Exhibit W

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Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade?

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Abstract. To investigate the extent and causes of recent quaking aspen (*Populus tremuloides*) recruitment in northern Yellowstone National Park, we measured browsing intensity and height of young aspen in 87 randomly selected aspen stands in 2012, and compared our results to similar data collected in 1997–1998. We also examined the relationship between aspen recovery and the distribution of Rocky Mountain elk (*Cervus elaphus*) and bison (*Bison bison*) on the Yellowstone northern ungulate winter range, using ungulate fecal pile densities and annual elk count data. In 1998, 90% of young aspen were browsed and none were taller than 200 cm, the height at which aspen begin to escape from elk browsing. In 2012, only 37% in the east and 63% in the west portions of the winter range were browsed, and 65% of stands in the east had young aspen taller than 200 cm. Heights of young aspen were inversely related to browsing intensity, with the least browsing and greatest heights in the eastern portion of the range, corresponding with recent changes in elk density and distribution. In contrast with historical elk distribution (1930s–1990s), the greatest densities of elk recently (2006–2012) have been north of the park boundary (~5 elk/km^2), and in the western part of the range (2–4 elk/km^2), with relatively few elk in the eastern portion of the range (<2 elk/km^2), even in mild winters. This redistribution of elk and decrease in density inside the park, and overall reduction in elk numbers, explain why many aspen stands have begun to recover. Increased predation pressure following the reintroduction of gray wolves (*Canis lupus*) in 1995–1996 played a role in these changing elk population dynamics, interacting with other influences including increased predation by bears (*Ursus* spp.), competition with an expanding bison population, and shifting patterns of human land use and hunting outside the park. The resulting new aspen recruitment is evidence of a landscape-scale trophic cascade in which a resurgent large carnivore community, combined with other ecological changes, has benefited aspen through effects on ungulate prey.

Key words: Bison; *browsing effects;* Canis lupus; Cervus elaphus; *gray wolves; large carnivore restoration;* Populus tremuloides; *predation risk; quaking aspen; Rocky Mountain elk; trophic cascade; Yellowstone National Park.*

Introduction

Quaking aspen (*Populus tremuloides*) stands declined in northern Yellowstone National Park (YNP) during the 20th century, as aging trees died but were not replaced. This decline was primarily due to intensive browsing of young aspen by Rocky Mountain elk (*Cervus elaphus*) in winter (White et al. 1998, NRC 2002, Barmore 2003, Larsen and Ripple 2005). The extirpation of gray wolves (*Canis lupus*) in the 1920s may have contributed to suppression of aspen, through effects on elk population dynamics and behavior (White et al. 1998, Ripple and Larsen 2000) and a resulting trophic cascade (Terborgh and Estes 2010, Ripple et al. 2014*b*).

In 1995–1996, wolves were reintroduced in YNP, restoring the native community of large carnivores (Smith et al. 2003), and elk numbers subsequently declined (White and Garrott 2005*a*, Eberhardt et al. 2007, White et al. 2013). In 2006 and 2010, young aspen in the eastern portion of the northern ungulate winter range (northern range) were found to be significantly taller in association with reduced browsing, an important change from past conditions (Ripple and Beschta 2007, 2012*b*). Much of the browsing reduction occurred in riparian (streamside) stands, while many non-riparian stands were still suppressed by browsing. Riparian areas were often in complex terrain that could discourage ungulate access and increase predation risk (Kauffman et al. 2007). Aspen stands with many fallen trees also showed signs of recovery, suggesting that downed logs might be avoided by ungulates as impediments to access or escape (Kuijper et al. 2013). Ripple and Beschta (2007) hypothesized that, in addition to reduced elk density, behavioral responses by elk to predation risk

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may have contributed to a trophic cascade benefiting aspen (White et al. 2003). Other plant species browsed by elk, including cottonwood (*Populus* spp.), willow (*Salix* spp.), serviceberry (*Amelanchier alnifolia*), and other palatable shrubs, have also shown signs of release from suppression by browsing following wolf reintroduction (Ripple and Beschta 2006, 2012*b*, Beyer et al. 2007, Tercek et al. 2010, Beschta and Ripple 2014, Ripple et al. 2014*a*).

Not all researchers agreed that aspen were recovering on the northern range. Kauffman et al. (2010:2742), sampling aspen during 2004–2006 on the northern range, reported that "aspen are not currently recovering in Yellowstone, even in the presence of a large wolf population." Browsing rates were high, and young aspen in sampling plots were short, with no saplings taller than 200 cm, the height at which saplings begin to escape from elk browsing. Kauffman et al. (2010) concluded that elk herbivory was still limiting the growth and survival of young aspen in northern YNP, as it had in previous decades.

The studies by Kauffman et al. (2010) and Ripple and Beschta (2007, 2012) differed in both timing and design, and this may explain their divergent conclusions regarding aspen recovery (Beschta and Ripple 2013). Kauffman et al. (2010) randomly selected 16 aspen stands across the northern range, and measured browsing and height of young aspen in random sampling plots in these stands. This method had the potential to detect a strong, widespread recovery of aspen stands, but might have missed a patchy recovery, or a recovery just beginning. Ripple and Beschta (2007, 2012) selected the five tallest young aspen in a stand, as an indication of new sapling recruitment, in 98 aspen stands located in the eastern portion of the northern range. Intensive sampling by Ripple and Beschta of a limited area ensured that riparian stands, some of the first to show signs of new recruitment, were included. The disparate findings from these studies raised questions about the extent and timing of a beginning aspen recovery on the northern range.

To update and expand information about the condition of aspen stands on the northern range, we sampled 87 randomly selected aspen stands in 2012, and compared these measurements to data collected from the same stands in 1997–1998 (Larsen 2001). We used two different sampling methods for young aspen: randomly located sampling plots within stands, and selecting the five tallest stems in a stand, methods comparable to those of previous studies. We analyzed variations in browsing intensity, young aspen height, and ungulate distribution to investigate the following questions:

1) How have browsing intensity and height of young aspen changed since 1998? What was the spatial extent and timing of new aspen recruitment, if any has occurred?
2) What factors explain variation in browsing rates and heights of young aspen among stands in 2012? Browsing intensity may be related to the large-scale distribution of elk, and perhaps bison (*Bison bison*), and may also vary in response to site characteristics.
3) How have bison affected aspen? We expected more browsing at sapling heights accessible to bison ($<$100 cm) in areas of high bison concentration in the eastern part of the range.
4) How are elk and bison distributed in northern YNP? We mapped the distribution of elk and bison scat in 2012, and calculated trends in elk density.

METHODS

Study area

The climate, topography, and vegetation of the northern Yellowstone ungulate winter range and the history of the northern Yellowstone elk herd have been described by Houston (1982) and others (YNP 1997, Lemke et al. 1998, White and Garrott 2005*b*, Wagner 2006, Eberhardt et al. 2007, White et al. 2012, 2013). In northern YNP and extending north along the Yellowstone River, open valleys at a relatively low elevation provide winter range (~1500 km^2) for elk and other ungulates, including bison, deer (*Odocoileus* spp.), and small numbers of pronghorn (*Antilocapra americana*) and moose (*Alces alces*). Aspen is a preferred browse species for elk, and important for habitat diversity in the Rocky Mountains (White et al. 1998). Aspen occupy only a small percentage of the landscape on the northern range, persisting for centuries in scattered stands in moist locations. In the absence of fire, almost all aspen regeneration is from root sprouts, the trees in a stand sharing a common root system. Our study area included that portion of the northern range (~1000 km^2) inside the park boundary (Fig. 1a). Elk share the range with bison, deer (*Odocoileus* spp.), and small numbers of pronghorn (*Antilocapra americana*) and moose (*Alces alces*).

White et al. (2012) examined changes in elk density in four sectors of the northern range (Coughenour and Singer 1996), which we have called east, central, west, and northwest (Fig. 1a). The elk herd using this range was composed of two herd segments: the Lamar River segment spending winter in the upper-elevation Lamar River valley and surrounding area (east and central sectors), and the Yellowstone River segment wintering in the lower-elevation Gardiner River and Yellowstone River valleys (central, west, and northwest sectors) both in and out of the park. Some elk varied their migration strategy over time, and there has been mixing between herd segments (White et al. 2010). Prior to the return of wolves, winter elk densities were usually greatest inside the park boundary including the east sector (Houston 1982, White et al. 2012), even when elk numbers were kept low (~5000 elk) by culling in the park in the 1960s. Severe winters drove elk out of the park to the northwest

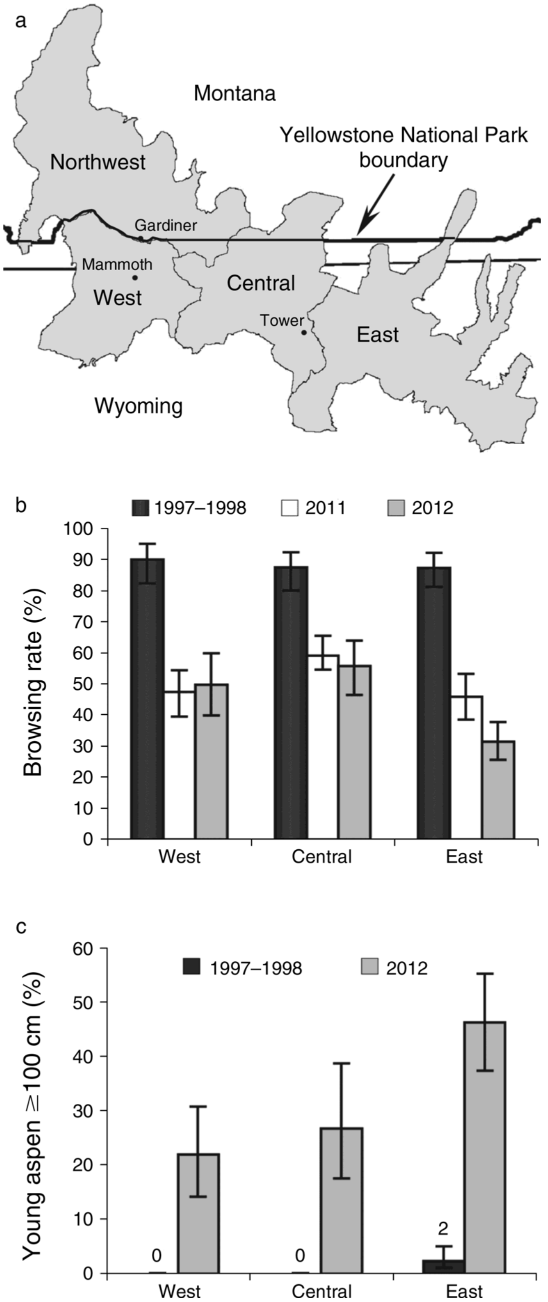

FIG. 1. Sector map along the Wyoming-Montana border, USA, and changes in aspen between 1998 and 2012 in sampling plots in 87 aspen (*Populus tremuloides*) stands in three range sectors within the Yellowstone National Park (YNP) boundary. (a) Map of the northern Yellowstone ungulate winter range (northern range) in gray, divided into four sectors. (b) Mean browsing rates (percentage of top leaders browsed in the previous year, spring through winter, including summer sprouts); error bars show 95% CI. (c) Percentage of young aspen >100 cm tall; error bars show 95% CI. The numbers above the black bars are percentages (y-axis values).

sector, but the shift of range was temporary. After culling ended in 1969, elk counts increased to ~17 000+ and the herd's winter range expanded northward outside the park, despite increased hunting (Lemke et al. 1998).

Since wolf reintroduction in 1995–1996, elk numbers have steadily decreased and were recently the lowest that they have been since the 1960s, with ~4200 counted in 2012 (Wyman and Smith 2012). Corresponding with this decrease, elk density declined in the park, but in the northwest sector outside the park, elk density remained about the same despite significant removals by human hunters (White and Garrott 2005*a*, Eberhardt et al. 2007, White et al. 2012). After 2005, winter harvests were much reduced; nevertheless, elk density continued to decrease within the park, with the greatest reduction in the east sector (White et al. 2012). Wolves and bears were the primary causes of elk mortality in the park, and these predator densities were higher inside than outside the park (Barber-Meyer et al. 2008, Hamlin and Cunningham 2009, White et al. 2010, White and Garrott 2013). This differential pattern of predation pressure provides a compelling hypothesis to explain the decline of the elk population within, but not outside of, the park. Bottom-up factors also may have affected elk distribution and density. Bison have greatly increased within the park and compete with elk for forage (White and Garrott 2005*b*, Plumb et al. 2009, Ripple et al. 2010, Wallen 2012, Frank et al. 2013). Outside the park in the northwest sector, irrigated pastures and reduced cattle densities may have benefited elk, particularly during times of drought (Haggerty and Travis 2006, Wilmers and Levi 2013). Drought between 1999 and 2006 could have reduced elk recruitment in the park and has been suggested as a reason for elk decline (Cook et al. 2004, Vucetich et al. 2005), but there was no evidence of a strong effect on elk pregnancy rates (White et al. 2011) or survival as a result of this drought (Cook et al. 2004, Barber-Meyer et al. 2008, White and Garrott 2013).

Data collection

In 1997–1998, Larsen (2001) marked with GPS the locations of 87 randomly selected aspen stands on the northern range within YNP (i.e., west, central, and east sectors) and measured browsing intensity and heights of young aspen in 79 stands. We used these data as a baseline for measuring change over time. In 2012, we revisited the 87 marked stands and again measured browsing and height of young aspen (Painter 2013). In each stand, young aspen were sampled with a randomly placed 2 × 30 m belt transect plot, replicating the methods of Larsen (2001). An aspen "tree" was defined as >5 cm dbh (diameter at breast height); "young aspen" included all aspen with dbh ≤ 5 cm, including "saplings" (i.e., young aspen ≥ 200 cm in height and ≤5 cm dbh). For young aspen in the sampling plots, we recorded the height and browsing status (browsed or not) of the tallest leader for fall 2012 (top height), spring 2012, and spring 2011, as indicated by bud scars and browsing scars (Ripple and Beschta 2007). We also located the five tallest young aspen in each stand and used plant architecture to assess height and browsing status during previous years (Ripple and Beschta 2007). Because we were interested in the effects of herbivory, young aspen that were protected by a physical barrier and had no evidence of past browsing were not included, although these were rare. For each stand, we recorded slope, aspect, and topographic position (riparian if associated with a stream, or not riparian). We counted the number of fallen trees and boulders >30 cm above the ground within 3 m of sampling plots, and within 3 m of the five tallest young aspen (Ripple and Beschta 2007).

As an index of ungulate use (Ripple et al. 2001, White et al. 2003), we counted ungulate fecal piles, including those of elk, bison, deer, and pronghorn, in four parallel 2×50 m belt transects spaced 7 m apart, placed outside of the stand perimeter in the nearest open area within 10 m of the stand. These plots were not placed within aspen stands because many stands were wet or mesic, with very dense ground cover and standing water for part of the spring and summer. Scat piles were unlikely to persist and difficult to detect in these conditions. Placing the scat plots in the adjacent grassland resulted in more consistent scat persistence and detection. Scat densities are likely to be higher in these locations compared to the stand interior (White et al. 2003). This method provided an index of relative ungulate densities in association with aspen stands in recent years, but scat densities were partially decoupled from some small-scale site factors such as the number of logs or complexity of terrain in the interior of stands. Elk pellets may persist for five years or more in xeric grassland (E. J. Larsen and W. J. Ripple, *unpublished data*), and all piles were counted regardless of age. An index for openness of view was calculated from the average distance (to 900 m, the rangefinder limit) at which view was obstructed (>50%) in the four directional quadrants (Ripple and Beschta 2006), viewed from the ungulate scat plots.

Analysis

Mean annual browsing rate (percentage of top leaders browsed in the previous year, spring through winter) and mean height of young aspen were calculated first within each stand and then averaged across all stands within a sector. Heights in 1997–1998 were categorical, so the percentage ≥100 cm was used for comparison with 2012. Browsing rate calculations did not include saplings (i.e., ≥200 cm tall). We compared browsing rates and heights between 1997–1998 and 2012 using bias-corrected 95% confidence intervals (CI) calculated by the adjusted bootstrap percentile method (Davison and Hinkley 1997) with 10 000 iterations, using the function "boot.ci" in the software R (R Development Core Team 2008). Bootstrapping was used because data from 1997–1998 had much greater skew than data from 2012. In the 1997–1998 data, new aspen sprouts of the summer were not distinguished from older young aspen, so the calculated browsing rate underestimated the actual browsing rate for the previous year in stands with new sprouts. Although we used this method for comparison with the 1997–1998 baseline (Fig. 1b), for further analysis of 2012 data we removed new sprouts, resulting in a slightly higher estimate of the percentage browsed. Using *t* statistics, we calculated 95% CI for mean browsing rate, spring height, and elk or bison scat density in 2012 for each sector. Confidence intervals showed that significant differences between sectors were primarily between the east and west sectors, so *t* tests (unequal variance) were used to analyze differences between these sectors.

We compared explanatory models for the following response variables: browsing rate in 2012, young aspen spring height in 2012 (in random plots and of the five tallest), and elk or bison scat density in 2012 (Appendix: Table A1). Models included variables hypothesized to influence these response variables, and were compared using the corrected Akaike information criterion, AIC_c (Burnham and Anderson 2002). Models with an AIC score within 2 units of the lowest score were considered equivalent. A natural logarithm transformation was used where needed for constant variance. Explanatory variables are shown in the Appendix (Table A1), and include range sector (East, Central, West), slope, aspect (South or not, where south includes southwest and southeast), Leader length, Browsing rate (for sampling plots), number of logs and boulders (Logs), topographic position (Riparian or not), openness of view (View), and distance to coniferous forest (Conifer distance). Not all explanatory variables were used for each response variable; see Table A1. We expected an inverse relationship between height and browsing. We expected gentle slopes, southerly aspect, and location in the west sector to be positively related to ungulate scat density and browsing rate. Browsing was expected to decrease and height to increase with number of logs, greater distance from conifers, and riparian position. We expected both height and browsing to be positively related to leader length, because greater growth could result in greater height after release from browsing, and elk may prefer browsing on more vigorous plants.

We calculated scat densities by sector, and used kriging (ArcMap v.10, Spatial Analyst; cell size and search distance 3 km; ESRI 2010) for an interpolated map of elk and bison scat density. To assess the possibility that bison may affect aspen recruitment, we calculated browsing rates for young aspen in sampling plots pooled in two groups by height, <100 cm (spring height) and 100–200 cm. Most browsing by bison occurs at heights <100 cm (Painter and Ripple 2012). Second, we hypothesized that high densities of bison in the east sector have resulted in more browsing of aspen in summer, and tested this by comparing summer browsing rates between east and west sectors. We also calculated an average browsing rate for nine stands with high bison scat densities but very low elk scat densities, where browsing probably would be from bison.

Elk population density

We calculated elk population density by sector (Fig. 1a) (White et al. 2012) for all years for which count unit data were available, 1987–2012 (except 1989, 1995–1997, and 2001). Winter elk count data were collected by the Northern Yellowstone Cooperative Wildlife Working Group (*unpublished data*), including the area of each count unit. Total counts for each sector were divided by the area of that sector to estimate density. We mapped average elk density by count unit for the years 1987–1994 and 2005–2011. A sightability correction (count/0.75) is often applied to elk counts (Wagner 2006, Eberhardt et al. 2007), but having no data on how this factor might vary by sector or unit, we did not adjust for sightability, consistent with similar previously published estimates (White et al. 2012; P. J. White, *personal communication*). We also summed the elk counts for units inside the park, and calculated the ratio of elk inside/outside the park annually. To test for a shift in distribution to the northwest sector outside the park, the ratio of elk inside/outside was averaged for the years 1987–1994 ($n = 7$, one year missing), and was compared with the average for 2005–2012 ($n = 8$ years), using a t test with unequal variance (Welch's).

SWE and precipitation

As an index to winter severity, we combined SWE (snow-water equivalent) data from two snow course monitoring stations (NRCS 2012), Lupine Creek (Station 10e01) in the west-central part of the northern range, and Northeast Entrance (Station 10d07s) near the eastern edge. Measurements for the first day of each month (January–April for Lupine Creek, January–May for Northeast Entrance) were averaged for the years 1985–2012, and the yearly averages used to calculate a mean SWE for this period.

RESULTS

Aspen

In 1997–1998, browsing rates were near 90% (Fig. 1b) and young aspen were consistently short (Fig. 1c), as in earlier studies that found young aspen on the northern range to be generally < 50 cm tall (Barmore 1967, 2003, Kay 1990). In 2011 and 2012, browsing rates were lower and more variable compared with 1997–1998 (Fig. 1b). Although there was wide variation within sectors in 2012 (Appendix: Fig. A1), stands with the lowest browsing rates and tallest young aspen were mostly in the east. In 2012, browsing rates (not counting new sprouts) averaged 37% (95% CI: 30–45%) in the east, 62% (95% CI: 53–71%) in the central, and 63% (95% CI: 53–74%) in the west sector. Comparing the east and west sectors in 2012, browsing rates in the east were significantly lower ($t_{58} = 3.9$, $P < 0.001$) and spring heights significantly taller ($t_{58} = 4.0$, $P < 0.001$). Variance in young aspen height was also greater in the east ($F_{36,22} = 2.84$, $P = 0.006$). The summer browsing rate in 2012 was 15 points higher ($t_{26} = 2.1$, $P = 0.001$) in the west (20% of leaders browsed in summer) compared to the east (5% browsed in summer), despite high bison densities in the east in summer. Browsing rates by height were: east sector, 48% below 100 cm and 14% at 100–200 cm; central sector 66% and 21%; and west sector 62% and 25%, respectively. The five tallest young aspen in each stand were older ($t_{58} = 4.0$, $P < 0.001$) and taller ($t_{57} = 4.9$, $P < 0.001$) in the east than in the west (Fig. 2a), with more saplings (i.e., $\geq$200 cm tall) in the east (Fig. 2b), matching the pattern seen in sampling plots. In 2007, there were few stands with saplings in any sector (Fig. 2b).

The multiple regression model for spring height of young aspen explained 67% of height variation, of which 62% was explained by browsing rate alone (Appendix: Table A1, Fig. A1). Range sector was the most influential variable for the percentage browsed, height of the five tallest, and scat density (Appendix: Table A1). The signs of regression coefficients were as expected in most cases, except that elk scat density was inversely related (weakly) to openness of view (Table A1). Height of the five tallest young aspen was positively related to the number of logs and riparian location, as expected. For the five tallest saplings, browsing rates were not available for all stands because many of the tallest young aspen were beyond the reach of elk (>200 cm) and therefore were not included in browse rate calculations.

Elk, bison, and climate

Elk accounted for 57%, bison 42%, deer 0.8%, and pronghorn 0.3% of all ungulate fecal piles in scat sampling plots. The west sector had greater elk scat density than the east ($t_{25} = 4.6$, $P < 0.001$), whereas bison scat density was greater in the east ($t_{37} = 8.7$ $P < 0.001$). The interpolated density map (Fig. 3a, b) showed the greatest elk scat density near the border with the northwest sector (Mt. Everts, Mammoth/Gardiner area), and the greatest bison scat density in the east (Lamar River) and part of the central sector (Blacktail Plateau). Nine stands with very low elk scat densities <1 pile/100 m^2 had high bison scat density of 13 piles/100 m^2. Browsing rates in these nine stands averaged 57% (range 30–85%), probably due to bison.

Winter elk densities declined overall in 1998–2012, but were stable in the northwest sector (Figs. 3c, d, 4a–d). Estimates of winter elk densities in March 2012 by sector were: east, 0.2 elk/km^2; central, 2.2 elk/km^2; west, 2.4 elk/km^2; and northwest, 5.7 elk/km^2. Average elk density for the east, central, and west sectors combined was 1.3 elk/km^2. These elk densities corresponded with elk scat densities: east, 4 groups of scat/100 m^2; central, 11 groups/100 m^2; and west, 17 groups/100 m^2. Scat counts may be inflated relative to elk density due to recent declines in elk density and the persistence of pellets. Nevertheless, these pellet pile densities indicate a

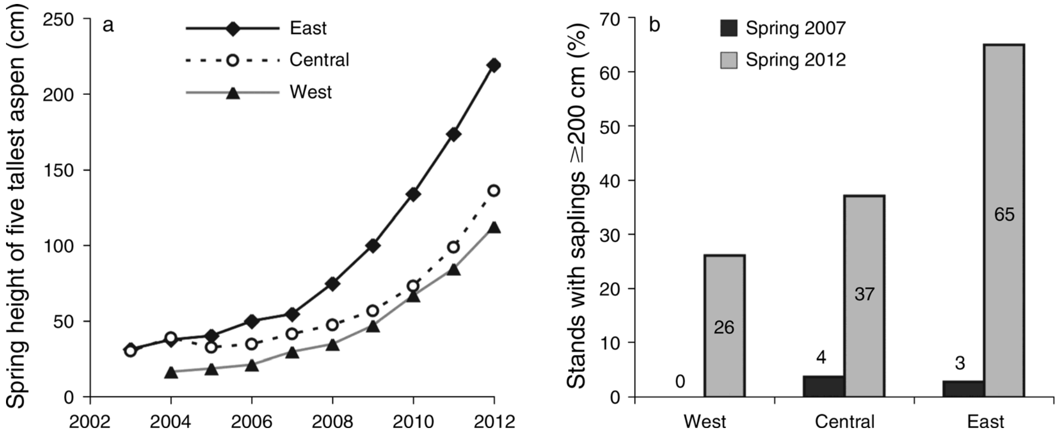

FIG. 2. Height and recruitment of the five tallest young aspen in each stand, averaged for each of three range sectors for each year, based on plant architecture measured in 2012. (a) Height over time (east and central range values overlapped in 2003 and 2004). (b) Percentage of stands with at least one sapling ≥200 cm spring height in 2007 and 2012. The height at which saplings begin to escape from elk browsing is considered to be 200 cm. Numbers above and inside the bars are percentages (*y*-axis values).

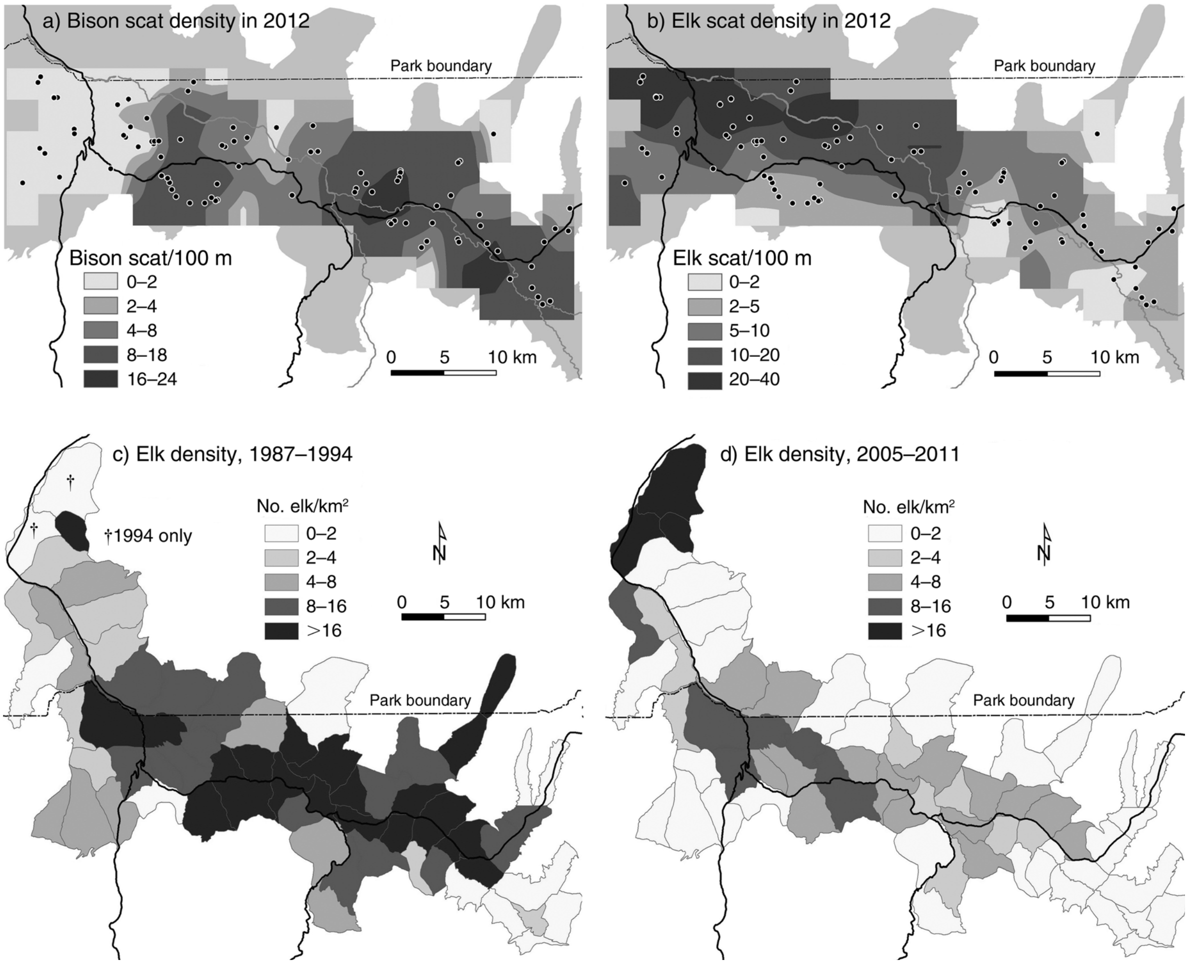

FIG. 3. (a) Bison and (b) elk scat density distribution in northern YNP, interpolated from data at 87 aspen stands (black dots show sampling locations). The gray background is the northern Yellowstone ungulate winter range. Interpolation did not include consideration of topographic variation. (c) Elk population density in each count unit was averaged for (c) the years 1987–1994 and (d) the years 2005–2011. The two northernmost units had no count data prior to 1994 (Lemke et al. 1998).

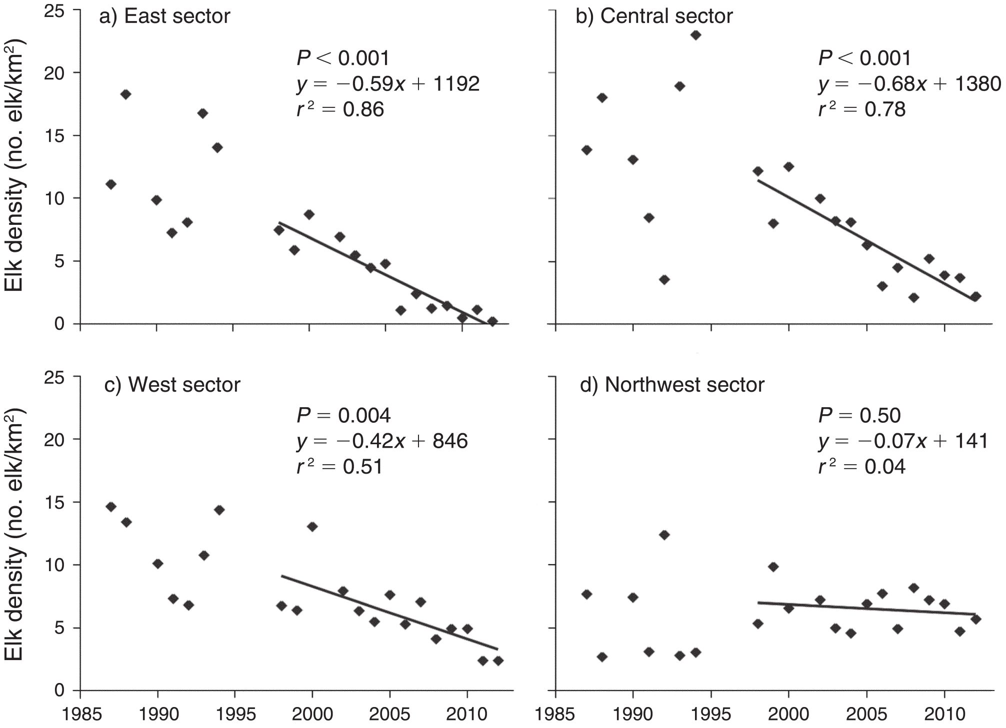

FIG. 4. Elk population density on the northern range by sector using winter aerial counts, 1987–2012, with regression results for the post-wolf period, 1998–2012. Count data were not available for 1989, 1995–1997, and 2001. In the 1980s and early 1990s, elk herd size fluctuated in response to environmental conditions and elk movements were strongly affected by winter severity (Singer et al. 1997, White and Garrott 2005*a*).

substantial reduction in elk density when compared with count densities of 20–40 groups/100 m^2 found in northern YNP in 1999 throughout the range (Ripple et al. 2001). Estimated winter elk densities in the east sector (from count data) were <2 elk/km^2 for six of the last seven years 2006–2012, whereas those in the west and central sectors were 2–6 elk/km^2 (Fig. 4). The ratio of elk counted inside/outside the park averaged 7.2 (95% CI: 2.5–11.9) in 1989–1994, and declined to 1.0 (95% CI: 0.58–1.5) in 2005–2012, a statistically significant reduction in this ratio ($P = 0.02$). Sample variance also was much greater in 1989–1994, 26 compared to 0.27 in 2005–2021. In the period of record 1987–2012, the ratio of elk inside/outside the park was <1 for the first time in 2006, and remained ≤ 1 in 2008–2012. After the extreme winter of 1996–1997, SWE was above average in 1999 and 2011, and below or near average for 2001–2010 and 2012 (Appendix: Fig. A2).

DISCUSSION

Aspen recruitment

Recent growth of aspen saplings above the browsing height of elk (Fig. 2) is evidence of a beginning aspen recovery in northern YNP (see Plate 1), mediated by changes in elk density and distribution. These new saplings are tall enough that they are likely to survive to replace dying overstory trees (Kay 1990, White et al. 1998). This patchy increase in aspen recruitment represents a fundamental shift in aspen dynamics, because recruitment of new aspen trees declined and virtually ceased by the mid-20th century due to intensive herbivory by elk (Ripple and Larsen 2000, Kauffman et al. 2010, Beschta and Ripple 2013, Painter et al. 2014). In 2012, browsing rates were lower and young aspen taller in all three range sectors within the park compared to conditions in 1997–1998 (Fig. 1), with the greatest change in the east sector, where signs of aspen recovery were first reported in 2006 (Ripple and Beschta 2007). This pattern was consistent with the fact that elk densities declined earlier and to lower levels in the east than in the rest of the range (Figs. 3d and 4a). Browsing and height varied greatly (Fig. A1), and browsing intensity appeared to be the primary driver of differences in young aspen height among stands (Appendix: Table A1, Fig. A1).

Timing and distribution of the release of aspen from suppression by browsing serve to explain the discrepancy between the findings of Ripple and Beschta (2007, 2012) and those of Kauffman et al. (2010). Although some aspen stands in the east sector had saplings (i.e., young aspen $\geq$ 200 cm in height) by 2006 (Ripple and Beschta 2007), most stands on the northern range did not (Fig. 2). Furthermore, patchy elk distribution resulted in some areas having high elk densities and high browsing rates even as the overall elk population declined. Outside of the park in 2006, in the northwest sector of the range, Kimble et al. (2011) found some new aspen saplings, but most stands were still suppressed by herbivory from elk and cattle, consistent with continued high elk densities in the northwest sector (Fig. 4d). More recently, aspen recruitment increased in a portion of the northwest sector as a result of decreased browsing (Runyon et al. 2014). Similarly, our data inside the park show that the percentage of stands with saplings has increased since about 2005 as browsing rates have declined (Fig. 2). If elk densities continue to decline, browsing rates may be further reduced. Alternatively, if densities stabilize at recent levels of 2–4 elk/km^2 on the west side of the range, aspen may be partially suppressed as in some other elk–wolf systems with similar elk densities (White et al. 1998, 2003). A more complete aspen recovery may require lower elk densities, <2 elk/km^2, as recently occurred in the east sector.

Changes in elk density and distribution

From 1950 to 1970, northern Yellowstone elk numbers were similar to the low numbers of the last decade, due to culling by the park service that ended in 1969, yet aspen herbivory remained intensive in the park, preventing significant aspen recruitment (Barmore 1967, 2003, Houston 1982, YNP 1997). In the 1960s, and for most of 20th century, most of the elk herd wintered within the park boundary, maintaining high densities (>4 elk/km^2) even when overall numbers were low (Houston 1982). The difference in the last decade, in which a similar elk population size has been associated with reduced herbivory, appears to be due to changes in the distribution of elk, resulting in a large proportion of the herd spending winter outside the park (Fig. 3d). Without this departure from historical patterns, elk densities would likely have remained high enough to suppress aspen recruitment, even with a reduction in overall elk numbers. For example, elk density inside the park in 2012 was 1.3 elk/km^2, but most of the herd wintered outside the park in the northwest sector. If 90% of the total herd had wintered in the park, as happened in the 1960s, elk density in the park would have been nearly three times greater (3.6 elk/km^2). The number of elk killed annually by wolves in the park (Smith et al. 2004, White and Garrott 2005*a*) has been comparable to rates of culling in the park in the 1960s (Houston 1982), but the outcome has been very different, with a large-scale shift in distribution of elk to the northwest sector of the range, even before the winter hunt was reduced in 2006 (Fig. 4).

Despite the near elimination of winter elk hunting after 2005 (White et al. 2012), lower wolf numbers after 2007 (Smith et al. 2013), mild winters after 1999 (Appendix: Fig. A2), and the end of the regional drought by 2007 (McMenamin et al. 2008, White and Garrott 2013, Painter et al. 2014), the trend of declining elk density inside the park continued through 2012 (Fig. 4). Other elk populations in the region experiencing a similar climate regime did not decline except where wolves and grizzly bears (*Ursus arctos*) were relatively abundant (Hamlin and Cunningham 2009, Creel et al. 2013, White and Garrott 2013), pointing to predation as a likely cause. Furthermore, suppression of elk recruitment due to drought or predation cannot explain the steady decline in elk numbers inside the park after 1997 without the additional factors of (1) a strong shift in elk winter range selection, or (2) increased mortality of adult elk wintering in the park, of which wolves have been the leading cause (White and Garrott 2005*a*, White et al. 2010). Although bears take many elk calves in spring (Barber-Meyer et al. 2008), they rarely take adults and do not prey on elk in winter.

In addition to higher mortality and lower recruitment of elk in the Lamar River herd segment (White et al. 2012), there is some evidence for changes in habitat selection by elk in response to wolves (Proffitt et al. 2009, White et al. 2009). After wolf reintroduction, elk home ranges increased in size and elk movements were more dynamic, with some elk dispersing to new areas (Gower et al. 2009, White et al. 2010). Although most cow elk tracked on the northern range between 2000 and 2008 showed a high degree of fidelity to their winter range, 39% changed their winter range toward the west and northwest (White et al. 2010). These changes suggest that some of the shift in distribution of the elk herd may have been behavioral. The factors most different now inside the park compared to the past century are the presence of wolves, increased predation by bears, and a larger bison population. Outside the park, elk have benefited from reductions in hunting and hunting access, fewer predators than in the park, and access to irrigated fields with high-quality forage, human influences that may contribute to a shift in elk distribution (Haggerty and Travis 2006, Berger 2007, Proffitt et al. 2009, 2013, Wilmers and Levi 2013). In a similar pattern, after wolves recolonized Banff National Park, Canada, elk distribution shifted toward areas of high human activity and low predator density (human shielding), reducing browsing on aspen and willow in remote areas (White et al. 2003, Hebblewhite et al. 2005, Hebblewhite and Merrill 2011). Regardless of the mechanism, the result has been a reduction in elk density in some areas of the northern range and an associated reduction in herbivory of aspen. Elk densities also became less variable as the population declined (Fig. 4), and since 1997, mortality inside the park has been primarily due to predation (Barber-Meyer et al. 2008, White et al. 2010), suggesting that top-down limitation of elk has been occurring without additional culling for probably the first time since elk counts began in the 1930s (Houston 1982, White and Garrott 2005*a*).

Behavioral responses to predation and the importance of scale

Trophic cascades involving wolves, elk, and plants are usually discussed as either density mediated at a

PLATE 1. Tall young aspen saplings in the eastern sector of the Yellowstone northern range. Recently recruited saplings were about 4 m tall when this photo was taken in September 2010, well above the height of most elk browsing. Photo credit: W. J. Ripple. Additional aspen photos from the study area in 2010 (Ripple and Bescheta 2012*b*) are available online at: http://hdl.handle.net/1957/25603

landscape scale (White et al. 2012), or behaviorally mediated at the small scale of topographic features, or piles of logs (Ripple and Beschta 2007, Kauffman et al. 2010, Winnie 2012). This paradigm, however, may be inadequate to describe recent changes on the northern range, where large-scale changes in elk density and distribution may have a behavioral component in response to predators as well as human hunters. Furthermore, behavioral responses by elk at an intermediate scale could also affect plants, such as changes in movements, grouping behavior, range size, and habitat use that occurred when wolves returned to Yellowstone (Mao et al. 2005, Gude et al. 2006, Gower et al. 2009, White et al. 2009, 2012). A more complete understanding of the interactions of predators, ungulates, and woody browse plants may result from consideration of responses to predation at multiple scales (White et al. 2003).

Our results suggest that widespread aspen recovery required a substantial reduction in elk density. Small-scale behavioral responses to risk may have had local effects on browsing (e.g., Ripple and Beschta 2007), but were not sufficient to relieve suppression of aspen on a broad scale. With elk densities reduced, behavioral effects of predation may explain some of the variation in browsing among stands in the same area (Appendix: Fig. A1). White et al. (2003) found evidence of small-scale effects of predation risk on aspen recruitment in Canadian national parks, but only in areas of low-to-moderate elk density (<4 elk/km^2). We found that young aspen were taller in riparian stands and stands with more logs (Appendix: Table A1), as did Ripple and Beschta (2012*b*) These variables could be related to the risk of predation (Ripple and Beschta 2007, Eisenberg 2012, Kuijper et al. 2013), but also to the convenience of accessing young aspen by elk or bison. Both factors may be operating, and would be difficult to distinguish as elk densities decline and bison increase. Also, predation risk effects may be temporally variable (Creel and Winnie 2005), and even a short period of browsing can prevent aspen growth (Fitzgerald and Bailey 1984), reducing the potential for behavioral responses to benefit aspen. For example, much browsing of aspen occurs in late fall (Barmore 1967, 2003) when predation risk may be less than later in winter, when elk are weak and snow is deep.

Bison distribution and browsing

Distributions of bison and elk on the northern range differed, as evidenced by scat densities and annual counts (Fig. 3). Timing of range use was different as well, with bison remaining year-round in places that elk use primarily in winter (Painter and Ripple 2012, Frank et al. 2013). Bison may have been limited by competition with elk in the past (Houston 1982, Coughenour 2005, White and Garrott 2005*b*), but bison on the northern range increased threefold between 1998 and 2012 (Plumb et al. 2009, Ripple et al. 2010, Wallen 2012), expanding into range vacated by elk, or perhaps displacing elk. The extent to which bison may have affected elk distribution is unknown, but the situation is clearly different from the past, with intensive range use by bison in some places removing forage that otherwise would be available for elk.

In recent years, bison have intensively browsed willow and cottonwood in portions of the east sector (Painter and Ripple 2012, Rose 2012), and we have observed bison browsing on aspen. High browsing rates in stands with very low elk density but high bison density suggest that bison may reduce or prevent aspen recruitment in some stands; however, bison have not prevented a general trend toward aspen recovery. Browsing rates on young aspen were generally low in the east sector, despite high bison density. Browsing rates of aspen on the northern range were very low (<25%) at heights above the reach of bison (>100 cm), suggesting that aspen taller than 100 cm may no longer be strongly suppressed by herbivory from either elk or bison.

Conclusions

The complex relationship of aspen and elk in YNP's northern range will continue to unfold, interacting with large predators (Hamlin et al. 2009, Creel et al. 2013), an increasing bison population (Painter and Ripple 2012), changing climate and fire regimes (Wilmers and Getz 2005, Wilmers et al. 2012), changes in land use and hunting outside the park (Haggerty and Travis 2006, Proffitt et al. 2013, Wilmers and Levi 2013), and other facets of the Yellowstone ecosystem (White and Garrott 2013). In 1997–1998, young aspen on the northern range remained suppressed by browsing, as had been the case for decades. By 2006 there was an important shift in aspen dynamics beginning in the east sector, following reductions in rates of browsing (Fig. 4), and by 2012, all three sectors of the range in the park had stands with saplings taller than the browse height of elk (Fig. 2b). Where herbivory has been reduced, bottom-up factors such as site productivity may become more important drivers of young aspen height, as has happened with willow (*Salix* spp.) in some places on the northern range (Tercek et al. 2010, Marshall et al. 2013).

Although elk mortality, recruitment, and habitat use may be affected by various factors, it is likely that predation in the park, especially from wolves, played a substantial role in declining elk numbers and shifting elk distribution (White and Garrott 2013). The resulting increase in aspen recruitment is evidence of a trophic cascade at a landscape scale. Changing elk dynamics and the beginning aspen recovery in Yellowstone are consistent with top-down control of large ungulate prey by large carnivores (Ripple and Beschta 2012*a*, Creel et al. 2013, White and Garrott 2013), with cascading effects in the ecosystem.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-0712.1.sm