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Short communication

Restoring Yellowstone's aspen with wolves

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ABSTRACT

Wolves (*Canis lupus*) were reintroduced to Yellowstone National Park in 1995–1996. We present data on a recent trophic cascade involving wolves, elk (*Cervus elaphus*), and aspen (*Populus tremuloides*) in Yellowstone's northern winter range that documents the first significant growth of aspen in over half a century. Results indicate reduced browsing and increased heights of young aspen during the last 4–5 years, particularly at high predation risk sites (riparian areas with downed logs). In contrast, young aspen in upland settings generally showed continued suppression with only a slight decrease in browsing levels and only a slight increase in height. Our findings are consistent with the combined effects of a behaviorally-mediated and density-mediated trophic cascade. Results provide an improved perspective for understanding trophic dynamics and spatially variable plant community growth patterns in this recovering ecosystem.

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The strength of top-down forces (trophic cascades) in terrestrial food webs is highly debated, as few examples exist illustrating the cascading effects of large mammalian carnivores in structuring terrestrial ecosystems (Ripple and Beschta, 2004a; Borer et al., 2005; Hebblewhite et al., 2005; Ray et al., 2005). Predators can directly influence prey populations through density-mediated effects (lethal), which in turn affect herbivory pressure on plants. A second, less understood mechanism involves behaviorally-mediated effects (non-lethal) whereby herbivores, under the risk of predation, alter foraging patterns and habitat use (Lima and Dill, 1990; Schmitz et al., 1997). For prey species, foraging decisions made in a landscape of fear may differ from a foraging strategy based on maximizing nutrient intake in the absence of predators (Laundré et al., 2001). Although little studied, the magnitude of behaviorally-mediated effects on plants may be equal to or even greater than cascading effects resulting from den-

sity-mediated effects of predation (Schmitz et al., 1997). While the effects of predation most likely occur as a combination of behaviorally-mediated and density-mediated effects on plants, disentangling the relative influence of these effects remains difficult (Ripple and Beschta, 2004a).

We recently examined a potential trophic cascade involving wolves (*Canis lupus*), elk (*Cervus elaphus*), and aspen (*Populus tremuloides*) in Yellowstone National Park. Aspen clones, with longevities of centuries and perhaps millennia, and other woody browse species in the park's northern winter range have declined substantially since wolf extirpation in the 1920s, likely attributable to ungulate browsing (Ripple and Larsen, 2000; National Research Council (NRC), 2002; Barmore, 2003; Beschta, 2005).

Although highly controversial, wolves were reintroduced into Yellowstone National Park during 1995 and 1996 following approximately seven decades of absence. After ten years

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of increasing wolf presence (Fig. 1a) and declining elk populations (Fig. 1b), we set out to assess if aspen recovery was underway within the Lamar Valley in the northeastern part of the park. To our knowledge, there have been no reports of significant growth of young aspen to heights greater than

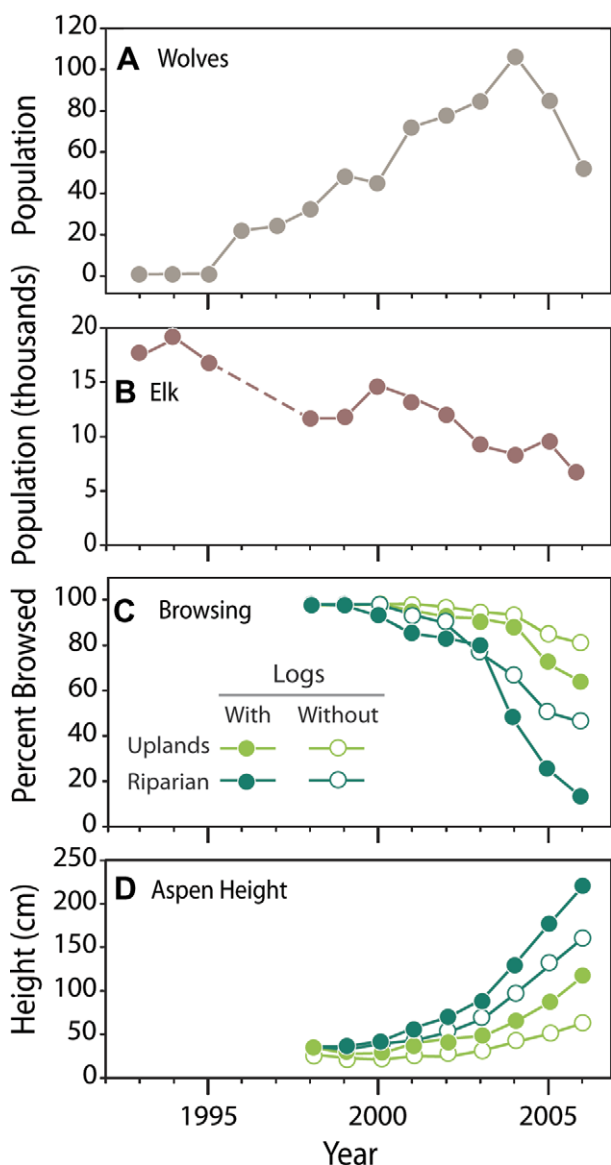


Fig. 1 – (A) Wolf populations, (B) elk populations, (C) percentage of aspen leaders browsed, and (D) mean aspen heights in Yellowstone’s northern range (early springtime heights after winter browsing but before summer growth). The percentage of aspen leaders browsed decreased the most and aspen grew tallest at high predation risk sites (riparian areas with downed logs). Wolf data from Smith et al. (2006); 1993–2004 elk data from White and Garrott (2005); and 2005–2006 elk data unpublished from Yellowstone National Park. The elk population estimate for 2006 is believed to be inaccurate due to poor weather conditions during the count. Animal data presented here are based on reporting year protocol suggested by White and Garrott (2005).

200 cm on the northern range since wolf reintroduction. Our objective was to test a set of *a priori* hypotheses potentially linking any recent aspen growth (measured as aspen height) to risk-sensitive foraging by elk (see covariates below).

The Lamar Valley lies within Yellowstone’s 1500 km² northern elk winter range. Lower elevations have predominately steppe and shrub-steppe plant communities, dominated by big sagebrush (*Artemisia tridentata*), that grade into conifers, principally lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*), at higher elevations. Cottonwoods (*Populus* spp.) and willows (*Salix* spp.) are found along flood plains, with aspen occurring in both riparian and upland settings (Meagher and Houston, 1998; National Research Council (NRC), 2002).

In August of 2006, we searched for and selected all riparian areas having seven or more aspen clones within the Lamar Valley study area. We paired each riparian area with a similar number of aspen clones in the adjacent upland. This allowed us to compare aspen height between riparian areas and uplands (position, see Table 1). Mean distance (\bar{x}) between an upland clone and the nearest riparian clone was 411 m. The total area in which aspen clones were sampled comprised ~450 ha of riparian/upland terrain along four streams: crystal Creek (1st-order stream [map scale=1:127,000], number of clones [N] = 25); Rose Creek (2nd-order, N = 14); Slough Creek (3rd-order, N = 25); and Lamar River (4th-order, N = 34).

Using plant architecture methods (Keigley and Frisina, 1998), we measured the recent history of browsing and height for the five tallest young aspen in each clone ($n = 490$ aspen). Inspection of individual leaders for terminal bud scars and browsing allowed us to determine annual heights for as many as nine previous years and the percentage of leaders browsed over time. All sampled aspen were accessible to ungulate browsing and each measured aspen had been browsed at least once during the last nine years.

To index potential escape impediments for elk, we recorded the number of downed logs >30 cm diameter (logs, $\bar{x} = 1.7$) within a 3 m radius of each measured aspen. For each aspen clone we also determined its distance to the nearest conifer forest (conifer edge, $\bar{x} = 264$ m) and nearest road (road, $\bar{x} = 1015$ m) using a hand-held laser rangefinder and a global positioning system.

We used an information theoretic criterion (AIC) approach for data analysis and developed ten *a priori* candidate models from our covariates (Burnham and Anderson, 2002). Based on previous studies (Ripple and Beschta, 2004b; Fortin et al., 2005; Mao et al., 2005; Beyer, 2006), we hypothesized that aspen would be taller (1) in riparian areas than in upland areas, (2) at sites with downed logs, (3) away from conifer forest edges, and (4) near roads. Our *a priori* model set included single-factor models (both linear and log-linear) of all four covariates and both additive and interactive two-factor models of landscape position and number of logs. The null model (intercept-only) was also included in our *a priori* model set. Plots of the best models suggested model residuals were independent and normally distributed with homogeneous variances, requiring no transformation.

To rank the models, we used the corrected AIC for small sample sizes (AIC_c), the difference in AIC_c between candidate models and the model with the lowest AIC_c value (ΔAIC_c), and

Table 1 – Results of AIC_c analysis for a priori generalized linear models explaining mean aspen height (N = 98 clones)

Model	k	AIC _c	Δ AIC _c	–2log L	ω_i
logs + position	4	1067.89	0.00	1.00	0.73
logs* position + logs + position	5	1069.82	1.93	0.38	0.28
Logs	3	1113.06	45.16	0.00	0.00
Position	3	1113.08	45.19	0.00	0.00
ln [logs]	3	1121.08	53.19	0.00	0.00
ln [conifer edge]	3	1148.35	80.45	0.00	0.00
Conifer edge	3	1153.43	85.54	0.00	0.00
Null Model	2	1158.24	90.35	0.00	0.00
ln [road]	3	1159.94	92.05	0.00	0.00
Road	3	1160.36	92.46	0.00	0.00

The variables include the number of downed logs (logs), riparian or upland area (position), distance to conifer forest (conifer edge), and distance to the nearest road (road). The number of parameters estimated in the model (k), the AIC_c, the difference in AIC_c values between any given model and the model with the lowest Δ AIC_c, the negative 2 log-likelihood (–2log L), and the Akaike's weight (ω_i) are listed for each candidate model.

Akaike weights (ω_i). We calculated slope coefficients (β_i), associated standard errors, and 95% confidence intervals to evaluate the strength of support for specific effects for competing models (<2 Δ AIC_c values). The extent to which the confidence intervals for β_i overlapped zero was used to assess the strength of support for specific effects in competing models. Unless confidence intervals on slope coefficients indicated otherwise, the model with the lowest AIC_c score was considered best (Burnham and Anderson, 2002).

Since 1997, average heights of young aspen were inversely related to the percentage of aspen leaders browsed (Fig. 1C and D). Our plant measurements indicated that by early spring of 2006 average aspen heights in riparian areas (\bar{x} = 214 cm, 95% CIs: 166–262, N = 44 clones) were above the normal browse level of elk (Figs. 1D, 2A). Conversely, aspen in uplands remained shorter (\bar{x} = 105 cm, 95% CIs: 89–121, N = 54 clones) and generally had not grown into tall saplings (Figs. 1D and 2B). We also found less browsing and taller aspen at sites with downed logs (\bar{x} = 167 cm, 95% CIs: 148–186, N = 77 clones) compared to sites without logs (\bar{x} = 105 cm, 95% CIs: 71–139, N = 21 clones). Model selection results suggest that the combined effects of landscape position (riparian vs. uplands) and number logs were most important for explaining aspen height differences (next best model Δ AIC_c > 43, Table 1). As hypothesized, aspen was taller in riparian areas compared to uplands (β = –87.8; 95% CIs: –65.8 to –109.9) and at sites with downed logs (β = 25.4; 95% CIs: 19.0 to 31.8). AIC offered no support for models containing other covariates including distance to either forest or roads.

Our results indicate the first significant growth of young aspen in the northern range for over half a century. In order to help understand the potential mechanism for the specific results we document herein, we formulated conceptual models (Fig. 3) illustrating the potential growth of young aspen growth in riparian and upland areas with “wolves absent” and “wolves present”. Since upland areas represent the vast majority of the northern range, we assumed in our model that upland elk densities follow the general pattern of decreasing elk populations represented in Fig. 1. Additionally, we assumed that elk densities are correlated with elk browsing levels. For our initial conditions of wolves absent, we represent riparian elk densities at levels greater than upland densities for “A”, equal for “B”, and

lower for “C” (Fig. 3). Because the results of this study indicated browsing levels in riparian areas were lower in recent years than in adjacent uplands, with wolves present we thus assume elk densities to be lower in riparian areas than in uplands. Two scenarios (Fig. 3A and B) represent a combination of behavioral- and density-mediated responses and show elk densities in riparian areas decrease at a faster rate than in uplands. For the third scenario (Fig. 3C), depending upon initial elk densities in riparian areas when wolves were absent, it is possible for them to decrease more rapidly, the same as, or less rapidly than that of uplands. In Fig. 3C we show elk densities declining at an equal rate in both riparian and upland areas; this unique solution represents the occurrence of density-mediation. The results from our study are consistent with Fig. 3A and B (combined behavioral and density effects) in that browsing levels were initially high at both locations (wolves absent) and have declined more in riparian areas than upland areas in recent years (wolves present).

Much of the aspen growth observed in riparian areas after the reintroduction of wolves appears to have been due to reduced browsing by elk at sites with poor escape terrain and reduced visibility (sites with high predation risk). Results from a recent willow study (Ripple and Beschta, 2006) indicated that the greatest decrease in browsing and the most plant growth occurred in riparian areas at sites with deep draws, tall cutbanks, or high terraces. The sharply decreasing elk browsing rate, and increasing height in riparian areas after about 2003 could reflect the steep Type 2 elk-aspen functional response described by White et al. (2003) where once aspen “thickets” develop, browsing rates decline even more rapidly due to localized aspen patch avoidance by elk. However, it could also be because elk are increasingly wary of riparian areas and are generally avoiding them as has been shown by recent elk telemetry data (Beyer, 2006).

The aspen height differences we found are apparently not attributable to differences in site productivity as the current annual growth of unbrowsed leaders showed no significant differences between riparian areas and uplands (\bar{x} = 50 vs. 49 cm, p = 0.60).

It is also unlikely that these aspen height differences were due to climate influences, as riparian areas share a similar climate with adjacent uplands. However, in the presence of key



Fig. 2 – August 2006 photographs of (A) recent aspen recruitment (aspen 3–4 m tall) in a riparian area along Lamar River and (B) a lack of recent aspen recruitment (aspen <1 m tall) in an adjacent upland. The dark, furrowed bark comprising approximately the lower 2.5 m of aspen boles in (B) represents long-term damage due to bark stripping by elk.

predators, climatic fluctuations might influence wolf-elk predation patterns (Hebblewhite, 2005) or allow for increased aspen growth in riparian areas due to the combination of reduced herbivory and a series of moist years (Romme et al., 1995). Thus, in the presence of strong predator effects, there could be climate interactions with landscape position if riparian areas have deeper snow or greater soil moisture in some years relative to uplands. These factors may only be of significance when coupled with strong predation effects, otherwise taller aspen would have occurred in past decades when no wolves were present.

Through the use of plant architecture techniques we are able to assess the recent history of browsing and growth of

individual plants. Collectively, these measurements provide a means of assessing the effects of herbivores in space and time. From a spatial perspective, the relative amount of herbivory of a particular forage species, such as aspen in this study, provides perhaps our best measure of predation risk occurring at local (e.g., within individual aspen stands) and landscape (e.g., riparian vs. upland) scales. Although radio telemetry can provide important data on elk locations and patterns of movement, it is unable to discern fine-scale spatial detail regarding browsing patterns on individual plants. From a temporal perspective, plant architecture measurements also allowed us to identify the recent browsing history and height status of recovering aspen communities, and of

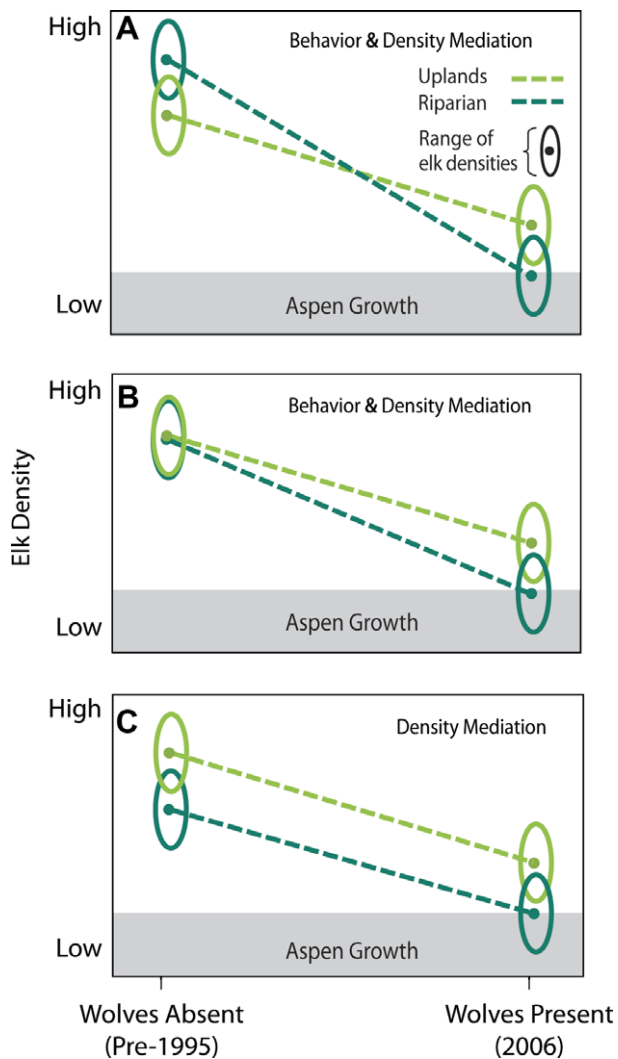


Fig. 3 – Conceptual model of elk density changes in the northern elk winter range from pre-1995 (wolves absent) to 2006 (wolves present). “Aspen growth” (shaded gray area) represents a range of elk densities at which aspen sprouts can grow above the normal upper browse level of elk. Scenarios include “A” and “B” where elk densities (and browsing) decline in both upland and riparian habitats, but declines occur more rapidly in riparian zones (behavioral response), and “C” a density-mediated effect since elk densities decline at an equal rate in both habitats.

those that were not. Conversely, we recognize that plant architecture techniques might not be useful for differentiating between upland and riparian elk use when elk browsing levels are sufficiently intense that little plant architecture remains (pre-2000 conditions, Fig. 1D).

The difference in aspen height increases in the uplands versus the riparian areas found in the current study is consistent with a recently reported patchy release of willow in Yellowstone’s northern winter ranges (Beyer, 2006; Ripple and Beschta, 2006). In this study we also found recent aspen height increases to be patchy. Elk may be avoiding browsing certain riparian areas (Beyer, 2006) as an anti-predator strategy to avoid wolf encounters, detect wolves, escape from

wolves, and/or evade wolves by hiding in nearby upland conifer forests.

It should be noted that the research reported herein was based upon a “natural experiment” with limitations such as: (1) there was no experimental control for the predator since the whole study area was recolonized by wolves; (2) it is possible that there were significant differences in elk use between the riparian and upland areas prior to the year 2000, but aspen suckers were so impacted in both that these past differences are not easily detectable in recently collected aspen morphology data; and (3) our data are only representative of the first recovering aspen (5 tallest per clone) and not an estimate of the aspen population response across Yellowstone’s northern winter range. In addition to elk, it should be noted that the northern range’s resident bison population may be affecting the status of aspen communities (Ripple and Beschta, 2006). Although typically not considered browsers, we have repeatedly witnessed bison foraging on woody species in our study area.

While results are encouraging for the recovery of aspen at some riparian sites, upland clones represent a different situation. Since the extirpation of wolves in the mid-1920s, aspen clones in the northern range typically have experienced high levels of herbivory and have been unable to regenerate. Many upland clones have already died. If high browsing levels continue, such as those found in this study, more clones are likely to disappear from the northern range in the coming years. To what extent this loss can be prevented by the continued presence of wolves, either through density-mediated or behaviorally-mediated effects, is not currently known. Research is needed integrating long-term elk densities, elk browsing, and aspen growth against control areas having no wolves or very low wolf densities. Investigating the complex predator/prey behavioral dynamics involving wolves and elk (e.g., Creel et al., 2005), while considering effects of other large carnivores, weather events, and wildfire on aspen recruitment within a context of altered anthropogenic processes, such as historic hunting and burning (White et al., 2003), will continue to pose a major challenge to researchers.

Yellowstone’s wolves are part of an ecological experiment in time, since this apex predator was first removed and later replaced. Based on recent growth responses of aspen in the northern range of Yellowstone, as well as growth responses of other woody browse species, wolves appear to represent a key component in helping to passively restore these complex and wild ecosystems. While wolf recovery remains controversial, the potential importance of these effects for maintaining biodiversity indicates they should be included in any wolf conservation debate.

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