

# Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration

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**Citation:** Painter, L. E., R. L. Beschta, E. J. Larsen, and W. J. Ripple. 2018. Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. *Ecosphere* 9(8):e02376. 10.1002/ecs2.2376

**Abstract.** Quaking aspen (*Populus tremuloides*) recruitment during the 1980s–90s was suppressed by Rocky Mountain elk (*Cervus canadensis*) herbivory on winter ranges in the Yellowstone region, and saplings (young aspen taller than 2 m) were rare. Following the 1995–96 reintroduction of gray wolves (*Canis lupus*), browsing decreased and sapling recruitment increased in Yellowstone National Park. We compared aspen data from inside the park to data collected in three winter ranges outside the park. For most areas, the percentage of young aspen browsed annually was 80–100% in 1997–98, decreasing to 30–60% in 2011–15. Sapling recruitment was inversely correlated with browsing intensity, and increased despite climate trends unfavorable for aspen. Browsing decreased with decreasing elk density, a relationship suggesting that densities greater than about 4 elk/km<sup>2</sup> resulted in consistently strong browsing effects likely to suppress aspen recruitment. Changes in elk density and distribution were influenced by predators, as well as human hunters. Most evidence for trophic cascades involving large terrestrial mammals has been from protected areas within national parks. This study provides evidence of widespread changes in plant communities resulting from large carnivore restoration, extending outside a protected national park to areas with hunting, livestock grazing, and other human activities.

**Key words:** aspen recruitment; *Canis lupus*; *Cervus canadensis*; Greater Yellowstone; herbivory; indirect effects; passive restoration; *Populus tremuloides*; trophic cascade; wapiti.

**Received** 28 April 2018; revised 28 June 2018; accepted 3 July 2018. Corresponding Editor: Debra P. C. Peters.

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## INTRODUCTION

Quaking aspen (*Populus tremuloides*) forms a small but important component of ecosystems in the northern Rocky Mountains, with a large effect on habitat diversity and biodiversity as one of the few deciduous tree species in the region. Rocky Mountain elk (wapiti, *Cervus canadensis*) forage on young aspen in fall and winter, and high levels of herbivory by elk can suppress heights of young aspen. This process over time can result in a loss of understory aspen and shrubs in aspen stands, and eventually loss of entire stands, as old trees die and are not

replaced (Romme et al. 1995, White et al. 1998, Barmore 2003, Smith et al. 2016). Gray wolves (*Canis lupus*) and other large carnivores, by affecting prey density and behavior, may indirectly affect plant communities through a trophic cascade (White et al. 2003, Peterson et al. 2014, Flagel et al. 2015). So far, most of the evidence for trophic cascades associated with wolves and elk has been from protected areas in national parks (Soulé et al. 2003, Hebblewhite et al. 2005, Beschta and Ripple 2007, 2009, Kuijper et al. 2013, Muhly et al. 2013). Outside of parks, human hunters may also influence elk density and behavior (Proffitt et al. 2013), possibly

resulting in synergistic effects by predators and hunters on herbivores and plant communities. Alternatively, trophic effects of predators may be weakened by human influences such as predator control, forage subsidies, and livestock grazing (Muhly et al. 2013, Wilmers and Levi 2013).

The ecosystem of Yellowstone National Park (YNP) provides an example of the relationships between aspen, elk, and large carnivores. In the late 1800s and early 1900s, aspen stands covered much more area than they do now in the valleys of northern Yellowstone (YNP 1997, NRC 2002). After wolves were extirpated in the 1920s and other predators were greatly reduced, browsing by elk was intensive and aspen stands in the northern Yellowstone elk winter range (northern range) failed to recruit new trees (Romme et al. 1995, Ripple and Larsen 2000). Although elk in the park were culled to reduce their impacts, young aspen rarely grew above the reach of elk (YNP 1997, Barmore 2003, Wagner 2006). Culling in the park ended in 1968, and elk herds grew to record numbers in the 1980s–90s (Coughenour and Singer 1996), expanding beyond the park boundary and suppressing aspen recruitment in winter ranges both inside and outside the park (St. John 1995, Kay 2001, Larsen and Ripple 2003, 2005, Halofsky and Ripple 2008).

During the first two decades after the return of wolves in 1995–96, elk densities decreased in northern YNP, and an increasing number of aspen stands produced saplings (young aspen >2 m in height), an indication that some aspen were escaping from browsing (Ripple and Beschta 2007, 2012, Painter et al. 2014, 2015, Klapotsky 2016, Beschta et al. 2018). These changes were associated with reduced herbivory, consistent with a trophic cascade whereby wolves, combined with bears (*Ursus* spp.) and cougars (*Puma concolor*), benefited aspen through effects on elk density or behavior (Hernandez and Laundre 2005, Hamlin et al. 2009, Peterson et al. 2014, Beschta and Ripple 2016). Human hunters outside the park also took many elk before 2006 (Vucetich et al. 2005, Eberhardt et al. 2007), but similar harvests previously had not been sufficient to limit the northern Yellowstone herd (Lemke et al. 1998, White and Garrott 2005).

We examined evidence for trophic cascades involving aspen, elk, and wolves in the

Yellowstone region, using surveys of aspen stands in elk winter ranges north, west, and east of the park, as well as inside the park boundary. Young aspen in these ranges were suppressed by browsing in the 1980s–90s, but after the return of wolves in the late 1990s, elk densities and distributions changed (Hamlin et al. 2009, Christianson and Creel 2014). We investigated the possibility that browsing intensity decreased and aspen recruitment increased in winter ranges outside the park, as has occurred in northern YNP (Painter et al. 2014, 2015), and that browsing intensity was linked with recent changes in elk abundance and distribution.

## METHODS

### Study areas

Some elk remain inside YNP during winter, but many elk in the Yellowstone region spend summer in high-elevation meadows in or near the park, migrating in winter to lower ranges outside the park (Lovaas 1970, Craighead et al. 1972, Houston 1982, Rudd et al. 1983, Hamlin et al. 2009). Elk share the winter ranges with deer (*Odocoileus* spp.), and a small number of moose (*Alces alces*) and pronghorn (*Antilocapra americana*). Bison (*Bison bison*) are present in northern YNP, and livestock (cattle and horses) graze some areas outside the park.

Aspen trees typically grow in clonal stands that may persist for thousands of years, as new root sprouts replace dying trees. Many such stands in northern Yellowstone were dying out in the late 20th century as herbivory suppressed recruitment of new trees. Coniferous trees also may eventually replace some aspen stands without fire to reset forest succession, a process that accounts for some of the loss of aspen in Yellowstone. Fire stimulates new aspen sprouts and seedlings, but intensive herbivory may suppress growth of these new sprouts, as happened in northern Yellowstone after the fires of 1988 (Romme et al. 1995, YNP 1997, Halofsky et al. 2008, Hansen et al. 2016, Smith et al. 2016).

We surveyed aspen during 2011–2015, in three winter ranges in the Yellowstone region (Craighead et al. 1972, Houston 1982), with the following study areas inside and outside the park boundary (Fig. 1, Table 1):

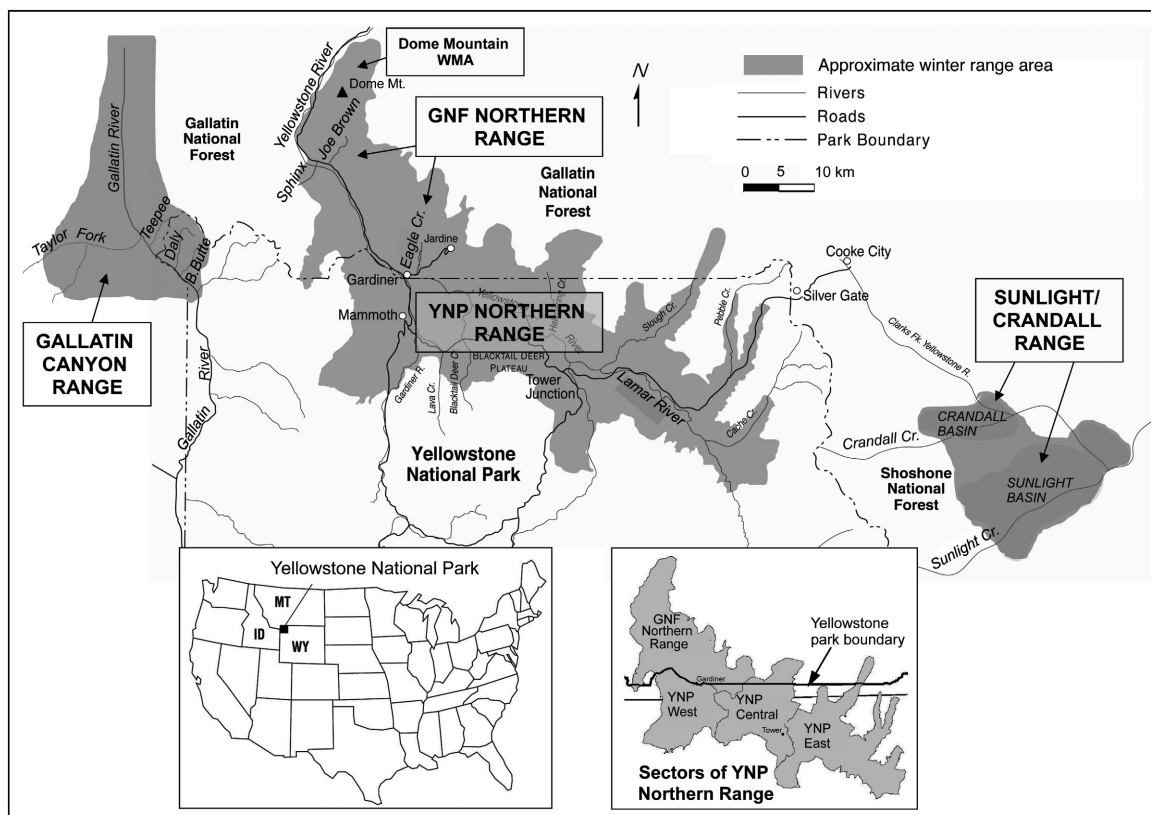


Fig. 1. Map of elk winter ranges in the northern Yellowstone region. Gray shading indicates the approximate area used by wintering elk. Lower right inset shows West, Central, and East sectors of Yellowstone National Park (YNP) Northern Range within the park, and Gallatin National Forest Northern Range north of the park. Lower left inset shows location of YNP in the United States.

1. YNP Northern Range—The northern Yellowstone elk winter range inside YNP, divided into West, Central, and East sectors (Painter et al. 2014, 2015).
2. Gallatin National Forest (GNF) Northern Range and Dome Mountain WMA—The portion of the northern range north of the YNP boundary divided into two areas: (1) the GNF Northern Range, in Gardiner Basin; and (2) the area north of Dome Mountain, including the Dome Mountain Wildlife Management Area (WMA).
3. Gallatin Canyon Range—The winter range of the Gallatin Canyon elk herd in the north-west corner of YNP and GNF to the west (Lovaas 1970), with study areas inside YNP (Daly and Black Butte creek basins), and outside (Taylor Fork and Teepee Creek).
4. Sunlight/Crandall Range—Sunlight Creek and Crandall Creek basins, in the Shoshone National Forest east of the park (Rudd et al. 1983, Painter 2013).

Aspen surveys in 1997–98 (Larsen and Ripple 2005) in the YNP Northern Range, GNF Northern Range, and Sunlight/Crandall Range provided a baseline for aspen conditions when wolves were beginning to colonize these areas.

When elk numbers were low in northern Yellowstone in the 1960–70s (Appendix S1: Fig. S1a), most elk wintered inside the park (Houston 1982, YNP 1997). This resulted in low elk densities outside the park, which likely contributed to new recruitment of aspen trees in the GNF Northern Range and Sunlight/Crandall Range (Larsen and Ripple 2003, Wagner 2006).

Table 1. Year and method of aspen sampling for ten study areas in three winter ranges and thus are lower than those previously published by Larsen and Ripple (2003, 2005).

Study area	Year	Stand selection	Sampling method	<i>n</i>
YNP Northern Range, in YNP, 3 areas: YNP East, YNP Central, YNP West	1997–98†	Random, aerial photograph	Random plot	79
	2012‡	Previous GPS locations	Random plot + 5 tallest	87
GNF Northern Range, north of YNP	1998†	Random, aerial photograph	Random plot	52
	2015	Previous GPS locations	Plotless+count >2 m	22
Dome Mountain WMA	2015	Visible from roads/trails	Plotless+count >2 m	7
Gallatin Canyon Range, 1 area in YNP: Daly/Black Butte	2014	Random, aerial photograph§	Plotless+count >2 m	30
Gallatin Canyon Range, 2 areas in Gallatin NF: Taylor Fork, Teepee Creek.	2014	Visible from roads/trails	Plotless+count >2 m	46
Sunlight/Crandall Range in Shoshone NF, 2 areas: Sunlight, Crandall	1998†	Random, aerial photograph	Random plot	36
	2011	Previous GPS locations	Random plot + 5 tallest	43

Notes: GNF, Gallatin National Forest; WMA, Wildlife Management Area; YNP, YNP, Yellowstone National Park.

Counts (*n*) for 1997–98 exclude those located on scree slopes.

† Larsen and Ripple (2003, 2005).

‡ Painter et al. (2014, 2015).

§ Halofsky and Ripple (2008).

As elk increased to high numbers in the 1980–90s, more elk migrated to winter ranges north, west, and east of the park (Houston 1982, Rudd et al. 1983, Lemke et al. 1998), suppressing young aspen there (St. John 1995, Kay 2001, Larsen and Ripple 2005). Wolves colonized the Gallatin Canyon Range in 1997 (Appendix S1: Fig. S1) and the Sunlight/Crandall Range in 1998 (USFWS 2000–2011, Creel and Winnie 2005, Hamlin et al. 2009), and hunting subsequently was reduced (Appendix S1: Fig. S1) in response to decreases in these herds (WGFD 1980–2014, Hamlin and Cunningham 2009). In northern Yellowstone, the winter elk hunt (Gardiner Late Elk Hunt) that affected elk migrating from the park was greatly reduced in 2006 and ended in 2010 (Eberhardt et al. 2007, White et al. 2012).

### Aspen stand selection

Aspen stands in YNP Northern Range, GNF Northern Range, and Sunlight/Crandall were selected randomly from aerial photographs and mapped with GPS in 1997–98 (Table 1). Aspen trees separated by >30 m were considered separate stands, consistent with previous work in northern Yellowstone by Kay (1990), and this definition was applied in all of our surveys. Unlike the large hillside expanses of aspen sometimes seen in the mountain west following fires, aspen stands in northern Yellowstone are typically relatively small clonal stands with >50% overstory aspen dominance (Painter et al. 2014).

In YNP Northern Range and Sunlight/Crandall Range, we revisited all of these mapped stands (Painter 2013, Painter et al. 2014). In GNF Northern Range, we surveyed stands in Eagle, Joe Brown, and Sphinx Creek basins, because of the prevalence of aspen there. We added a study area north of Dome Mountain and Yankee Jim Canyon in Dome Mountain WMA (Fig. 1), where we surveyed all stands visible from the access road, or encountered while hiking to these stands. Stands on steep (>20 degrees) or scree slopes were excluded because these conditions may inhibit ungulate access (St. John 1995, Larsen and Ripple 2003).

On the west side of the park in the Gallatin Canyon winter range (Table 1), aspen stands in lower Daly and Black Butte Creek basins were mapped from aerial photographs by Halofsky and Ripple (2008). We relocated and surveyed every second stand (half of the stands) in these areas. Outside the park boundary in Taylor Fork and Teepee Creek basins, we surveyed stands visible from roads or trails, or encountered while hiking to stands. Because of the proximity of roads used by hunters in Taylor Fork, we required that sampled stands be >100 m from a road.

### Aspen sampling

Sampling was focused primarily on young aspen, those <6 cm dbh (diameter at breast height), while trees were defined as >6 cm dbh.



Young aspen in the 1990s typically were browsed heavily, and <1 m tall, so the presence of aspen saplings, defined as young aspen taller than 2 m, was an indication of significant change (Romme et al. 1995, Kay 2001, Larsen and Ripple 2005, Winnie 2012, Painter et al. 2014). Two meters is the height at which young aspen typically escape from elk browsing. In YNP Northern Range (2012) and Sunlight/Crandall Range (2011), browsing rates and young aspen heights were measured in each stand in a randomly placed 2 × 30 m sampling plot, from the edge of the stand toward the centroid, as was done in 1997–98 (Larsen and Ripple 2003, 2005, Painter et al. 2014). Browsing rates were measured as the percentage of young aspen <2 m in spring height that were browsed on the top leader in the previous year (annual browsing rate), or the current growing season (summer browsing). In addition to these random plots, we measured browsing and growth histories of the five tallest young aspen in each stand (excluding aspen protected from browsing by obstacles), by examining annual growth nodes on the plant stem (plant architecture; Keigley and Frisina 1998, Ripple and Beschta 2012, Painter et al. 2014). The tallest were a useful indicator of new recruitment and changes in browsing pressure, given the gap in recruitment that resulted from past suppression by browsing (Ripple and Beschta 2007). The combination of random sampling plots and the five tallest in a stand gave two different perspectives on young aspen dynamics, one the population average (comparable to data from 1998) and the other providing the earliest indicators of new height growth. In the 1997–98 data, and for comparison to those data, the presence of one or more saplings in a sampling plot was used as an indicator of recruitment. For areas sampled in 2011–15, an additional index of recruitment rate was measured as the percentage of stands with five or more saplings in the entire stand.

For Gallatin Canyon (2014) and GNF Northern Range (2015), we used plotless sampling for rapid assessment of browsing and recruitment (Table 1). To test this plotless method for consistency with the previous work, we also measured browsing in 18 stands using a random 30-m sampling plot, and compared these duplicate measurements. A stand was entered at a point representative in slope and young aspen height

and density. The closest overstory tree was selected as a sampling location and its dbh recorded. Browsing was estimated from the ten closest young aspen <2 m tall and >2 yr of age. The number of saplings in each stand was recorded, excluding those protected by physical barriers. Five of the tallest young aspen in the stand were examined for the number of years elapsed (growth nodes) since they had been <1 m in height. This measurement represented the time since the stand began to be released from browsing, as suppressed stands typically had no young aspen >1 m (Kay 2001, Larsen and Ripple 2005).

In all areas, conifer cover in a stand was estimated as 0%, <10%, 10–50%, or >50%. Ungulate scat piles (of elk, deer, moose, bison, cattle, and horses) were counted in two belt transects, each 2 m wide and 50 m long, adjacent to each stand. Scat transects were located with sparse ground cover and low slope, in xeric grassland or open forest edges, providing an index of ungulate density in an area but not within an aspen stand.

### Analysis

Aspen stands were grouped for analysis based on geographic boundaries and land ownership (Table 1, Fig. 1). Hunting has been much more restricted in Teepee Creek basin than in Taylor Fork, so these areas were analyzed separately. For each stand, we calculated a browsing rate and then a grand mean for each study area. Data from 1997–98 lumped new summer sprouts (not yet exposed to winter browsing) with older sprouts, but in later surveys, we did not include new sprouts in browsing rate calculations. To correct this bias in the 1997–98 data, we added 10 percentage points to browsing rates from 1997–98, based on our finding of 13% new sprouts in YNP Northern Range in 2012. This raised the highest browsing rate in 1997–98 to 100% and provided an estimate more comparable to other sampling methods, but did not affect the significance of any statistical tests.

Logistic regression was used to test for a relationship between aspen recruitment and browsing rate, using R statistical software (R Development Core Team 2008). We also compared different methods of browsing rate estimation (i.e., random plot vs. plotless; random plot vs. 5 tallest in stand) to evaluate whether the

methods produced similar results. We compared estimates made at different times in different field studies, to assess the validity and repeatability of estimating past browsing using growth nodes of the five tallest young aspen (stand data were pooled in each area). To test the link between herbivory and ungulates, we examined browsing rate as a function of ungulate scat density (cervids, bison, and cattle) for areas surveyed in 2011–2015.

#### *Elk counts, hunting harvest, and wolf predation*

Annual aerial elk count data (1987–2015) for the northern Yellowstone elk herd were obtained from the Yellowstone Center for Resources. Counts were done once in winter, providing a snapshot of elk distribution. Mapped count units allowed for calculation of elk densities for sectors of the northern range (Painter et al. 2015). For density calculations only, a correction factor of 1.32 was used to compensate for elk missed in the counts (Eberhardt et al. 2007). We tested the hypothesized relationship between browsing rate and elk density by combining datasets from surveys of aspen on the northern range and Sunlight Creek basin. Two aspen surveys in the East sector of YNP (Ripple and Beschta 2012, Painter et al. 2014) provided a time series of browsing rates for 1999–2012 (Fig. 3a). These data were combined with aspen surveys in: the West, Central, and East sectors of YNP Northern Range (years 1998 and 2012); GNF Northern Range north of the park (1998 and 2015); and Sunlight Creek basin (1998 and 2011), as shown in Table 1 and Fig. 2. For Sunlight basin, counts were divided by the area of the Sunlight Creek drainage (350 km<sup>2</sup>), and the 1999 count was used as there was no count in 1998 (Appendix S1: Fig. S1c).

We estimated the annual percentage of the northern Yellowstone elk herd inside the park based on winter count data from Houston (1982), combined with count unit data that began in 1987. Harvest data for the Gardiner Late Elk Hunt 1975–2006 were from published sources (Coughenour and Singer 1996, Lemke et al. 1998, Vucetich et al. 2005, White and Garrott 2005, White et al. 2012, Canfield 2014). The number of elk killed in 1995–2014 by wolves on the YNP Northern Range was estimated from annual wolf counts (Smith et al. 2015), using a kill rate of

1.6 elk·wolf<sup>-1</sup>·month<sup>-1</sup>, based on a rate of 1.9 in winter and 1.3 in summer (Smith et al. 2004, White and Garrott 2005). Elk counts and harvest data for Gallatin Canyon and Sunlight/Crandall were provided by Montana Fish Wildlife and Parks, and Wyoming Game and Fish Department.

The annual northern range elk counts by map unit were used to calculate the percentage of the total herd found north of Dome Mountain (count units 66, 67, and 68) in 1987–2015. Additional winter counts of the number of elk north of the park and the maximum number north of Dome Mountain began in 1975 (Canfield 2014, Loveless 2017), as late winter migration surveys. We used these winter migration data, which included years missing from annual northern range unit counts, to compare means (*t*-test for unequal variance; *F*-test for difference in variance) for the period of high elk counts on the northern range prior to wolf restoration (1978–1994), vs. the recent period of low counts (2005–2015), for three areas: YNP Northern Range inside the park; GNF Northern Range (Gardiner Basin); and the area north of Dome Mountain. Some years had no counts, but these time intervals provided a minimum of 10 counts in each group. Mean elk counts represent the average browsing pressure on aspen during these two time periods, as suppression or release of aspen recruitment results from a pattern of browsing over time, not a single year.

## RESULTS

Aspen stands lacked intermediate sizes (young trees), evidence of a past gap in recruitment that confirmed a history of aspen suppression, in all areas except at Dome Mountain WMA. All areas surveyed in 1997–98 had high annual browsing rates (84–100%) and very low rates of aspen recruitment (Fig. 2a); few plots had any saplings, and these were all outside the park. In 2011–15, however, rates of recruitment varied widely by study area and were distributed along a gradient of browsing intensity, with a strong inverse relationship between browsing and aspen recruitment (Fig. 2b, *P* < 0.01). Most aspen saplings grew taller than 1 m within the last decade, as browsing decreased (after 2004; Table 2, Fig. 3). Sunlight/Crandall and GNF Northern Range had

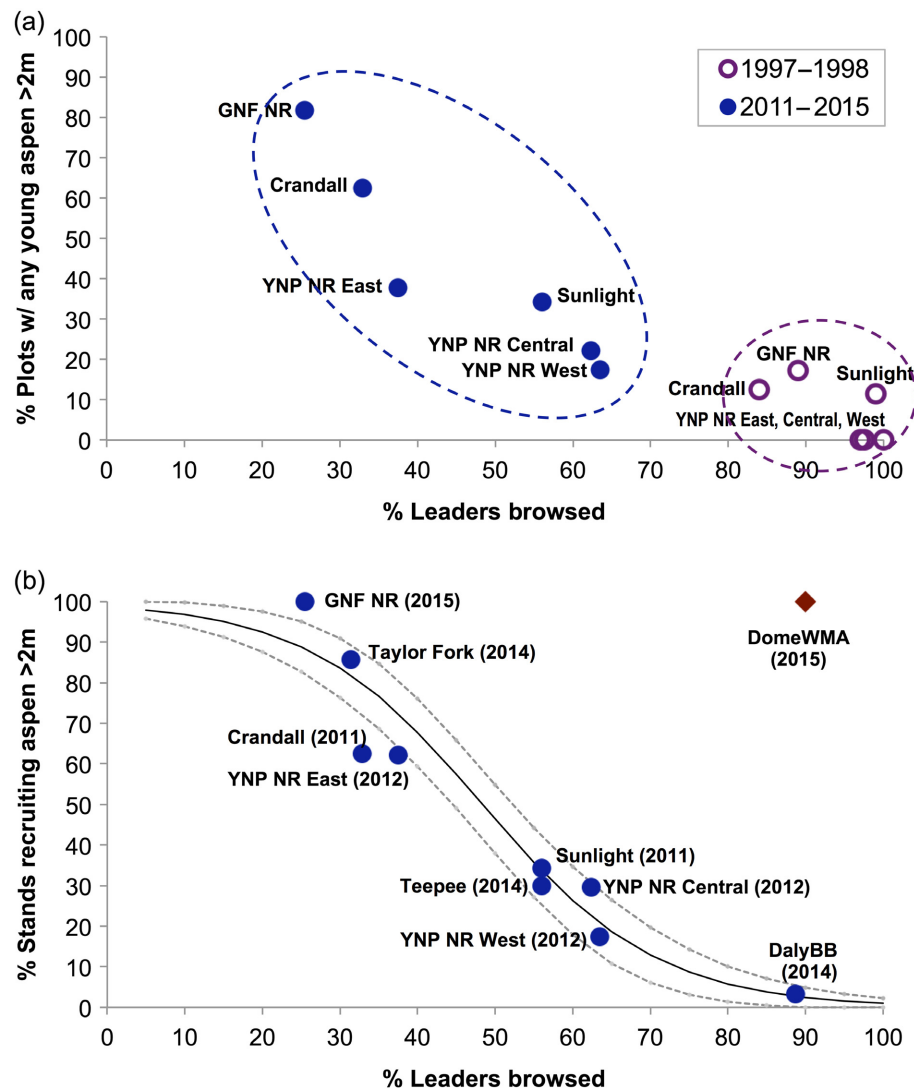


Fig. 2. (a) Average browsing rate and percentage of stands with at least one aspen sapling (aspen >2 m tall and <6 cm dbh) in random plots in 1997–98 and 2011–2015. (b) During 2011–2015, most study areas reflected a new state of low to moderate herbivory; dotted lines show 95% confidence interval for logistic regression,  $P < 0.01$  (excluding Dome Mt. Wildlife Management Area); recruitment was indicated by the presence of at least five aspen saplings per stand. Gallatin National Forest (GNF) Northern Range (GNF NR) in 2015 included Eagle, Sphinx, and Joe Brown creeks; Yellowstone National Park (YNP) Northern Range inside the park (YNP NR) was divided into West, Central, and East sectors (see map, Fig. 1). Daly and Black Butte Creeks (DalyBB), Teepee Creek, and Taylor Fork were in the Gallatin Canyon range.

some aspen recruitment in the 1970s (Larsen and Ripple 2003), and we found evidence of this as well in Taylor Fork where some stands had trees 12–20 cm dbh, but lacked smaller trees. Dome Mountain WMA had a different history of elk use, and aspen stands had a continuous

multi-age structure with no past gap in recruitment; therefore, this area was not included in the regression analysis of browsing and recruitment (Fig. 2b). Summer browsing rates in all areas were low on average (Table 2), but much greater in some individual stands (range 0–65%).

Table 2. Characteristics of aspen stands sampled during 2011–15 in the Yellowstone region.

Study areas	Age >1 m (yr)	Browsing (%)	Summer browsing (%)	Cervid scat (/100 m <sup>2</sup> )	>50% conifer (%)
YNP Northern Range (all)	2	52	1	10	18
YNP Northern Range West	1	64	20	17	30
YNP Northern Range Central	2	62	10	11	7
YNP Northern Range East	3	38	5	4	19
GNF Northern Range	8	26	5	11	23
Dome Mountain WMA	(no age gap)	90	7	52	0
Gallatin Canyon Range					
Taylor Fork	7	31	2	3	17
Teepee Creek	2	56	2	6	30
Daly/Black Butte	0	89	4	16	33
Sunlight/Crandall Range	4	52	5	21	60

Notes: GNF, Gallatin National Forest; WMA, Wildlife Management Area; YNP, Yellowstone National Park.

Age is years since the tallest young aspen were <1 m in height (age >1 m); browsing is percentage of leaders browsed previous year (annual browsing); summer browsing is percentage of leaders browsed in the growing season (summer browsing); cervid scat is density of cervid scat piles; final column is percentage of stands with >50% conifer cover.

### Cross-checking and validation of sampling methods

1. A paired *t*-test showed no difference between mean browsing rates obtained by the plotless method vs. a 2 × 30 m plot in the same stands (mean = 40.6% vs. 38.9%;  $P = 0.59$ ;  $n = 18$  stands).
2. Estimates of browsing in random plots vs. the five tallest in each stand were very similar in 1997–99 for the YNP East sector, in 2011 for Sunlight/Crandall, and in 2011 and 2012 for YNP (regression slope = 1.02,  $r^2 = 0.99$ ,  $P < 0.01$ ,  $n = 4$  study areas, summarizing 130 sample plots; see Appendix S1: Table S3, Fig. S4).
3. Browsing rate estimates made in 2012 for the years 2005, 2006, and 2010, using plant architecture of the five tallest young aspen, were very close to direct measurements made in 2006 and 2010, verifying this method (Fig. 3a). Estimates of past browsing from growth histories of the tallest young aspen were consistent with other methods, confirming these estimates and the downward trend they demonstrate.

### Elk density and ungulate scat

Browsing was positively correlated with elk density (Fig. 3b,  $r^2 = 0.58$ ,  $P < 0.01$ ,  $n = 25$ ), supporting the hypothesis that the recent reduction in browsing was linked to changes in elk density

and distribution. Browsing rates were consistently high (70–100%) where elk densities were greater than about 4 elk/km<sup>2</sup>. Browsing rates were significantly correlated with cervid scat density for the ten areas surveyed in 2011–2015 ( $r^2 = 0.47$ ,  $P = 0.03$ ,  $n = 10$ ). In addition to cervids, some areas had livestock or bison, but inclusion of these scat counts did not improve the regression model.

Cervid scat piles were almost all (92%) from elk (Table 2), the rest from deer and moose. Elk, deer, and moose all browse aspen, but these results show that elk were by far the dominant influence on browsing intensity. Cattle accounted for 20% of all scat piles in the GNF Northern Range (at Joe Brown and Sphinx Creeks), and 23% in Sunlight/Crandall. Bison accounted for 42% of all scat piles in the YNP Northern Range, and 1.4% at Eagle Creek. Eagle Creek and most of the Taylor Fork area had no livestock grazing (S. LaMont, Gallatin National Forest, *personal communication*). Grazing was reduced in the study period in the Crandall Creek area due to conflicts with wolves, but continued with full stocking rates at Sunlight Creek (J. Hicks, Shoshone National Forest, *personal communication*).

### Elk counts, hunting harvest, and wolves

The percentage of the northern Yellowstone elk herd wintering inside the park was high prior to 1995 (mean 83% for 1927–1994), then declined sharply after the return of wolves ( $P < 0.01$ , Fig. 4a). Harvest in the Gardiner Late Elk Hunt



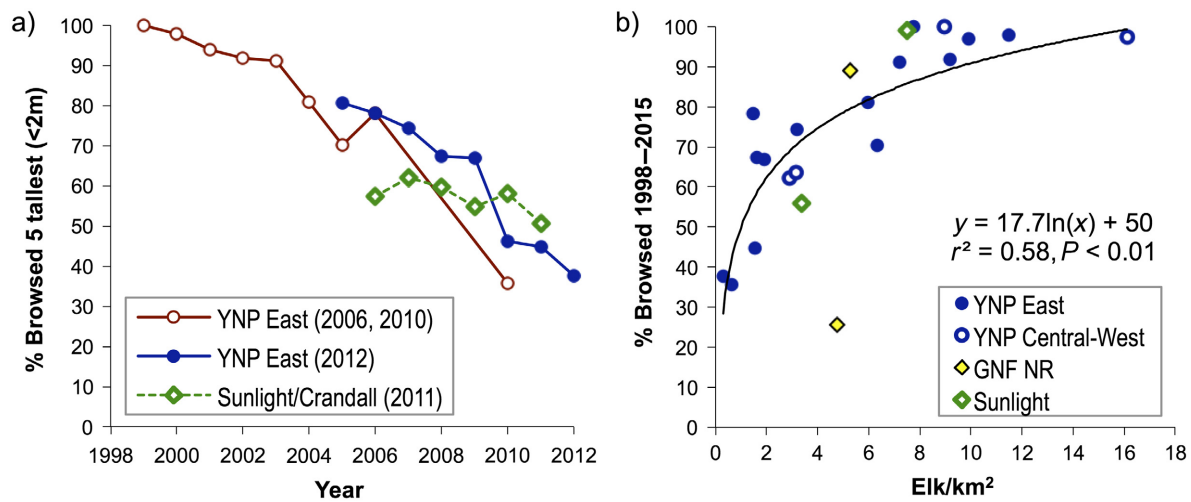


Fig. 3. (a) Browsing rates over time for the five tallest young aspen in each stand, excluding those >2 m in height, for the east sector of the YNP Northern Range (Fig. 1). Measurements were made in the year indicated, by analysis of annual growth nodes for past years (Ripple and Beschta 2007). Stands sampled in 2006 and 2010 by Ripple and Beschta (2012) were different from those sampled in Yellowstone National Park (YNP) East in 2012 by Painter et al. (2015). Browsing rates for YNP East in 2006 and 2010 are higher than published previously (Ripple and Beschta 2007, 2012) due to our analysis excluding saplings (>2 m in height). (b) Average browsing rates as a function of elk density combining several datasets: YNP East sector 1999–2012 (Fig. 3a); YNP West, Central, and East sectors (sampled 1998 and 2012); Gallatin National Forest (GNF) Northern Range north of the park (sampled 1998 and 2015); and Sunlight Basin (sampled 1998 and 2011). Each study area was represented by two measurements, separated by 13–17 yr, with additional years for YNP East. Elk densities were corrected for sightability.

was highly variable before 1996, then more consistent until permits were reduced (Fig. 4b). The estimated number of elk killed by wolves fluctuated with the number of wolves and then stabilized at about 700 elk/yr after 2008 (Fig. 4b). Elk counts in the lower Madison Valley (HD 360 and 362) increased strongly during the study period, while counts of the Madison Headwaters elk in the park and Gallatin Canyon elk near the park decreased (Appendix S1: Fig. S3).

The percentage of the entire northern range herd north of Dome Mountain (count units 66, 67, 68) in the annual elk count increased during the study period 1998–2015 ( $P < 0.01$ ) and was about 30–50% of the total herd after 2005. Comparing the period of high elk numbers before wolves (1978–1994) to the recent period of low elk numbers (2005–15; Fig. 5) produced the following results:

1. Total northern range elk count (Appendix S1: Fig. S2a) decreased ( $P < 0.01$ ), and variance decreased ( $P = 0.02$ ).
2. Counts of elk migrating north of the park (Fig. 5, Appendix S1: Fig. S2b) did not change significantly ( $P = 0.85$ ), but variance decreased ( $P < 0.01$ ).
3. Elk counts decreased ( $P = 0.04$ ) in GNF Northern Range (Gardiner Basin, Fig. 5, Appendix S1: Fig. S2d), and the variance of counts decreased ( $P < 0.01$ ).
4. North of Dome Mountain (Fig. 5, Appendix S1: Fig. S2c), elk counts increased ( $P < 0.01$ ), and variance decreased ( $P = 0.01$ ).

These tests showed a general pattern during the study period of elk distribution shifting toward the extreme northern end of the northern range, north of Dome Mountain.

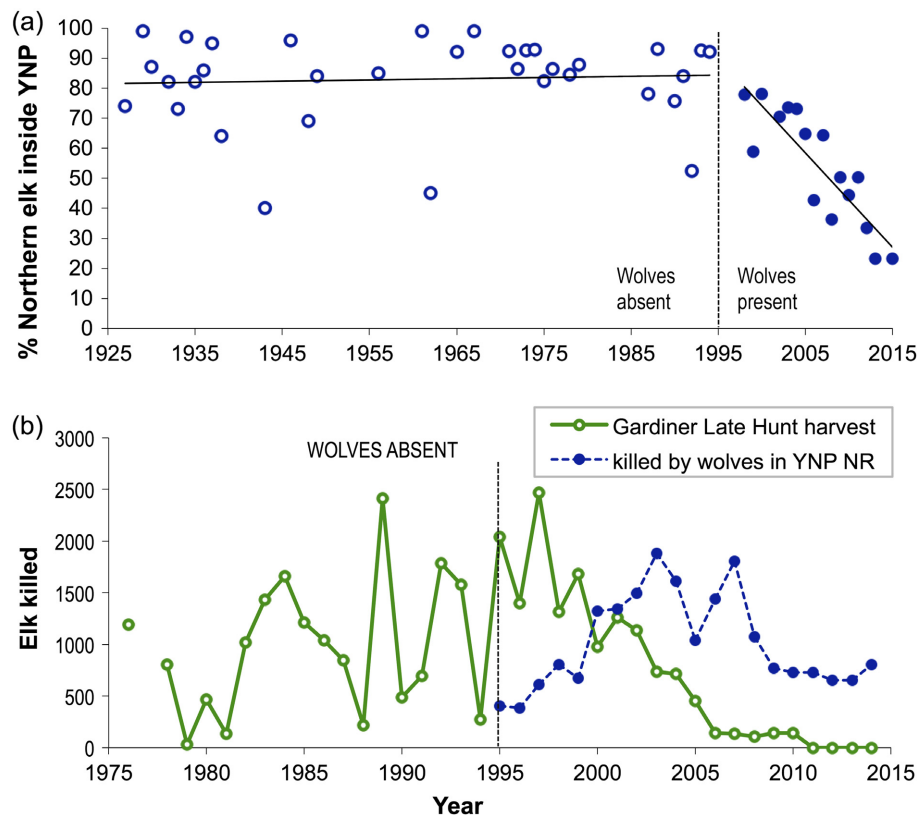


Fig. 4. (a) Percentage of northern Yellowstone elk herd counted in winter in Yellowstone National Park during 1927–2015 (1927–94: slope = 0.04,  $r^2 = 0.04$ ,  $P = 0.72$ ; 1998–2015: slope =  $-3.1$ ,  $r^2 = 0.74$ ,  $P < 0.01$ ; test for difference  $P < 0.01$ ). (b) Estimated number of elk killed annually by hunters north of Yellowstone National Park in the Gardiner Late Elk Hunt, 1976–2010, and by wolves inside the park in YNP Northern Range. Late hunt permits were greatly reduced after 2005, and none were issued after 2010. Wolf kills were estimated based on the number of wolves in YNP Northern Range (see text for methods).

## DISCUSSION

Following the return of wolves to the Yellowstone region in 1995–96, browsing of young aspen decreased and aspen recruitment increased in three elk winter ranges, outside as well as inside the park (Fig. 2a). The proportion of aspen stands with saplings was inversely correlated with browsing intensity (Fig. 2b), and browsing intensity was linked with elk density (Fig. 3b), which decreased in most areas after the return of wolves (Appendix S1: Figs. S1, S2) and concurrent recovery of grizzly bears (*U. arctos*) (Barber-Meyer et al. 2008). Thus, changes in browsing and aspen recruitment followed the reduction and redistribution of elk herds, which was influenced by predators, interacting with the effects of human

hunters (Fig. 4; Eberhardt et al. 2007, Hamlin et al. 2009, White et al. 2012, Creel et al. 2013, White and Garrott 2013). The recent changes in aspen browsing and recruitment we documented were consistent with a trophic cascade over a broad scale resulting from large carnivore restoration, on lands with hunting and grazing outside YNP, as well as protected areas inside the park. The increase in aspen saplings on elk winter ranges in and near the park breaks the historical pattern of suppressed aspen recruitment, strongly suggesting that aspen have been a “beneficiary” of wolf reintroduction (Klaptosky 2016).

### New aspen growth

When elk numbers were high in the 1990s, browsing was intense, young aspen were

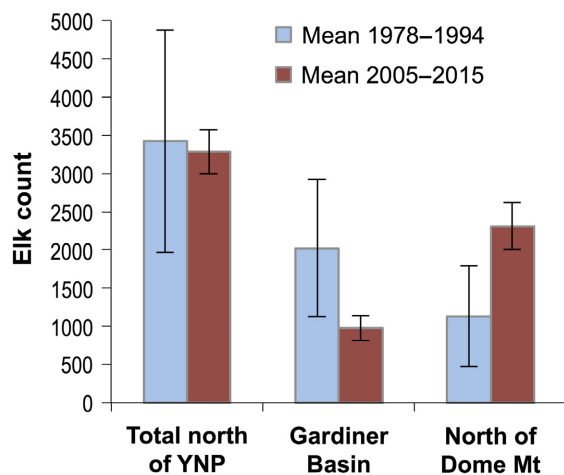


Fig. 5. Aspen recruitment is affected by browsing pressure over time, not a single year. Figure shows average of elk counts north of the Yellowstone National Park (YNP) boundary, for time periods before and after large carnivore restoration: 1978–1994, when the northern Yellowstone elk herd (including in the park) was at historically high numbers; and 2005–2015, when overall counts were low. Total is equal to the sum of the other two areas: Gardiner Basin (Gallatin National Forest Northern Range) plus the area north of Dome Mountain. Error bars indicate two standard errors. Mean and variance between the time periods were significantly different for Gardiner Basin (mean,  $P = 0.04$ ; variance,  $P < 0.01$ ) and north of Dome Mt. (mean,  $P < 0.01$ ; variance,  $P = 0.01$ ), but not for the combined total. Counts of elk were obtained from Canfield (2014) and Loveless (2017; Appendix S1: Fig. S2).

consistently short (Fig. 2a), and aspen trees were decreasing in winter ranges in the Yellowstone region (St. John 1995, Kay 2001, Larsen and Ripple 2005). These conditions were confirmed in our recent aspen surveys by a lack of young trees, which was evidence of a distinct gap in recruitment between mature trees and a new cohort of young aspen. This gap demonstrated that there was a period of low recruitment, but then something changed recently, resulting in new saplings (Table 2). This change has been widespread but uneven, with much new recruitment in most but not all study areas (Fig. 2b). Since young aspen in these areas have only recently begun growing taller, it is likely that recruitment rates will increase over time as the

ecosystem responds to the new browsing regime. With moderate rates of browsing, young aspen grow taller slowly, as they are still browsed in some years. In some areas, such as Daly Creek basin, aspen remained suppressed due to locally high rates of browsing (Winnie 2012).

#### *The cause of new aspen recruitment*

Our results support the hypothesis that a reduction in browsing intensity since the late 1990s has released young aspen to grow taller in the Yellowstone region. The significant spatial variation in this aspen response is explained by the relationship between browsing and recruitment: Only where browsing rates were relatively low (<50% of young aspen browsed) did most aspen stands have saplings (Fig. 2b), and in some areas, aspen have remained suppressed by high rates of browsing. An alternative hypothesis is that aspen grew taller because of favorable climate trends such as a longer growing season or increased atmospheric carbon dioxide (Cole et al. 2010), and then browsing rates decreased due to the increase in height. This climate-driven or favorable conditions hypothesis makes predictions that can be evaluated by the evidence:

1. Climate effects would be broadly similar across the region (e.g., a wet or dry period, or long-term climate change). Instead, we found strong differences in recruitment between study areas, even in the same range, such as Daly Creek compared to Taylor Fork, or the East and West sectors of the YNP Northern Range (Fig. 2). The bark of new saplings usually was not stripped as it would have been if elk were simply unable to reach the top leader. By contrast, in Dome Mountain WMA browsing was heavy and bark was stripped from saplings, indicating a recent increase in herbivory (Keigley and Frisina 2008), the opposite of other study areas. Changing elk distribution and an uneven release from browsing explain these results, but climate does not.
2. If increased productivity (e.g., from moisture, carbon dioxide, or longer growing seasons) were responsible for increased height, then sites with the greatest rates of growth would be the ones with the tallest young aspen. Ripple and Beschta (2007) and

Painter et al. (2014, 2015) tested this prediction, but found no significant relationship between annual height growth increment and height of young aspen in northern YNP. Instead, young aspen with high browsing rates were consistently short, while those with less browsing were taller and more variable, regardless of growth rates. Our new aspen surveys confirmed this relationship between browsing and aspen recruitment on a larger scale (Fig. 2b).

3. The climate-driven hypothesis posits favorable conditions to explain an increase in aspen recruitment (Houston 1982, YNP 1997). In fact, recent climate trends in the Yellowstone region have been unfavorable for aspen, particularly on low, dry winter ranges (Romme and Turner 2015, Beschta and Ripple 2016, Hansen et al. 2016). Aspen recovery began during the regional drought of 1999–2007 (McMenamin et al. 2008, Painter et al. 2014), and long-term warming and drying trends would not be expected to stimulate aspen growth (Hanna and Kulawski 2012, Worrall et al. 2013). These climate trends have adversely affected aspen elsewhere in the western United States (Rogers and Mitten 2014). Furthermore, aspen recruitment inside exclosures has confirmed that, regardless of climate, a release from herbivory was sufficient for young aspen to grow tall (Kay 2001, Beschta et al. 2016).

Our findings, and those of other published research, provide compelling evidence that browsing intensity has been the dominant factor affecting aspen recruitment in the Yellowstone region, while the alternative hypothesis, based on climate and productivity, results in predictions not supported by the data. Consistently, high browsing rates in the late 1990s (80–100% of young aspen leaders browsed) decreased to more moderate levels (30–60%) in most areas within 10–15 yr (Figs. 2a, 3), breaking a pattern of aspen suppression that had persisted for decades. This trend has been confirmed by repeated measurements during 1999–2013 in marked aspen plots (Klaptosky 2016). Thus, it is not changes in climate but a widespread and uneven reduction in herbivory that has been the driver of new aspen

recruitment. Reduced herbivory followed the reduction and redistribution of elk herds (Figs. 3b, 4a, 5, Appendix S1: Figs. S1–S3). Inside YNP, elk densities were very high in the 1990s (White et al. 1998, Wagner 2006, Painter et al. 2015), so a larger reduction was required to reach a density at which reduced browsing was possible (Fig. 3b), compared to areas outside the park where hunting was already limiting elk density.

#### *Aspen recruitment in the YNP Northern Range: Why now?*

If young aspen have recently grown taller due to a reduction in browsing, following a decrease in the elk herd, why then were aspen in northern YNP unable to escape browsing in the 1950–60s, when elk numbers were also relatively low (Appendix S1: Fig. S1a)? This difference can be explained by the changing distribution of elk (White et al. 2012, Painter et al. 2015). For most of the 20th century, most northern Yellowstone elk wintered inside the park (Fig. 4a; Appendix S1: Fig. S2), except in severe winters when driven out by starvation (Houston 1982, Lemke et al. 1998, NRC 2002). Even in the 1960s when culling greatly reduced elk numbers and there was no winter hunt outside the park, the proportion of the herd in the park remained high, >80%. This pattern changed after wolf reintroduction, as shown by trends in elk count data (Fig. 4a). Total elk counts decreased, but most of the decrease was inside the park (Appendix S1: Fig. S2).

Aerial counts in 2013 and 2015 found 77% of northern Yellowstone elk wintering north of the park, and the lowest numbers ever recorded (915 elk in 2013) inside the park (Canfield 2014, Wyman and Smith 2015). Although total elk numbers since about 2005 have been comparable to the lows of the 1960s (Appendix S1: Fig. S1a), this similarity was only superficial, as elk densities in the park have been much lower recently than in the 1960s (Houston 1982). With relatively low elk densities, browsing rates also decreased (Fig. 3). Responses from woody forage plants might be expected to follow, and increases in height or recruitment have been documented not only for aspen, but also for cottonwood (*Populus* spp.), willow (*Salix* spp.), thinleaf alder (*Alnus incana* spp. *tenuifolia*), and other shrubs (Beschta and Ripple 2016).



### ***GNF Northern Range and Dome Mountain WMA***

Researchers in the GNF Northern Range found young aspen to be suppressed by herbivory in 1994 and 1998 (St. John 1995, Larsen and Ripple 2005). A 2006 study found patchy new growth of saplings, but in most stands young aspen still were suppressed (Kimble et al. 2011). By 2012, aspen recruitment had increased at Eagle Creek (Runyon et al. 2014), and in 2015, we found that almost all stands in the GNF Northern Range contained large numbers of saplings that had grown tall in the previous decade, with low to moderate rates of browsing on average (Fig. 2b, Table 2). As in the park, this reduction in browsing was associated with changes in elk distribution (Fig. 3b). Although the total number of elk wintering north of the park did not significantly change, since about 2005 most have been migrating to the area north of Dome Mountain (Fig. 5), where Dome Mountain WMA is located (Fig. 1), at the extreme northern end of the northern range (Lemke et al. 1998, Hamlin and Cunningham 2009, Painter et al. 2015). Consequently, relatively few elk have been left to occupy Gardiner Basin, south of Dome Mountain (Fig. 5, Appendix S1: Fig. S2d). This redistribution of elk can explain the reduction in browsing (Fig. 3b) and the increase in aspen recruitment (Fig. 2b) in the GNF Northern Range during the last decade.

Few elk migrated north of Dome Mountain until the winter after the 1988 fires (Lemke et al. 1998, NRC 2002), when many elk starved and unusual numbers left the park (Appendix S1: Fig. S2c, S2d). Annual counts there generally increased until the late 1990s, then remained high after wolf reintroduction as elk counts decreased elsewhere (Fig. 5, Appendix S1: Fig. S2). Thus, the history of elk north of Dome Mountain has been much different from that of the rest of the northern range. This explains the aspen stand conditions found there in 2015, with dense thickets of saplings and no gap in age and size distribution, but many saplings were stripped of bark and shorter aspen were heavily browsed. The fact that saplings could grow in the past but now are being killed by browsing demonstrates the recent increase in elk herbivory that has occurred there (Keigley and Frisina 2008). It will take time for elk to completely suppress aspen recruitment in dense multi-age stands at Dome Mountain WMA, a process that

took decades when it happened in the park (Beschta et al. 2016), but this may occur if new patterns of elk distribution continue.

### ***Elk distribution and aspen recruitment***

Consistent with trends in the northern range, elk counts decreased markedly in the Gallatin Canyon range following the return of wolves (Appendix S1: Figs. S1b, S3), while in the valley of the lower Madison River to the west, elk numbers increased 240% between 1994 and 2008 (Hamlin and Cunningham 2009). Over the last two decades, elk distribution has shifted away from the park toward the valleys of the lower Yellowstone River north of the park, the lower Madison River to the west, and the Clark's Fork River to the east (Hamlin et al. 2009, Middleton et al. 2013, Proffitt et al. 2013, Christianson and Creel 2014). More elk have been wintering in these lower valleys, and resident (non-migratory) elk there have increased (Hamlin and Cunningham 2009, Wilmers and Levi 2013). Close to the park, elk recruitment, population densities, and harvests have decreased, while high elk densities in these other areas have caused concern about disease transmission, range damage, and competition with cattle (Haggerty and Travis 2006, Dickson 2014, Proffitt et al. 2015).

Although ranges and migration routes of Yellowstone elk remained the same after wolf reintroduction (Mao et al. 2005, White et al. 2010), the proportions of the herds wintering in or near the park decreased (Fig. 4a), even as harvest near the park decreased (Appendix S1: Fig. S1). Elk recruitment was strong in surrounding areas with fewer predators, suggesting predation as a primary cause of the decrease (Hamlin and Cunningham 2009, Cunningham et al. 2010, Middleton et al. 2013, Christianson and Creel 2014). Other possible causes of this shift away from the park included (1) reductions in hunting and closures of private lands to hunters, providing hunting refuges for elk (Haggerty and Travis 2006, Proffitt et al. 2013, Dickson 2014); (2) reduced forage on high-elevation summer ranges with warmer, drier climate (Vucetich et al. 2005, Middleton et al. 2013), while high-quality forage may be had in irrigated fields outside the park (Muhly et al. 2013, Wilmers and Levi 2013); and (3) an increased bison population inside the park competing with elk for forage (Plumb et al. 2009,

Ripple et al. 2010, Painter et al. 2015). While these factors may have contributed, most researchers have concluded that recent changes in elk distribution were due, at least in part, to greater rates of predation in the ranges in and near the park, where predators may be more numerous and deeper snow makes elk more vulnerable (Barber-Meyer et al. 2008, Hamlin et al. 2009, White et al. 2009, 2012, Creel et al. 2013, Middleton et al. 2013, Wilmers and Levi 2013).

Our finding that aspen are likely to be suppressed by browsing where elk densities exceed about 4 elk/km<sup>2</sup> (Figs. 2, 3b) is consistent with previous research in other areas, and with other recent work in Yellowstone (Beschta et al. 2018). White et al. (1998, 2003) found that aspen recruitment in Rocky Mountain national parks in the United States and Canada was suppressed by elk browsing, except where predation by wolves was moderate to high and elk densities moderate to low, <4 elk/km<sup>2</sup>. Olmsted (1979) estimated that herbivory of more than 30% of annual twig production could reduce stand densities, while we found strong increases in recruitment with browsing rates of 40–50% of top leaders, and moderate increases with browsing of 50–60% of leaders (Fig. 2). However, Olmsted (1979) measured total utilization of annual production, so these measurements of browsing intensity, while similar, are not directly comparable. Other researchers have confirmed that high rates of aspen herbivory consistently suppressed aspen recruitment except where elk densities were relatively low (Durham and Marlow 2010, Rogers and Mittenack 2014).

#### *Behavioral effects of predation*

In addition to direct mortality of elk, behavioral responses to both predators and human hunters could be a factor in the recent shift in elk distribution. Studies of elk movements, vigilance, group sizes, habitat selection, and foraging patterns have shown significant effects on elk behavior from both wolves and human hunters (Laundré et al. 2001, Creel and Winnie 2005, Fortin et al. 2005, Hernandez and Laundré 2005, Mao et al. 2005, Gower et al. 2009b, White et al. 2009, Proffitt et al. 2013). Such behavioral responses could cause variations in elk density and habitat use at both large and small scales, adding to the spatial variation in elk browsing

(White et al. 2003, Kuijper et al. 2013, Flagel et al. 2015, Painter et al. 2015). For example, in the Sunlight/Crandall Range, many stands with new recruitment were away from open areas where elk tend to congregate, a pattern that can be explained by a greater tendency for elk to group together (Gower et al. 2009a, White et al. 2012), thereby reducing foraging in peripheral locations. In the Gallatin Canyon Range, risk from hunting (Proffitt et al. 2013) can explain differences between Daly Creek inside the park with high browsing rates (Winnie 2012), compared to Taylor Fork which was open to hunters and had much lower browsing rates and lower scat density (Fig. 2b, Table 2). Because elk density changed concurrently with changes in behavior, it is difficult to separate these interacting variables.

Greater predation in the park and recent limitations on hunting have increased benefits and reduced risks for elk migrating out of the park (Hamlin et al. 2009, White et al. 2012). Even before the return of wolves, elk left higher elevation ranges in greater numbers in severe winters, demonstrating the potential for a range shift (Houston 1982, Lemke et al. 1998, Eberhardt et al. 2007). As wolves recolonized, most elk returned to the same portion of winter range each year, but some changed (Gower et al. 2009b, Hamlin and Cunningham 2009, White et al. 2010). The percentage of the northern Yellowstone herd in the park decreased steadily after 1997 (Fig. 4a), despite mild winters and large harvests outside the park (Fig. 4b). These facts suggest that large-scale effects of predation on elk migratory behavior may have contributed to changes in elk density (Hamlin and Cunningham 2009, White et al. 2009).

#### *Top-down limitation of elk herds*

After culling inside the park ended in 1968, the rapid increase of northern Yellowstone elk in the 1970s was typical of an irrupting ungulate population with abundant resources (Appendix S1: Fig. S1a). However, starvation limited elk numbers in the 1980s, with large die-offs in severe winters followed by increases (Coughenour and Singer 1996). The last of these population crashes was in 1997 (White and Garrott 2005, Eberhardt et al. 2007). Rather than again increasing as before, elk continued to decrease, with large

harvests outside the park and comparable numbers killed by wolves inside (Fig. 4b). Predation by bears and cougars also increased, adding to the effects of wolves (Barber-Meyer et al. 2008, Garrott et al. 2009, Hamlin et al. 2009).

Vucetich et al. (2005) argued that the decline of northern Yellowstone elk during 1997–2004 could be accounted for by hunting, and perhaps also drought, so the effect of wolves was largely compensatory. For example, in the severe winter of 1997, many elk died of starvation, so predation from a small population of wolves made little difference. In subsequent years, thousands of female elk of prime breeding age were killed by hunters north of the park, a greater impact than that of wolves (Fig. 4b). However, elk numbers north of the park remained fairly stable, while decreasing in the park (Fig. 4a, 5, Appendix S1: Fig. S2a, S2b). In the past, hunting had never been sufficient to stabilize or reduce elk numbers inside the park except for the short term, without additional culling in the park as in the 1930–60s (Appendix S1: Figs. S1a, S2a). After wolf restoration, predators culled elk in the park, combining with the effect of hunters outside the park (Fig. 4b). The drought ended by 2007 and hunting was greatly reduced, yet the northern Yellowstone elk herd continued to decrease to low densities inside the park. Predation replaced starvation as the leading cause of elk calf mortality (Barber-Meyer et al. 2008), and the previous starvation cycles were essentially eliminated.

The northern Yellowstone elk herd following the restoration of wolves is an example of a switch from bottom-up to top-down limitation, first by hunters and predators, then primarily by predators (White and Garrott 2005, Eberhardt et al. 2007, White and Garrott 2013). The Madison Headwaters elk herd in central Yellowstone (Appendix S1: Fig. S3) also was reduced by predation following wolf reintroduction (Garrott et al. 2009, White et al. 2009), as was the Gallatin Canyon herd (Hamlin et al. 2009). Wildlife managers attributed these changes in elk populations primarily to predation and emigration (Hamlin and Cunningham 2009, Cunningham et al. 2010, Middleton et al. 2013).

Elk counts in the Sunlight/Crandall Range did not decrease as much as in other study areas (Appendix S1: Fig. S1c), as hunting was reduced to compensate for predation and low elk

recruitment. This herd had previously been regulated by hunting (WGFD 1980–2014), and when wolves returned may already have been near the low density at which browsing was moderated (Fig. 3b). Smaller changes were sufficient to reduce browsing pressure to a level at which aspen recruitment was possible, as previously occurred in the 1970s.

#### *Bison and livestock effects on aspen*

Browsing by bison has suppressed willow and cottonwood in some places where bison forage year-round, such as the Lamar Valley (Painter and Ripple 2012, Beschta and Ripple 2014). Although herbivory prevented recruitment in some aspen stands frequented by bison (Bork et al. 2013), this browsing did not result in a general suppression of young aspen in the YNP Northern Range, or the Eagle Creek area, as demonstrated by this and other recent aspen studies (Runyon et al. 2014, Painter et al. 2015, Klapotosky 2016). Some stands were heavily browsed by bison, but the effect was not ubiquitous.

Browsing rates of aspen were moderate, on average, in areas grazed by cattle or horses outside the park, compared to high browsing rates in these areas in 1998 (Fig. 2a). Aspen may have benefited from reduced cattle grazing in the Crandall Creek area (Painter 2013), but livestock grazing was unchanged in most areas. Therefore, the general and substantial reduction in browsing we documented cannot be explained by changes in livestock grazing practices. Although cattle are known to suppress aspen, and we found evidence of this in some stands, our results confirmed that elk were the primary browsers affecting aspen (Bork et al. 2013).

#### *Aspen persistence vs. aspen expansion*

Many aspen stands in the Yellowstone region have begun to grow new saplings and young trees, where they were losing trees for decades. This may not, however, restore aspen to a much greater area of aspen cover, as in the early years of the park (Houston 1982, NRC 2002). In some places, expansion of aspen stands may require a synergy of fire with low levels of herbivory (Romme et al. 1995, Smith et al. 2016). For example, in Sunlight/Crandall, 60% of stands had >50% conifer cover (Table 2). With browsing



reduced so that aspen recruitment is no longer suppressed, these ecosystem processes may be restored, and future fires may stimulate regeneration and expansion of aspen stands in Yellowstone (Ripple and Beschta 2004, Halofsky et al. 2008). Warmer and drier conditions, however, may result in less aspen on winter ranges over the long term, possibly with elevational changes in aspen distribution (Brodie et al. 2011, Hanna and Kulakowski 2012, Worrall et al. 2013, Romme and Turner 2015, Hansen et al. 2016).

## CONCLUSIONS

Large carnivore restoration has indirectly benefited aspen recruitment in the Yellowstone region through a trophic cascade. This hypothesis was supported by evidence from aspen surveys and elk counts. In winter ranges in and near the park, browsing generally decreased and aspen recruitment increased. Yet, in some places such as Daly Creek, intensive browsing by elk continued and aspen were still suppressed. Elk use of the Dome Mountain WMA area has increased, beginning to suppress young aspen there. These exceptions to the general pattern demonstrate the importance of placing local phenomena into a broader context. As elk densities have decreased more in some areas than others, spatial variation in browsing has increased, resulting in a patchy increase in aspen recruitment.

Following the return of wolves to Yellowstone, elk herds that formerly were limited by forage or hunting have become limited by predators, and the proportion of the elk population wintering in or near the park has decreased. Surveys of aspen both in and out of the park found reduced herbivory and increased aspen recruitment within the last decade, despite climate trends unfavorable for aspen. This decrease in herbivory of aspen has followed changes in elk densities and distribution, suggesting that relatively low elk densities are required for widespread aspen recruitment (Fig. 3b). If predation has been a significant cause of these changes, as the evidence supports, then the new aspen recruitment we observed was, at least in part, an indirect effect of wolf restoration. In addition to direct mortality of elk, behavioral responses to predators and human hunters may have influenced elk range selection, foraging, and use of habitat. These

results provide evidence of a trophic cascade involving wolves outside of a protected park, in a complex landscape with hunting, livestock, and other human influences. The consequences of large carnivore restoration in Yellowstone continue to unfold, with cascading effects over large scales, as prey balance the pressures of predation and hunting with other environmental factors.

## ACKNOWLEDGMENTS

We received helpful cooperation and data from Doug Smith and P.J. White of the Yellowstone Center for Resources, Doug McWhirter of Wyoming Game and Fish Department, Julie Cunningham of Montana Game Fish and Parks, Joe Hicks of the Shoshone National Forest, and Susan LaMont of the Gallatin National Forest. Ariel Muldoon advised portions of the statistical analysis. Thanks to field technicians Jonathan Batchelor and Jeff Stephens. Two anonymous reviewers provided comments that improved this paper. Aspen sampling in Yellowstone National Park was funded in part by the University of Wyoming—National Park Service Research Station.

## LITERATURE CITED

- Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* 169:1–30.
- 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, USA.
- Beschta, R. L., L. E. Painter, T. Levi, and W. J. Ripple. 2016. Long-term aspen dynamics, trophic cascades, and climate in northern Yellowstone. *Canadian Journal of Forest Research* 46:548–556.
- Beschta, R. L., L. E. Painter, and W. J. Ripple. 2018. Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone. *Forest Ecology and Management* 413:62–69.
- Beschta, R. L., and W. J. Ripple. 2007. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research* 37:1873–1885.
- Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142:2401–2414.
- Beschta, R. L., and W. J. Ripple. 2014. Divergent patterns of riparian cottonwood recovery after the



- return of wolves in Yellowstone, USA. *Ecohydrology* 8:56–66.
- Beschta, R. L., and W. J. Ripple. 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. *Biological Conservation* 198:93–103.
- Bork, E. W., C. N. Carlyle, J. F. Cahill, R. E. Haddow, and R. J. Hudson. 2013. Disentangling herbivore impacts on *Populus tremuloides*: a comparison of native ungulates and cattle in Canada's Aspen Parkland. *Oecologia* 173:895–904.
- Brodie, J., E. Post, F. Watson, and J. Berger. 2011. Climate change intensification of herbivore impacts on tree recruitment. *Proceedings of the Royal Society B: Biological Sciences* 279:1366–1370.
- Canfield, J. 2014. Northern Yellowstone Cooperative Wildlife Working Group 2013 Annual Report. Gallatin National Forest, Montana Fish and Game Commission, and Yellowstone National Park, Bozeman, Montana, USA.
- Christianson, D., and S. Creel. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: a before-after-control-impact approach. *PLoS ONE* 9:e102330.
- Cole, C. T., J. E. Anderson, R. L. Lindroth, and D. M. Waller. 2010. Rising concentrations of atmospheric CO<sub>2</sub> have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Global Change Biology* 16:2186–2197.
- Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecological Applications* 6:573–593.
- Craighead, J. J., G. Atwell, and B. W. O'Gara. 1972. Elk Migrations in and near Yellowstone National Park. *Wildlife Monographs* 29:3–48.
- Creel, S., J. A. Winnie, and D. Christianson. 2013. Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: an example with wolves and elk. *Ecology and Evolution* 3:5189–5200.
- Creel, S., and J. A. Winnie Jr. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69:1181–1189.
- Cunningham, J. A., K. Alt, and K. L. Hamlin. 2010. Management challenges from predator-prey effects on the Gallatin Canyon elk herd. Abstract presented at the Montana Chapter of The Wildlife Society, 48th Annual Meeting, Feb. 22–26, 2010, Helena, Montana. *Intermountain Journal of Sciences* 16:120–121.
- Dickson, T. 2014. Where are all the elk? *Montana Outdoors* 2014:36–39.
- Durham, D. A., and C. B. Marlow. 2010. Aspen response to prescribed fire under managed cattle grazing and low elk densities in southwest Montana. *Northwest Science* 84:141–150.
- Eberhardt, L. L., P. J. White, R. A. Garrott, and D. B. Houston. 2007. A seventy-year history of trends in Yellowstone's northern elk herd. *Journal of Wildlife Management* 71:594–602.
- Flagel, D. G., G. E. Belovsky, and D. E. Beyer Jr. 2015. Natural and experimental tests of trophic cascades: gray wolves and white-tailed deer in a Great Lakes forest. *Oecologia* 180:1183–1194.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Garrott, R. A., P. J. White, and J. J. Rotella. 2009. The Madison Headwaters elk herd: transitioning from bottom-up regulation to top-down limitation. Pages 489–517 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. *The ecology of large mammals in central Yellowstone*. Elsevier, Boston, Massachusetts, USA.
- Gower, C. N., R. A. Garrott, P. J. White, S. Cherry, and N. G. Yoccoz. 2009a. Elk group size and wolf predation: a flexible strategy when faced with variable risk. Pages 401–422 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. *The ecology of large mammals in central Yellowstone*. Elsevier, Boston, Massachusetts, USA.
- Gower, C. N., R. A. Garrott, P. J. White, F. G. R. Watson, S. S. Cornish, and M. S. Becker. 2009b. Spatial responses of elk to wolf predation risk: using the landscape to balance multiple demands. Pages 373–399 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. *The ecology of large mammals in central Yellowstone*. Elsevier, Boston, Massachusetts, USA.
- Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. *Geoforum* 37:816–830.
- Halofsky, J., and W. J. Ripple. 2008. Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA. *Forestry* 81:195–207.
- Halofsky, J. S., W. J. Ripple, and R. L. Beschta. 2008. Recoupling fire and aspen recruitment after wolf reintroduction in Yellowstone National Park, USA. *Forest Ecology and Management* 256:1004–1008.
- Hamlin, K. L., and J. A. Cunningham. 2009. Monitoring and assessment of wolf-ungulate interactions and population trends within the Greater Yellowstone Area, southwestern Montana, and Montana

- statewide: final Report. Montana Department of Fish, Wildlife, and Parks, Wildlife Division, Helena, Montana, USA.
- Hamlin, K. L., R. A. Garrott, P. J. White, and J. A. Cunningham. 2009. Contrasting wolf-ungulate interactions in the Greater Yellowstone Ecosystem. Pages 541–577 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. The ecology of large mammals in central Yellowstone. Elsevier, Boston, Massachusetts, USA.
- Hanna, P., and D. Kulakowski. 2012. The influences of climate on aspen dieback. *Forest Ecology and Management* 274:91–98.
- Hansen, W. D., W. H. Romme, A. Ba, and M. G. Turner. 2016. Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. *Forest Ecology and Management* 362:218–230.
- Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86:2135–2144.
- Hernandez, L., and J. W. Laundre. 2005. Foraging in the “landscape of fear”, and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology* 11:215–220.
- Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. Macmillan, New York, New York, USA.
- Kay, C. E. 1990. Yellowstone’s northern elk herd: a critical evaluation of the “natural regulation” paradigm. Dissertation. Utah State University, Logan, Utah, USA.
- Kay, C. E. 2001. Long-term aspen exclosures in the Yellowstone ecosystem. Pages 225–240 in W. D. Shepherd, D. Binkley, D. L. Bartos, T. J. Stohlgren, and L. G. Eskew, editors. Sustaining Aspen in Western Landscapes: symposium Proceedings, June 13–15, 2000, Grand Junction, Colorado. RMRS-P-18. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Keigley, R. B., and M. R. Frisina. 1998. Browse evaluation by analysis of growth form. Montana Fish, Wildlife and Parks, Helena, Montana, USA.
- Keigley, R. B., and M. R. Frisina. 2008. Aspen height, stem-girth and survivorship in an area of high ungulate use. *Northwest Science* 82:199–210.
- Kimble, D. S., D. B. Tyers, J. Robison-Cox, and B. F. Sowell. 2011. Aspen recovery since wolf reintroduction on the northern Yellowstone winter range. *Rangeland Ecology & Management* 64:119–130.
- Klaptosky, J. 2016. The plight of aspen: emerging as a beneficiary of wolf restoration on Yellowstone’s northern range. *Yellowstone Science* 24:65–69.
- Kuijper, D. P. J., C. de Kleine, M. Churski, P. van Hooft, J. Bubnicki, and B. Jędrzejewska. 2013. Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography*. <https://doi.org/10.1111/j.1600-0587.2013.00266.x>
- Larsen, E. J., and W. J. Ripple. 2003. Aspen age structure in the northern Yellowstone ecosystem: USA. *Forest Ecology and Management* 179:469–482.
- Larsen, E. J., and W. J. Ripple. 2005. Aspen stand conditions on elk winter ranges in the northern Yellowstone ecosystem, USA. *Natural Areas Journal* 25:326–338.
- Laundré, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79:1401–1409.
- Lemke, T. O., J. A. Mack, and D. B. Houston. 1998. Winter range expansion by the northern Yellowstone elk herd. *Intermountain Journal of Sciences* 4:1–9.
- Lovaas, A. L. 1970. People and the Gallatin Elk Herd. Montana Fish and Game Department, Helena, Montana, USA.
- Loveless, K. 2017. 2017 Hunting district 313 elk survey (Gardiner to 6-mile creek). Montana Fish, Wildlife & Parks, Bozeman, Montana, USA.
- Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69:1691–1707.
- McMenamin, S. K., E. A. Hadly, and C. K. Wright. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proceedings of the National Academy of Sciences of the United States of America* 105:16988–16993.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* 94:1245–1256.
- Muhly, T. B., M. Hebblewhite, D. Paton, J. A. Pitt, M. S. Boyce, and M. Musiani. 2013. Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. *PLoS ONE* 8:e64311.
- NRC (National Research Council). 2002. Ecological dynamics on Yellowstone’s northern range. National Academies Press, Washington, D.C., USA.
- Olmsted, C. E. 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain National Park. Pages 89–97 in M. S.

- Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior, and management. University of Wyoming, Laramie, Wyoming, USA.
- Painter, L. E. 2013. Trophic cascades and large mammals in the Yellowstone ecosystem. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Painter, L. E., R. L. Beschta, E. J. Larsen, and W. J. Ripple. 2014. After long-term decline, are aspen recovering in northern Yellowstone? *Forest Ecology and Management* 329:108–117.
- Painter, L. E., R. L. Beschta, E. J. Larsen, and W. J. Ripple. 2015. Recovering aspen follow changing elk dynamics in Yellowstone: Evidence of a trophic cascade? *Ecology* 96:252–263.
- 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.
- Peterson, R. O., J. A. Vucetich, J. M. Bump, and D. W. Smith. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annual Review of Ecology, Evolution, and Systematics* 45:325–345.
- Plumb, G. E., P. J. White, M. B. Coughenour, and R. L. Wallen. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation* 142:2377–2387.
- Proffitt, K. M., N. Anderson, P. Lukacs, M. M. Riordan, J. A. Gude, and J. Shamhart. 2015. Effects of elk density on elk aggregation patterns and exposure to brucellosis. *Journal of Wildlife Management* 79:373–383.
- Proffitt, K. M., J. A. Gude, K. L. Hamlin, and M. A. Messer. 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. *Journal of Wildlife Management* 77:514–524.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience* 54:755–766.
- Ripple, W. J., and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138:514–519.
- Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* 145:205–213.
- Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* 95:361–370.
- Ripple, W. J., L. E. Painter, R. L. Beschta, and C. C. Gates. 2010. Wolves, elk, bison, and secondary trophic cascades in Yellowstone National Park. *Open Ecology Journal* 3:31–37.
- Rogers, P. C., and C. M. Mitanck. 2014. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. *Journal of Vegetation Science* 25:457–469.
- Romme, W. H., and M. G. Turner. 2015. Ecological implications of climate change in Yellowstone: Moving into uncharted territory? *Yellowstone Science* 23:6–12.
- Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone Park. *Ecology* 76:2097–2106.
- Rudd, W. J., A. L. Ward, and L. L. Irwin. 1983. Do split hunting seasons influence elk migrations from Yellowstone National Park? *Wildlife Society Bulletin* 11:328–331.
- Runyon, M. J., D. B. Tyers, B. F. Sowell, and C. N. Gower. 2014. Aspen restoration using beaver on the northern Yellowstone winter range under reduced ungulate herbivory. *Restoration Ecology* 22:555–561.
- Smith, D. S., S. M. Fetting, and M. A. Bowker. 2016. Elevated Rocky Mountain elk numbers prevent positive effects of fire on quaking aspen (*Populus tremuloides*) recruitment. *Forest Ecology and Management* 362:46–54.
- Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management* 68:153–166.
- Smith, D. W., D. Stahler, E. Stahler, M. Metz, K. Cassidy, B. Cassidy, and R. McIntyre. 2015. Yellowstone Wolf Project: annual Report, 2014. YCR-2015-02. Yellowstone Center For Resources, Yellowstone National Park, USA.
- Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* 17:1238–1250.
- St. John, R. A. 1995. Aspen stand recruitment and ungulate impacts: Gardiner Ranger District, Gardiner, Montana. Thesis. University of Montana, Missoula, Montana, USA.
- USFWS (U.S. Fish and Wildlife Service). 2000–2011. Rocky Mountain Wolf Recovery Interagency Annual Reports. USFWS Ecological Services, Helena, Montana, USA.
- Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos* 111:259–270.
- Wagner, F. H. 2006. Yellowstone's destabilized ecosystem: elk effects, science, and policy conflict. Oxford University Press, New York, New York, USA.

- WGFD (Wyoming Game and Fish Department). 1980–2014. Cody region annual big game herd unit reports 1980–2014. Cheyenne, Wyoming, USA.
- White, C. A., M. C. Feller, and S. Bayley. 2003. Predation risk and the functional response of elk-aspen herbivory. *Forest Ecology and Management* 181:77–97.
- White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin* 26:449–462.
- White, P. J., and R. A. Garrott. 2005. Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin* 33:942–955.
- White, P. J., and R. A. Garrott. 2013. Predation: wolf restoration and the transition of Yellowstone elk. Pages 69–93 in P. J. White, R. A. Garrott, and G. E. Plumb, editors. *Yellowstone's wildlife in transition*. Harvard University Press, Cambridge, Massachusetts, USA.
- White, P. J., R. A. Garrott, S. Cherry, F. G. R. Watson, C. N. Gower, M. S. Becker, and E. Meredith. 2009. Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. Pages 451–476 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. *The ecology of large mammals in central Yellowstone*. Elsevier, Boston, Massachusetts, USA.
- White, P. J., K. M. Proffitt, and T. O. Lemke. 2012. Changes in elk distribution and group sizes after wolf restoration. *American Midland Naturalist* 167:174–187.
- White, P. J., K. M. Proffitt, L. D. Mech, S. B. Evans, J. A. Cunningham, and K. L. Hamlin. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. *Journal of Mammalogy* 91:827–837.
- Wilmers, C. C., and T. Levi. 2013. Do irrigation and predator control reduce the productivity of migratory ungulate herds? *Ecology* 94:1264–1270.
- Winnie, J. A. 2012. Predation risk, elk, and aspen: tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. *Ecology* 93:2600–2614.
- Worrall, J. J., G. E. Rehfeldt, A. Hamann, E. H. Hogg, S. B. Marchetti, M. Michaelian, and L. K. Gray. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management* 299:35–51.
- Wyman, T., and D. W. Smith. 2015. 2014–2015 Annual Winter Trend Count of Northern Yellowstone Elk. Northern Yellowstone Cooperative Wildlife Working Group, Yellowstone National Park, USA.
- YNP (Yellowstone National Park). 1997. *Yellowstone's Northern Range: complexity and Change in a Wildland Ecosystem*. National Park Service, Mammoth Hot Springs, USA.

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