. 2008 Leading indicators of trophic cascades. *Ecology Letters* 11: 128–138
- Chadde, S., C. Kay. 1991. Tall-willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm. Pages 231–262 in R.B. Keiter and M.S. Boyce, editors, *The Greater Yellowstone Ecosystem: redefining America's wilderness heritage*. Yale University Press, New Haven, CT.
- Estes, J.A. et al. 2011. Trophic downgrading of planet earth. *Science* 333: 301–306

- Fortin, D., L.B. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, J.S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86: 1320–1330
- Jewett, J. T., R. L. Lawrence, L. A. Marshall, P. E. Gessler, S. L. Powell, and S. L. Savage. 2011. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. *Forest Science* 57: 320–335.
- Kay, C. E. 1995. Browsing by native ungulates: effects on shrub and seed production in the Greater Yellowstone Ecosystem. In: Roundy, B.A., McArthur, E.D., Haley, J.S., Mann, D.K. (Compilers), *Proceedings: Wildland Shrub and Arid Land Restoration Symposium*. US Forest Service, INT-GTR-315, Ogden, UT, pp. 310–320
- Keigley, R.B., M.R. Frisina, and C. W. Fager. 2002. Assessing browse trend at the landscape level. I: Preliminary steps and field survey. *Rangelands* 24: 28–33.
- Marshall, K. N., N. T. Hobbs, and D. J. Cooper. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings of the Royal Society B: Biological Sciences* 280: 20122977.
- Marshall, K. N., D. J. Cooper, and N. T. Hobbs. 2014. Interactions among herbivory, climate, topography and plant age shape riparian willow dynamics in northern Yellowstone National Park, USA. *Journal of Ecology* 102:667–677.
- Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. In: Mech, L.D., Boitani, L. (Eds.), *Wolves: Behavior, Ecology, and Conservation*. Univ Chicago Press, pp. 131–160.
- Mech, L. D. 2012. Is science in danger of sanctifying the wolf? *Biological Conservation* 150: 143–149.
- Middleton, A. D., T. A. Morrison, J. K. Fortin, C. T. Robbins, K. M. Proffitt, P. J. White, D. E. McWhirter, T. M. Koel, D. G. Brimeyer, W. S. Fairbanks, and M. J. Kauffman. 2013. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences* 280: 20130870.
- Painter, L. E., and W. J. Ripple. 2012. Effects of bison on willow and cottonwood in northern

- Yellowstone National Park. *Forest Ecology and Management* 264: 150–158
- Ritchie, E.G., and C.N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12, 982–998.
- Ripple, W. J. and R. L. Beschta. 2003. Wolf reintroduction, predation risk and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184:299–313
- Ripple W.J., R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138: 514–519
- Ripple, W. J, and R. L. Beschta. 2012a. Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research* 58: 733-742.
- Ripple, W. J., and R. L. Beschta. 2012b. Trophic Cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation* 145: 205-213
- Ripple, W. J., A. J. Wirsing, C. C. Wilmers, and M. Letnic. 2013. Widespread mesopredator effects after wolf extirpation. *Biological Conservation* 160: 70–79.
- Ripple, W.J., R.L. Beschta, J.K. Fortin, and C.T. Robbins. 2014. Trophic cascades from wolves to grizzly bears in Yellowstone. *Journal of Animal Ecology* 83: 223–233.
- Sandom, C., S. Faurby, B. Sandel, and J. Svenning. 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proc. R. Soc. B* 281: 20133254
- Schullery, P. “The Greater Yellowstone Ecosystem”. *Our Living Resources*. U.S. Geological Survey. Archived 27 September 2006. Accessed 28 September 2014.
- Singer F. J., L.C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone’s northern winter range. *J. Range Manage.* 47: 435–443.
- Tercek, M. T., R. Stottlemeyer, and R. Renkin. 2010. Bottom-up factors influencing riparian willow recovery in Yellowstone National Park. *Western North American Naturalist* 70: 387–399
- Tveraa, T., P. Ferchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Høgda. 2007. What regulate and limit reindeer populations in Norway? *Oikos* 116: 706–715

- White, P. J., R. L. Wallen, C. Geremia, J. J. Treanor, D. W. Blanton. 2011. Management of Yellowstone bison and brucellosis transmission risk: implications for conservation and restoration. *Biol. Conserv.* 144: 1322-1334
- White, P. J., K. M. Proffitt, T. O. Lemke. 2012. Changes in elk distribution and group sizes after wolf restoration. *New American Midland Naturalist* 167: 174–187.
- Winnie, J.A. Jr. 2012. Predation risk, elk, and aspen: tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. *Ecology* 93: 2600–2614.
- Wolf, E.C., D.J. Cooper, and N.T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* 17: 1572–1587
- "Yellowstone Fact Sheet". National Park Service. August 10, 2006. Accessed 28 September 2014.
- Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. US Department of Interior, Yellowstone National Park, Mammoth Hot Springs, WY.