

Exhibit G

**Berry-producing shrub characteristics following wolf reintroduction
in Yellowstone National Park**

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Abstract

Gray wolves (*Canis lupus*) were reintroduced into Yellowstone National Park in 1995-96, thus completing the park's large predator guild. In the fall of 2010, approximately 15 years after wolf reintroduction, we sampled ten genera/species of berry-producing shrubs within 97 aspen (*Populus tremuloides*) stands in the park's northern ungulate winter range. Regression analysis indicated shrub heights for five of the ten genera/species were positively correlated with height of understory aspen; greater shrub richness was found in aspen stands with the tallest understory aspen. In addition, the proportion of shrubs with berries was positively correlated with shrub height for six of the ten genera/species. Results were consistent with the re-establishment of a tri-trophic cascade involving wolves, elk (*Cervus elaphus*), and palatable woody plants in northern Yellowstone. After multiple decades of browsing suppression by elk, it appears that aspen and at least some genera/species of berry-producing shrubs are in the early stages of recovery. If shrub recovery continues, improved food-web and habitat support could benefit a wide range of terrestrial wildlife species in northern Yellowstone.

Key words berry-producing shrubs, aspen, elk, wolves, Yellowstone National Park

1. Introduction

In tri-trophic systems, carnivores provide top-down forcing that can mediate the behavior and density of herbivores (consumers), thus allowing plant communities (producers) to maintain high levels of abundance, biomass, and productivity (Pace et al., 1999; Ripple and Beschta, 2012a). However, in the late 1800s-early 1900s, an increasing Euro-American presence in the western United States (US) resulted in widespread extirpation of gray wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), as well as reduced numbers of ungulates (Laliberte and Ripple, 2004). Although ungulate populations across much of this region were recovering by the mid-1900s, incomplete large predator guilds have remained.

Even national parks in the western US were not immune to the loss or displacement of large mammalian carnivores (e.g., Cahalane, 1941; Leopold et al., 1963) and increased herbivory by elk (*Cervus elaphus*) and/or deer (*Odocoileus* spp.) began to alter the structure and dynamics of plant communities as well as other ecosystem processes (Hess, 1993; White et al., 1998; Prichard, 1999; Beschta and Ripple, 2009). In the eastern US, intensive herbivory on young deciduous woody plants from an increased population of white-tailed deer (*O. virginianus*), in the absence of gray wolves and cougars (*Puma concolor*), similarly initiated major shifts in plant diversity and patterns of succession across many of the region's deciduous forests (Rooney et al., 2004).

Following the extirpation of wolves and grizzly bears in the American West, many aspen (*Populus tremuloides*) communities experienced long-term decline during the latter half of the 20th century due, in part, to high levels of herbivory from native and domestic ungulates (Kay, 1997; Bartos, 2001). The status and dynamics of these communities are of particular importance to the biodiversity and resilience of terrestrial ecosystems because numerous species of vascular

plants may occur in the understories, including multiple genera of shrubs (e.g., *Rosa*, *Symphoricarpos*, *Amelanchier*, *Prunus*, *Berberis*). These understory plants are key sources of food and physical habitat for an extensive array of wildlife species (DeByle and Winokur, 1985).

Gray wolves, initially extirpated from Yellowstone National Park in the early 1900s, were reintroduced in 1995-96, again completing the park's native predator guild (Smith et al., 2003). Consistent with the re-establishment of a tri-trophic cascade involving wolves-elk-plants, improved recruitment (i.e., growth of seedlings/sprouts above the browse level elk) of young aspen, cottonwood (*Populus* spp.), and willow (*Salix* spp.) plants have been documented in portions of the park's northern ungulate winter range (Beyer et al., 2007; Ripple and Beschta, 2012b; Baril, 2009; Beschta and Ripple, 2010). However, the status of shrub communities in aspen stands has not been previously reported. We hypothesized that the increased heights of young aspen (ramets) in recent years may similarly be reflected in shrub community dynamics. Thus, the objective of this study, some 15 years after wolf reintroduction, was to assess the heights, diversity, and presence/absence of fruit on berry-producing shrubs within recovering aspen stands in northern Yellowstone.

2. Study Area

Yellowstone's northern ungulate winter range contains a mix of grassland and forest vegetation distributed across the more than 1,500 km² of mountainous terrain (NRC, 2002; Barmore, 2003), two-thirds of which lies within the park's boundaries. Steppe and shrub-steppe plant communities are often dominated by big sagebrush (*Artemisia tridentata*) and, with increasing elevation, grade into coniferous forests comprised principally of lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*). Aspen stands occur in riparian and

upland settings and occupy 2.4% of the northern range (Savage, 2005), with cottonwood and willow communities predominantly found along stream courses and adjacent floodplains.

When ungulates in Yellowstone National Park were being protected during the early 1900s and wolves systematically removed, Smith et al. (1915) observed that willows and various shrubs such as “mountain maple, service berry, wild rose, snow-berry, fly honey suckle” were showing evidence of considerable winter browsing. Some four decades later, the park’s elk management plan indicated the severity of effects this large herbivore was having on northern range ecosystems (YNP, 1958; pp. 1-2):

“The cumulative effects of grazing and trampling by excessive numbers of elk for many decades are obvious today. Meadows once covered by lush thickets of willows now have a grass-type aspect; likewise former groves of aspen now have only a few trees which cannot be replaced while elk consume reproduction. Sagebrush has disappeared from ridges and other places where snow lies shallow, and even bunchgrass, which comprises the bulk of the elk’s diet, is in poor condition on that range where grazing animals must feed later in the winter.”

“Damaging effects of this abuse are manifold. Animals, whether they be the elk or bighorn which graze, the beaver which feeds on aspen and willow, small songbirds which demand food and protection from vegetation, ducks which suffer from fluctuating water levels, or fish which find a shortened food supply as silt fills stream beds, all suffer from this damaging chain reaction started by the elk.”

Based on long-term age structure data for aspen (Romme et al., 1995; Ripple and Larsen, 2000), cottonwood (Beschta, 2005), and willow (Wolf et al., 2007), the extent to which intensive browsing by elk impaired Yellowstone’s northern range deciduous plant communities during the last half of the 20th century was unprecedented. Trophic downgrading and impacts to channels

following the loss of wolves similarly occurred in the upper Gallatin elk winter range along the park's northwest corner (Ripple and Beschta, 2004; Beschta and Ripple, 2006; Halofsky and Ripple, 2008).

After wolves were reintroduced into Yellowstone during the mid-1990s, their numbers in the northern range increased annually, attaining a population of nearly 100 wolves in 2003. Since then, the northern range population has fluctuated between 40 and 95 wolves (Smith et al., 2011). Following the return of this apex predator, various changes in elk behavior were observed (Laundré et al., 2001) and their population declined from >15,000 elk in the 1990s to ~5,000 elk by 2010. Furthermore, annual population surveys (White et al., 2012) indicate that relatively few elk have been wintering in the eastern portion of the northern range in recent years.

3. Methods

In September of 2010, we revisited 98 aspen stands in the eastern portion of Yellowstone's northern range that had been previously sampled in August of 2006 (see Ripple and Beschta, 2007). They included 44 riparian and 54 upland stands distributed along Crystal Creek, Rose Creek, Slough Creek, and the Lamar River. One of the original riparian stands along Rose Creek had experienced conifer blowdown and human disturbance during removal of the downed conifers; it was thus excluded from remeasurement. In 2006 we had selected the five tallest understory aspen (i.e., of those that became established since the reintroduction of wolves) within each stand and determined temporal patterns of leader heights and browsing levels from plant architecture (e.g., Keigley et al., 2003). In 2010 we again selected the five tallest understory aspen and determined leader heights as of the spring of 2010 as well as whether each leader had been browsed during the winter of 2009-10. From the 2006 and 2010 data sets, we

summarized annual browsing intensity of aspen leaders (% browsed) by three height classes (i.e., 1-100, 101-200, and 201-800 cm). We were unable to consistently distinguish annual patterns of browsing and height growth for berry-producing shrubs from plant architecture measurements, thus we utilized browsing measurements of young aspen as an index of herbivory within each stand. The forage value of at least some of the shrubs we sampled (e.g., serviceberry and chokecherry) was similar to that of aspen (Nelson and Leege, 1982).

For each measured understory aspen, a 10-m radius plot was delineated around its base for sampling shrubs. Within the collective area of these 10-m radius plots in each stand, we measured the height (cm) of the five tallest berry-producing shrubs for each of ten genera/species as well as whether fruit were present/absent on an inventoried plant. The following genera/species were encountered (listed in frequency of occurrence from the most frequent to the least frequent): (1) rose (*Rosa woodsii* and *R. acicularis*); (2) snowberry (*Symphoricarpos albus* and *S. oreophilus*); (3) gooseberry (*Ribes lacustre* and *R. oxycanthoides*); (4) serviceberry (*Amelanchier alnifolia*); (5) buffaloberry (*Shepherdia canadensis*); (6) chokecherry (*Prunus virginiana*); (7) twinberry (*Lonicera involucrata*); (8) thimbleberry (*Rubus parviflorus*); (9) currant (*Ribes cereum*); (10) raspberry (*Rubus idaeus*). Except perhaps for snowberry, currant, and raspberry, most of these species are capable of attaining heights of 200 cm; serviceberry and chokecherry can attain heights considerably greater than 200 cm (Hitchcock and Cronquist, 1973; Cronquist et al., 1997).

We use the terminology “berry-producing shrubs” herein to collectively represent a diverse group of deciduous woody plants that produce a prominent fruit. While most of the shrubs evaluated in this study generate a fruit that meets the strict definition of a “berry” — a fleshy fruit developed from a single pistil (Derig and Fuller, 2001) — some do not. For example, rose

produces a rose hip, serviceberry a pome, and chokecherry a drupe. Nevertheless, we included them in our study since they have a fleshy fruit that is generally “berry-like.” Some of the shrubs we encountered in the field may hybridize (e.g., *Rosa* spp.), thus precluding easy confirmation of species.

We used linear regression of shrub height (y) and aspen height (x) for each genera/species category to assess whether the heights of berry-producing shrubs were associated with the increased heights of young aspen that had been occurring in recent years. We also calculated shrub richness (the average number of genera/species categories, $\pm 95\%$ CL) by height class of aspen leaders to identify possible relationships in shrub richness relative to the height of recovering understory aspen. Kay (1995) had earlier found that taller plants produced more fruit, thus we used logistic regression to identify potential relationships between the percentage of inventoried berry-producing shrubs with fruit (y) versus shrub height (x) for each genera/species category. Regression results were considered significant at $p \leq 0.05$.

4. Results

The intensity of browsing associated with aspen leaders 1-100 cm in height was $>90\%$ through 2006, decreasing to 68% by 2010 (Fig. 1a). For aspen leaders 101-200 cm in height, the browsing intensity ranged from 41-63% from 2000-06, declining to only 12% by 2010. A plant height of >200 cm is generally considered above the browse level of elk and only 1% of aspen leaders 201-800 cm in height had been browsed in 2010.

Understory aspen heights averaged ≤ 50 cm in height from 1998-2002, a period when browsing rates were relatively high. However, as the browsing intensity on young aspen began to decrease after about 2002, average heights (reflecting annual growth minus browsing effects) began to increase ~ 25 cm/yr (Fig. 1b). While none of the aspen leader heights were >200 cm in

2002, by 2010 over 60% of the sampled stands had understory aspen >200 cm in height. In 2010, leader heights of sampled understory aspen ranged from 41 to 715 cm. Examples of the contrasting conditions for understory aspen and berry-producing shrubs encountered in northern range aspen stands during September of 2010 is shown in Fig. 2. Photographs of all sampled aspen stands are available at <http://hdl.handle.net/1957/20842> and clearly show the characteristic two-tiered stand structure that resulted from high levels of elk herbivory during the period when wolves were absent in the park.

The number of stands (n) containing a particular genera/species of berry-producing shrub and their associated heights (minimum, average, and maximum) are presented in Table 1; at least one genera/species of berry-producing shrub was present in each of the 97 aspen stands we sampled. Significant linear regressions ($p \leq 0.05$) of shrub height (y) vs. aspen height (x) were obtained for half of the genera/species categories, including those of rose, snowberry, gooseberry, serviceberry, and twinberry (Fig. 3). Species richness of berry-producing shrubs within a given stand tended to be least where understory aspen were relatively short (<100 cm) and greatest where they were tall (>200 cm; Fig. 4). Although riparian stands, on average, had a greater number of berry-producing shrub categories than upland aspen stands, 2.6 vs. 1.6, respectively, these averages were not significantly different ($p = 0.11$, t-test, unequal variances). Significant logistic regressions were obtained between the percentage of shrubs with fruit (y) and shrub height (x) for six of the ten shrub categories, including snowberry, rose, twinberry, serviceberry, gooseberry, and chokecherry (Fig. 5).

5. Discussion

In the absence of an apex predator, ungulate herbivores such as elk and deer can reduce the abundance of flowers, fruits, and seeds as well as suppress the growth of palatable woody

species (Hester et al., 2006), potentially risking the capability of these plants to persist within a given landscape (Martin et al., 2011). Early field research in Yellowstone's northern range for the period 1935-89 found that the heights of young aspen, willow, and berry-producing shrubs outside of exclosures were being maintained at <100 cm in height due to intensive annual herbivory by elk (Kay, 1995; Singer, 1996; Barmore, 2003). Our 2010 results indicated that herbivory on aspen plant leaders in the 1-100 cm height class was still relatively high, a height class that contains the vast majority (68%) of berry-producing shrubs sampled in this study.

Although significant regressions ($p \leq 0.05$) between shrub height (y) and understory aspen height (x) were obtained for five of the ten categories of berry-producing shrubs assessed in this study, the lack of significant regressions for the other five categories may be due to various factors such as small sample sizes, slow plant growth rates, palatability and utilization differences, or a variety of site factors (e.g., soil nutrient availability, soil moisture, mycorrhizae, historical disturbances). Nevertheless, because decreased ungulate browsing of understory aspen has been generally occurring within the 97 aspen stands we sampled, this would suggest that the greater shrub richness observed with relatively tall aspen understory plants may also be associated with reductions in herbivory.

Our results contrast with previous research in Yellowstone's northern range when wolves were absent, research that indicated intensive elk herbivory had been suppressing the height growth of young deciduous plants. It would thus appear that a fundamental shift in the dynamics of aspen plant communities is underway for many of the stands we sampled and that understory aspen, and at least some genera/species of berry-producing shrubs, are also beginning to increase in height.

In another northern range study, Kay (1995) measured the heights and quantity of fruit associated with serviceberry, chokecherry, and buffaloberry shrubs inside and outside of long-term ungulate exclosures. Average shrub heights inside of exclosures ranged from 87-133 cm vs. 20-48 cm outside of exclosures. Approximately 1,100-2,100 berries per plant were measured on shrubs inside of exclosures but <3 berries per plant outside of exclosures, a three-order of magnitude difference. In an earlier study, Kay and Chadde (1992) noted that even where berry-producing shrubs are fully protected from browsing it may require 10 to 15 years, or longer, to attain their full potential for producing fruit.

Because berries have a high content of fatty acids indispensable for building-up specific depot lipids in birds, many avian species accelerate feeding activities and shift food selection towards fruit in late summer/early fall, a process known as “hyperphagia.” This process is often crucial for birds that depend on internally stored energy for long migratory flights and must therefore greatly increase energy reserves before departing in late summer (Bairlein, 2002).

Hollenbeck and Ripple (2007) reported on a three-year study of avian use in Yellowstone’s northern range aspen stands. Results of that study, which occurred prior to any recent improvements in understory aspen plant communities, indicated that bird species generally dependent upon aspen habitat, except for cavity nesters, were uncommon. Studies at the National Elk Refuge immediately south of Yellowstone National Park, where ungulate herbivory has also altered woody plant communities, similarly found that the abundance of bird species dependent upon aspen communities and riparian habitats was usually minimal relative to ecologically comparable habitats in the western US (Dobkin et al., 2002). Johnsgard (1983) indicated significant declines in riparian-associated bird species are common in areas where ungulate densities were high, including the smallest hummingbird regularly found in the United

States, the calliope hummingbird (*Stellula calliope*). This diminutive avian species (average weight of 2.5-3 grams) commonly utilizes gooseberry and currant flowers (Grinnell and Miller, 1944), two of the genera/species evaluated in this study.

Intensive ungulate browsing can suppress the capability of shrubs to provide flowers and nectar thereby having direct and indirect effects on pollinators (Nyoka, 2010). Kearns and Inouye (1997) suggested that “the ultimate fate of many plants may depend on preserving their mutualistic relationships with pollinators and with the web of organisms that affect both plant and pollinator.” Huffman et al. (2009) found arthropod abundances to be greater on Fendler’s ceanothus (*Ceanothus fendleri*) that were protected from elk and deer herbivory. Additionally, Martin et al. (2011) concluded there is a growing body of knowledge indicating that the regulation of cover and structure of understory vegetation by ungulates can profoundly affect bird assemblages. Thus, berry-producing shrubs may represent a potentially important biodiversity indicator (e.g., Ferris and Humphrey, 1999).

An early treatise of Yellowstone’s animals (Bailey, 1930) identified a broad assemblage of fauna categorized as “gnawing animals.” The various species of small mammals that comprised this grouping collectively utilized leaves, stems, flowers, roots, and fruit of deciduous woody plants to help meet food and shelter needs. Even food-web support for large mammals can be influenced by the status of berry-producing shrubs in northern Rocky Mountain ecosystems. For example, grizzly bears in Alberta (Munro et al., 2006), British Columbia (McLellan, 2011), and Glacier National Park, Montana (Martinka and Kendall, 1986) have been found to consume mostly berries during late summer in order to attain sufficient energy reserves for winter hibernation and reproduction. This late summer pattern of intensive frugivory is in sharp contrast to bear populations in Yellowstone National Park where berries are rarely consumed and

whitebark pine (*Pinus albicaulis*) seeds represent an important autumn food source (Mattson et al., 1991). However, whitebark pine has been in decline in Yellowstone (Tomback et al., 2001) and thus any recovery of berry-production from shrubs could provide additional capacity for supporting the caloric needs of Yellowstone's grizzlies during the late summer and fall. Clearly, any improvement in the abundance and productivity of berry-producing shrubs in Yellowstone's northern range could beneficially affect food-web support for a broad spectrum of invertebrates, birds, and mammals (Fig. 6).

To the best of our knowledge, this is the first study in Yellowstone's northern range to indicate an improving status for any genera/species of berry-producing shrubs since the early 1900s when herbivory impacts to deciduous browse species, by elk, were initially identified. Thus, our results may not only provide a baseline for comparison with future northern range studies but are also encouraging in that at least some berry-producing shrubs in aspen stands appear to be increasing in height and in the occurrence of fruit. However, it should be noted that: (1) our study encompassed aspen stands only in the eastern portion of the northern range where decreases in elk numbers have been the greatest, (2) not all of the genera/species of berry-producing shrubs showed significant increases in height or berry presence, and (3) shrub heights typically remain well-below those expected for mature plants. Furthermore, browsing by an enlarging population of bison (*Bison bison*) in northern Yellowstone National Park may be increasingly contributing to the suppression of shrubs in portions of the northern range (White et al., 2010; Ripple et al., 2010; Painter and Ripple, 2012).

6. Conclusions

One and one-half decades after the reintroduction of wolves into Yellowstone, decreased browsing levels and increased heights of young aspen have been documented in some northern

range aspen stands along with concurrent increases in the heights of several genera/species of berry-producing shrubs. In addition, a greater species richness of shrubs was found where young aspen plants were relatively tall and the presence of fruit for several of the sampled genera/species categories was positively correlated with shrub height. Collectively, these plant community indicators appear to represent the early stage of a recovering ecosystem, a recovery consistent with trophic cascades theory. If berry-producing shrubs continue to increase in height, abundance, and the production of fruit during coming years, this would likely have major implications regarding the various ecosystem services aspen plant communities can provide. Such changes could represent an important improvement in food resources and physical habitat for an array of wildlife species, ranging in size from invertebrates and hummingbirds to ungulates and bears. Any increased biomass and productivity of berry-producing shrubs, as well as that of other native understory plants, would not only help to recover biodiversity in Yellowstone northern range, but could also help improve its resiliency relative to any ongoing or impending changes in climate. Lastly, many of the shrub species evaluated in this study have wide distributions in the American West. Thus our results may have implications to plant communities outside of Yellowstone where wolves currently reside, where reintroduction/recolonization of wolves has occurred in recent years, or where recolonizations may occur in the future.

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1 Table 1

2 Heights of berry producing shrubs sampled in 97 aspen stands during September, 2010 (*n* represents number of stands where indicated
3 shrubs were encountered), northern range of Yellowstone National Park

<u>Berry-producing shrub category</u>	<u><i>n</i></u>	<u>Shrub height (cm)</u>		
		<u>Minimum</u>	<u>Average</u>	<u>Maximum</u>
(1) rose spp. (<i>Rosa woodsii</i> & <i>R. acicularis</i>)	90	35	88	198
(2) snowberry spp. (<i>Symphoricarpos albus</i> & <i>S. oreophilus</i>)	60	27	58	82
(3) gooseberry spp. (<i>Ribes lacustre</i> & <i>R. oxycanthoides</i>)	28	42	115	175
(4) serviceberry (<i>Amelanchier alnifolia</i>)	17	38	102	185
(5) buffaloberry (<i>Shepherdia canadensis</i>)	15	50	94	135
(6) chokecherry (<i>Prunus virginiana</i>)	14	64	92	163
(7) twinberry (<i>Lonicera involucrata</i>)	14	55	112	265
(8) thimbleberry (<i>Rubus parviflorus</i>)	10	40	87	123
(9) currant (<i>Ribes cereum</i>)	4	66	87	105
(10) raspberry (<i>Rubus idaeus</i>)	3	62	71	85

Figures

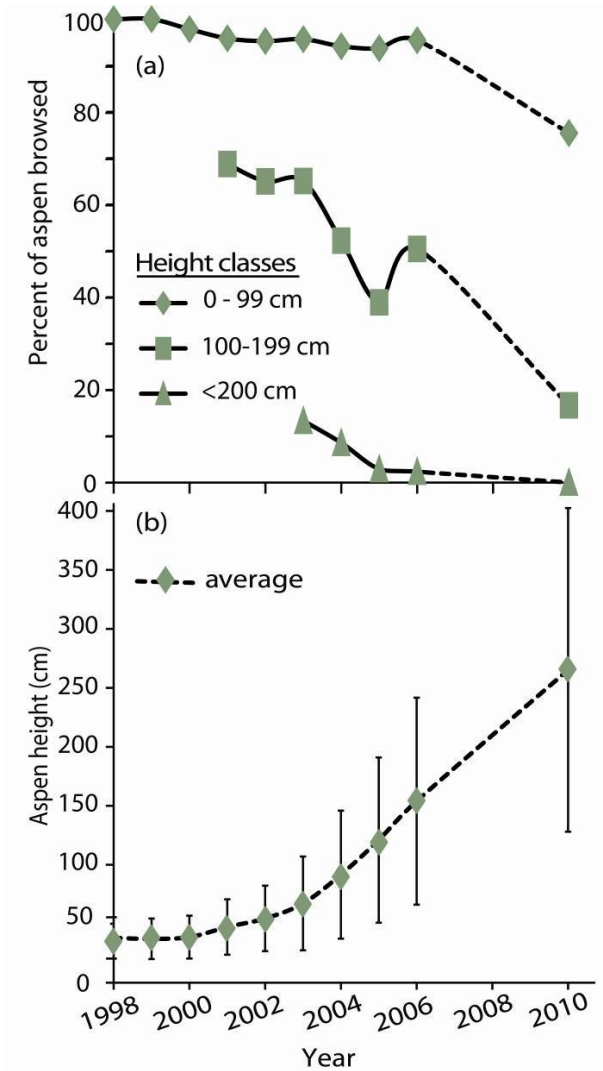


Fig. 1. (a) Average percent of aspen leaders browsed, by height class and (b) average leader height (\pm std. dev.) over the period 1998-2010. Data for 1998-2006 from Ripple and Beschta (2007).



Fig. 2. Fig. 2. Contrasting aspen sites in the northern range of Yellowstone (September 2010): (a) A riparian site that has experienced reduced ungulate browsing pressure in recent years with resultant increases in the heights of serviceberry and chokecherry (foreground) as well as increased aspen and mountain alder (*Alnus incana*) recruitment (i.e., growth above browse level of elk; background) and (b) an upland site experiencing continued high levels of ungulate browsing, no increased heights of berry-producing shrubs, and no aspen recruitment. Note the two-tiered aspen stand structure comprising an overstory of mature trees and an understory of young aspen; the missing intermediate size/age classes occurred over multiple decades when elk herbivory, in the absence of wolves, prevented aspen recruitment.

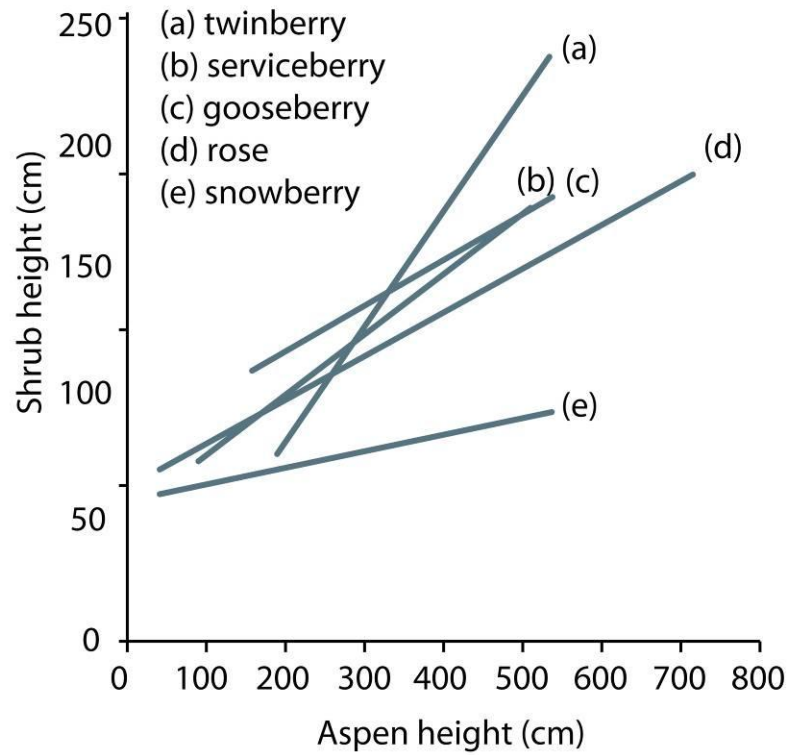


Fig. 3. Statistically significant linear regressions ($p \leq 0.05$) of berry-producing shrub height (y) vs. understory aspen height (x) for twinberry ($r^2 = 0.39$), serviceberry ($r^2 = 0.38$), gooseberry ($r^2 = 0.23$), rose ($r^2 = 0.35$), and snowberry ($r^2 = 0.26$).

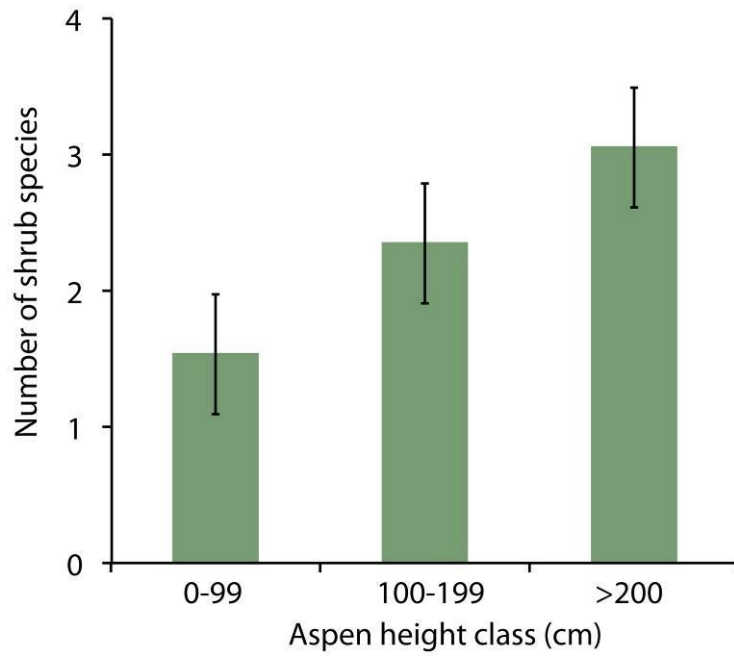


Fig. 4. Average number of berry-producing shrub genera/species categories in sampled aspen stands (\pm 95% confidence intervals) relative to the height of understory aspen.

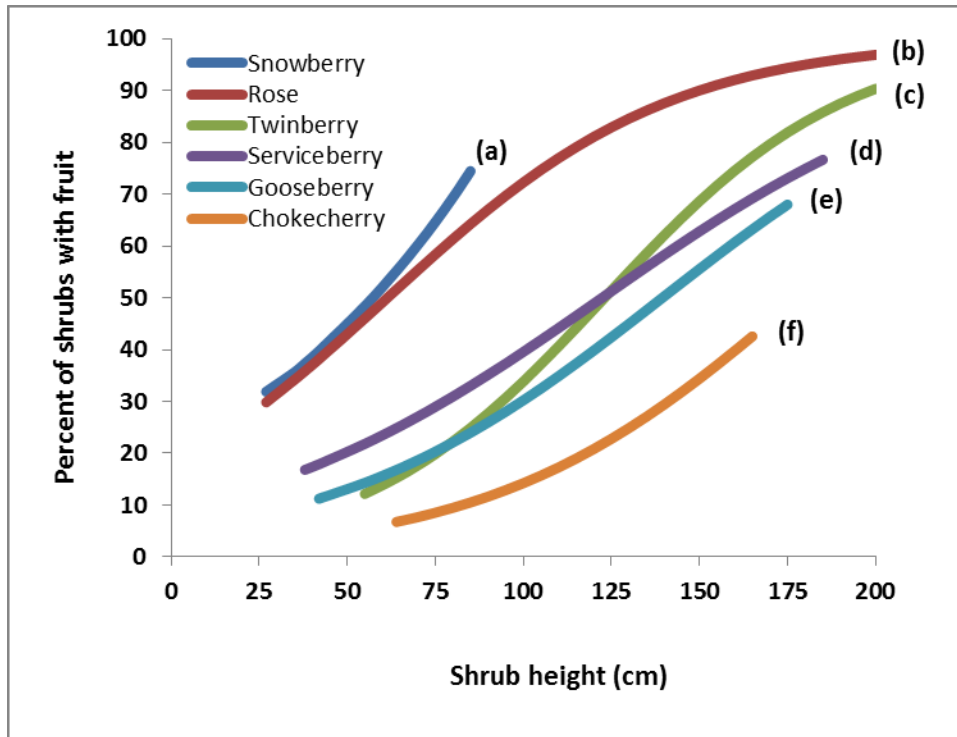


Fig. 5. Statistically significant logistic regressions ($p \leq 0.05$) of percent of berry-producing shrubs with fruit (y) vs. shrub height (x) for snowberry, rose, twinberry, serviceberry, gooseberry, and chokecherry.

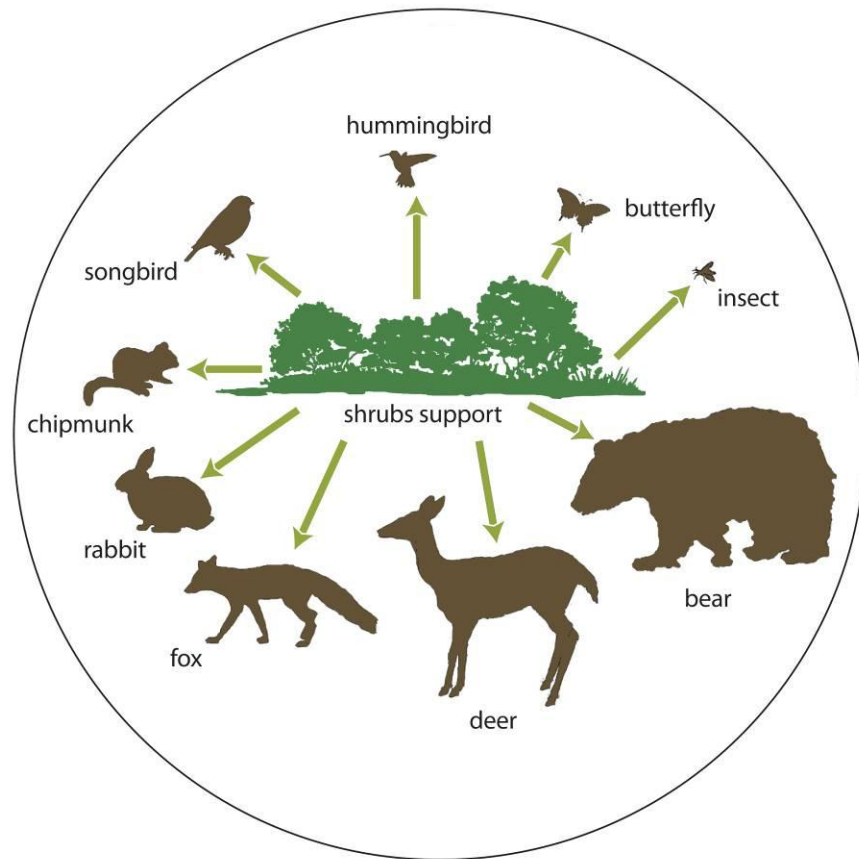


Fig. 6. Generalized diagram indicating a wide range of terrestrial faunal species in Yellowstone National Park that might benefit from the food-web support provided by an improving community of berry-producing shrubs (Bailey, 1930; Grinnell and Miller, 1944; Mattson et al., 1991; Bairlein, 2002; Hoffman et al., 2009).

References

- Bailey, V., 1930 Animal life of Yellowstone National Park. Charles C. Thomas, Baltimore, Maryland.
- Bairlein, F., 2002. How to get fat: Nutritional mechanisms of seasonal fat accumulation in migratory songbirds. *Naturewissenschaften* 89, 1-10.
- Baril, L.M., 2009. Change in deciduous woody vegetation, implications of increased willow (*Salix* spp.) growth for bird species diversity and willow species composition in and around Yellowstone National Park's northern range. MS thesis, Montana State University, Bozeman, Montana.
- Barmore, W.J., 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: Research and synthesis 1962–1970. Yellowstone Center for Resources, Yellowstone National Park, Mammoth Hot Springs, Wyoming.
- Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests. In: Shepperd, W.D., Binkley, D., Bartos, D.L., Stohlgren, T.J., Eskew, L.G. (Compilers), Sustaining Aspen in Western Landscapes: Symposium Proceedings. USDA Forest Serv., Proc. RMRS-P-18, Fort Collins, Colorado, pp. 5-14.
- Beschta, R.L., 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. *Ecology* 86, 391–403.
- Beschta, R.L., Ripple, W.J., 2006. River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA. *Earth Surface Processes and Landforms* 31, 1525-1539.
- Beschta, R.L., Ripple, W.J., 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142, 2401-2414.

- Beschta, R.L., Ripple, W.J., 2010. Recovering riparian plant communities with wolves, in northern Yellowstone, USA. *Restoration Ecology* 18,380-389.
- Beschta, R.L., Ripple, W.J., 2011. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade – Comment. *Ecology* doi:10.1890/11-0063.1.
- Beyer, H.L., Merrill, E.H., Varley, N., Boyce, M.S., 2007. Willow on Yellowstone's northern range: Evidence for a trophic cascade. *Ecological Applications* 17, 1563–1571.
- Cahalane, V.H., 1941. Wildlife surpluses in the national parks. *Transactions of the Sixth North American Wildlife Conference*, pp. 355-36.
- Cronquist, A., Holmgren, A.H., Holmgren, P.K., 1997. Intermountain flora: Vascular plants of the Intermountain West. Volume three, Part A, subclass Rosidae. The New York Botanical Garden, Bronx, New York.
- DeByle, N.V., Winokur, R.P. (Eds.), 1985. *Aspen: Ecology and management in the western United States*. USDA Forest Service, General Technical Report RM-119, Fort Collins, Colorado.
- Dobkin, D.S., Singer, F.J., Platts, W.S., 2002. Ecological condition and avian response in willow, aspen, and cottonwood communities of the National Elk Refuge, Jackson, Wyoming. Final report by the independent science panel, High Desert Ecological Research Institute, Bend, Oregon.
- Derig, B.B., Fuller, M.C., 2001. *Wild berries of the West*. Mountain Press Publishing Company, Missoula, Montana.
- Ferris, R., Humphrey, J.W., 1999. A review of potential biodiversity indicators for application in British forests. *Forestry* 72, 313-328

- Grinnell, J., Miller, A.H., 1944. The distribution of the birds of California. Pacific Coast Avifauna No. 27.
- Halofsky, J., Ripple, W., 2008. Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA. *Forestry: An International Journal of Forest Research* 81, 195-207.
- Hess, K, Jr., 1993. Rocky times in Rocky Mountain National Park: An unnatural history. University Press of Colorado, Niwot, Colorado.
- Hester, A.J., Bergman, M., Iason, G.R., Moen, J., 2006. Impacts of large herbivores on community structure and dynamics. In: Danell, K., Bergström, R., Duncan, P., Pastor, J. (Eds.), *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Cambridge University Press, Cambridge, pp. 97-141.
- Hitchcock, C.L., Cronquist, A., 1973. *Flora of the Pacific Northwest*. University of Washington, Seattle, Washington.
- Hollenbeck, J.P., Ripple, W.J., 2007. Aspen snag dynamics, cavity-nesting birds, and trophic cascades in Yellowstone's northern range. *Forestry Ecology and Management* 255, 1095-1103.
- Huffman, D.W., Laughlin, D.C., Pearson, K.M., Pandey, S., 2009. Effects of vertebrate herbivores and shrub characteristics on arthropod assemblages in a northern Arizona forest ecosystem. *Forest Ecology and Management* 258, 616-625.
- Johnsgard, P.A., 1983. *The hummingbirds of North America*. Smithsonian Institution Press, Washington, D.C.
- 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, Utah, pp. 310-320.
- Kay, C.E., 1997. Is aspen doomed? *Journal of Forestry* 95,4-11.
- Kay, C.E., Chadde, S., 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. In: Clary, W.P., McArther, E.D., Bedunah, D., Wambolt, C.L. (Eds.), Proceedings—Symposium on Ecology and Management of Riparian Shrub Communities. US Forest Service, INT-GTR-289, Ogden, Utah, pp. 92-99.
- Kearns, C.A., Inouye, D.W., 1997. Pollinators, flowering plants, and conservation biology. *BioScience* 47, 297-307.
- Keigley, R.B., Frisina, M.R., Fager, C., 2003. A method for determining the onset year of intensive browsing. *Journal of Range Management* 56, 33-38.
- Laliberte, A.S., Ripple, W.J., 2004. Range contractions of North American carnivores and ungulates. *BioScience* 54,123–138.
- Leopold, A.S., Cain, S.A., Cottam, C.M., Gabrielson, I.N., Kimball, T.L., 1963. *Wildlife Management in the National Parks: The Leopold Report*. Advisory Board on Wildlife Management, U.S. Department of Interior, National Park Service, Washington, D.C.
- Martin, T.G., Arcese, P., Scheerder, N., 2011. Browsing down our natural heritage: Deer impacts on vegetation structure and songbird populations across an island archipelago. *Biological Conservation* 144, 459-469.
- Martinka, C.J., Kendall, K.C., 1986. Grizzly bear habitat research in Glacier National Park, Montana, in Proceedings of Grizzly Bear Habitat Symposium, US Forest Service, INT-GTR-207, Ogden, Utah, pp. 19-23.

- Mattson, D.J., Blanchard, B.M., Knight, R.R., 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69, 1619-1629.
- McLellan, B.N., 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus acrtos*) bears. *Canadian Journal of Zoology* 89, 546-558.
- Munro, R.H.M., Nielsen, S.E., Price, M.H., Stenhouse, G.B., Boyce, M.S., 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87, 1112-1121.
- Nelson, J.R., Leege, T.A., 1982. Nutritional requirements and food habits. In: Thomas, J.W., Toweill, D.E (Eds.), *Elk of North America: Ecology and Management*. Stackpile books, Harrisburg, Pennsylvania, pp. 323-367.
- NRC (National Research Council), 2002. *Ecological Dynamics on Yellowstone's Northern Range*. National Academy Press, Washington, D.C.
- Nyoka, S.E., 2010. Can restoration management improve habitat for insect pollinators in Ponderosa Pine forests of the American Southwest? *Ecological Restoration* 28, 280-290.
- Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14, 483–488.
- Painter, L.E., Ripple, W.J., 2012. Effects of bison on willow and cottonwood in northern Yellowstone National Park. *Forest Ecology and Management* 264, 150-158.
- Prichard, J.A., 1999. *Preserving Yellowstone's natural conditions: Science and the perception of nature*. University of Nebraska Press, Lincoln, Nebraska.

- Ripple, W.J., Beschta, R.L., 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecology and Management* 200, 161-181.
- Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138, 514-519.
- Ripple, W.J., Beschta, R.L., 2012a. Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research*, doi 10.1007/s10344-012-0623-5.
- Ripple, W.J., Beschta, R.L., 2012b. Trophic cascades in Yellowstone: The first fifteen years after wolf reintroduction. *Biological Conservation* 145, 205-213.
- Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* 95, 361–370.
- Ripple, W.J., Painter, L.E., Beschta, R.L., Gates, C.C., 2010. Wolves, Elk, Bison, and Secondary Trophic Cascades in Yellowstone National Park. *The Open Ecology Journal* 3, 31-37.
- Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, elk and fire on the northern range of Yellowstone National Park. *Ecology* 76, 2097-2106.
- Rooney, T.P., Wiegmann, S.M., Rogers, D.A., Waller, D.M., 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology* 18, 787-798.
- Savage, S.L. 2005. Vegetation dynamics in Yellowstone's northern range: 1985-1999. MS Thesis, Montana State University, Bozeman, Montana.
- Singer, F.J., 1996. Differences between willow communities browsed by elk and communities protected for 32 years in Yellowstone National Park. In: Singer, F.J (Ed.), *Effects of Grazing*

by Wild Ungulates in Yellowstone National Park. ISDI, National Park Service, Natural Resource Information Division, Denver, Colorado, pp. 279–290.

Smith, C.L., Simpson, A.A., Bailey, V., 1915. Report on investigations of the elk herds in the Yellowstone Region of Wyoming, Montana, and Idaho. December 14, 1915 report to the Biological Survey and Forest Service. Washington, D.C.

Smith, D., Stahler, D., Albers, E., McIntyre, R., Metz, M., Irving, J., Raymond, R., Anton, C., Cassidy-Quimby, K., Bowersock, N., 2011. Yellowstone wolf project: Annual report 2010. Yellowstone Center for Resources, Yellowstone National Park, Mammoth Hot Springs, Wyoming.

Smith, D.W., Peterson, R.O., Houston, D.B., 2003. Yellowstone after wolves. *BioScience* 53, 330-340.

Tomback, D., Arno, S., Keane, R., 2001. Whitebark pine communities: Ecology and restoration. Island Press, Washington, DC.

White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, elk, and fire in the Rocky Mountain national Parks of North America. *Wildlife Society Bulletin* 26, 449–462.

White, P.J., Proffitt, K.M., Lemke, T.O., 2012. Changes in elk distribution and group sizes after wolf restoration. *New American Midland Naturalist* 167, 174-187.

White, P.J., Proffitt, K.M., Mech, L.D., Evans, S.B., Cunningham, J.A., Hamlin, K.L., 2010. Migration of northern Yellowstone elk: Implications of spatial structuring. *Journal of Mammalogy* 91, 827-37.

Wolf, E.C., Cooper, D.J., Hobbs, N.T., 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* 17,1572-1587.

YNP (Yellowstone National Park), 1958. Management plan for northern elk herd, Yellowstone National Park. National Park Service, Mammoth Hot Springs, Wyoming.