

Exhibit R

Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade

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Abstract. Behaviorally mediated trophic cascades (BMTCs) occur when the fear of predation among herbivores enhances plant productivity. Based primarily on systems involving small-bodied predators, BMTCs have been proposed as both strong and ubiquitous in natural ecosystems. Recently, however, synthetic work has suggested that the existence of BMTCs may be mediated by predator hunting mode, whereby passive (sit-and-wait) predators have much stronger effects than active (coursing) predators. One BMTC that has been proposed for a wide-ranging active predator system involves the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park, USA, which is thought to be leading to a recovery of trembling aspen (*Populus tremuloides*) by causing elk (*Cervus elaphus*) to avoid foraging in risky areas. Although this BMTC has been generally accepted and highly popularized, it has never been adequately tested. We assessed whether wolves influence aspen by obtaining detailed demographic data on aspen stands using tree rings and by monitoring browsing levels in experimental elk exclosures arrayed across a gradient of predation risk for three years. Our study demonstrates that the historical failure of aspen to regenerate varied widely among stands (last recruitment year ranged from 1892 to 1956), and our data do not indicate an abrupt cessation of recruitment. This pattern of recruitment failure appears more consistent with a gradual increase in elk numbers rather than a rapid behavioral shift in elk foraging following wolf extirpation. In addition, our estimates of relative survivorship of young browsable aspen indicate that aspen are not currently recovering in Yellowstone, even in the presence of a large wolf population. Finally, in an experimental test of the BMTC hypothesis we found that the impacts of elk browsing on aspen demography are not diminished in sites where elk are at higher risk of predation by wolves. These findings suggest the need to further evaluate how trophic cascades are mediated by predator–prey life history and ecological context.

Key words: behaviorally mediated trophic cascade; *Canis lupus*; *Cervus elaphus*; density-mediated indirect interactions; elk; herbivory; landscape of fear; *Populus tremuloides*; predation risk; predator hunting mode; trait-mediated indirect interactions; Yellowstone National Park.

INTRODUCTION

Predators indirectly influence plants in two main ways: by altering either the density or the foraging behavior of herbivores (Trussell et al. 2006, Heithaus et al. 2008). The latter influences are termed trait-mediated indirect interactions (TMIIs; Abrams 1996, Werner and Peacor 2003), and when such indirect interactions are strong enough to structure ecosystems, they are referred to as behaviorally mediated trophic cascades (BMTCs; Abrams 1984, Kerfoot and Sih 1987, Beckerman et al. 1997). Ecologists have documented numerous and well-known density-mediated trophic cascades in nature across a variety of ecological systems (Estes and

Palmisan 1974, Paine 1980, Carpenter et al. 1987, Power 1990, Terborgh et al. 2001, Croll et al. 2005), but the exploration of TMIIs has only recently attracted attention (McIntosh and Townsend 1996, Beckerman et al. 1997). TMIIs have been well documented on relatively small spatial scales. For example, studies of food chains involving spiders, insects, and plants (Beckerman et al. 1997, Gastreich 1999, Schmitz 2008), fish, invertebrates, and algae (McIntosh and Townsend 1996, Bernot and Turner 2001, Stief and Holker 2006), and insects, snails, and algae (Wojdak and Luttbeg 2005) have demonstrated strong TMIIs.

A growing number of ecologists have suggested that the strength of trait-mediated indirect effects equals or exceeds that of density-mediated effects (Peacor and Werner 2001, van Veen et al. 2005, Wojdak and Luttbeg 2005, Trussell et al. 2006). However, very few studies have assessed the existence and strength of TMIIs in

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systems where predators and prey interact over large geographic areas. In addition, recent syntheses (Schmitz et al. 2004, Schmitz 2005) have suggested that TMIIIs can be strongly mediated by predator hunting mode. Hunting modes range from passive, sit-and-wait predators, to active predators such as the wolf (*Canis lupus*) that course through groups of prey and chase down vulnerable individuals (MacNulty et al. 2007). Active predators, such as those common in many large mammal systems, are predicted to have the weakest (or nonexistent) fear-mediated effects, whereas passive predators should have the strongest indirect effects (Schmitz 2005). Active predators, especially those that roam over large landscapes, rarely produce consistent predation risk cues at any one spatial location or habitat type (Schmitz 2005). Given the high costs of antipredator behavior (Lima and Bednekoff 1999), prey of active-hunting predators may ultimately be relatively unresponsive to predators and thus unlikely to demonstrate risk-induced changes in foraging effort or habitat selection necessary to bring about BMTCs (Schmitz 2005). This variation in predation cues based on hunting mode is further altered by prey behavior related to risk allocation. The risk allocation hypothesis (Lima and Bednekoff 1999) suggests that prey should be more responsive to a pulse of risk against a background of relative safety and less responsive to more or less constant levels of risk. Creel et al. (2008) found evidence in support of this hypothesis with wolves and elk (*Cervus elaphus*), whereby elk in Yellowstone National Park (hereafter "Yellowstone"; many wolves, high risk) were less vigilant than elk in nearby drainages where wolf visitation was much less frequent. Although the strength and existence of TMIIIs appears to be mediated by predator hunting mode in small-scale systems involving spiders, grasshoppers, and plants (Schmitz and Suttle 2001), the generality of hunting mode mediation of TMIIIs (and that of risk allocation) has not been extended to large mammalian systems where predators and prey interact at the landscape scale.

The best-known TMII studies suggesting strong, behaviorally mediated effects (i.e., a BMTC) involving large mammals come from Yellowstone and the food chain involving wolves, elk, and aspen trees (*Populus tremuloides*) (Ripple et al. 2001, Fortin et al. 2005, Ripple and Beschta 2007). Because wolves are active predators, this system provides a rare opportunity to evaluate the influence of such a predator interacting with its prey on a landscape scale. Wolves were extirpated from most of their natural range in North America by the early 20th century as the continent was colonized by Euro-American settlers. In Yellowstone and the surrounding ecosystem, wolf extirpation is one factor that allowed elk to obtain high densities during much of the 20th century (Houston 1982). The precise date of wolf extirpation from Yellowstone is unknown, although it is clear they were no longer found in the region by 1930 (Schullery 2004). However, Schullery (2004) suggests

that the carcass poisoning that accompanied massive hunting efforts of ungulates may have largely reduced the Yellowstone wolf population to near extinction by 1880. In the last few decades, studies in Yellowstone have documented a decline of aspen resulting from a lack of new recruitment (Romme et al. 1995, Larsen and Ripple 2003). Aspen decline in Yellowstone parallels declines of this important deciduous tree species across the U.S. Intermountain West. The cause of aspen decline in Yellowstone has spawned considerable debate (e.g., Kay 1997, Huff and Varley 1999, NRC 2002), but most recognize that intense elk browsing of young shoots plays a crucial role (Romme et al. 1995, 2005, Huff and Varley 1999, Ripple et al. 2001, Barmore 2003).

The reintroduction of wolves to Yellowstone beginning in 1995 was heralded as a great success, not only because it reestablished an extirpated species, but because it was expected to restore ecosystem function through cascading indirect effects on other species. The original case made by the National Park Service for wolf reintroduction into Yellowstone did not predict BMTCs, but did predict that wolves would reduce elk numbers (White and Garrott 2005). However, once wolves were on the landscape and some plant monitoring was underway, suggestions were made that wolves might alter elk foraging behavior to the extent that aspen would be released from herbivory (Ripple et al. 2001, NRC 2002). Wolf reintroduction was, in fact, followed by a marked decline in elk numbers (Eberhardt et al. 2007). However, reduced forage due to a drought and a sustained increase in human hunting during this same period also negatively influenced the elk population (Vucetich et al. 2005). Detectable changes in elk foraging behavior (Laundré et al. 2001, Lung and Childress 2007, Liley and Creel 2008) and movement (Creel et al. 2005, Fortin et al. 2005, Gude et al. 2006) have been found where elk are now hunted by wolves. Recently, authors have claimed that aspen are benefiting from wolves via a BMTC, whereby aspen are recovering in areas where elk are at a high risk of predation (Ripple et al. 2001, Ripple and Beschta 2004, 2007, Fortin et al. 2005). Other researchers have claimed similar increases in willow (*Salix* spp.; Beyer et al. 2007) and cottonwood (*Populus* spp.; Beschta 2003) due to wolf-induced changes to elk foraging behavior, although recent work suggests that elk antipredator behavior is an unlikely mechanism for changes in willow growth (Creel and Christianson 2009). Since its reporting, the recovery of aspen has been attributed to a restored "landscape of fear" caused by wolf reintroduction. The notion that elk are now avoiding aspen in risky sites due to their fear of wolves has been hailed as an important conservation achievement, because it had been accomplished by reintroducing an ecological process (predation risk) rather than through direct intervention in aspen stands (Soulé et al. 2003, 2005, Donlan et al. 2006, Morell 2007). Yet despite the popular and scientific interest in the Yellowstone BMTC, its existence runs contrary to

the emerging view that active predators should be the least likely to produce BMTCs (Schmitz 2005).

Previous tests of the Yellowstone BMTC hypothesis have been limited by the inability to rigorously quantify predation risk and have relied instead on risk gradients based on untested assumptions about wolf and elk behavior (Ripple et al. 2001, Ripple and Beschta 2004; see *Discussion*). In this study, we used independent, empirically derived estimates of predation risk from a 10-year data set of winter wolf–elk predation events to evaluate risk effects on aspen (Kauffman et al. 2007) (Fig. 1). Our measure of landscape-level predation risk is estimated at a resolution of 30 m, which is consistent with the spatial scale of elk behavioral responses to wolves, according to recent evaluations. For example, Gude et al. (2006) found that elk distribution was influenced by wolf hunting patterns (based on kill locations), but not wolf activity patterns (based on wolf locations alone), which lends support to our measure of predation risk. Although some studies of BMTCs in Yellowstone (Ripple and Beschta 2003, Halofsky and Ripple 2008a) have inferred finer scale (i.e., 5–10 m) behavioral responses of elk, such fine-scale behavioral responses have yet to be verified, particularly in winter, when most elk foraging on aspen occurs (Romme et al. 1995).

The recent estimates of landscape-level predation risk by Kauffman et al. (2007) characterize the “landscape of fear” caused by the reintroduction of wolves to Yellowstone and set the stage for our analysis. Our primary objective was to evaluate the demographic response of aspen associated with the restoration of wolf predation risk to the landscape. First, we used a tree-ring study to assess whether the historical timing of recruitment failure among Yellowstone aspen stands coincided with wolf extirpation and the loss of this source of predation risk on the landscape. Next, we evaluated whether aspen stands are still failing to recruit new individuals to the adult class or whether a landscape-level recovery is underway. In addition, we tested whether differences in current levels of aspen recruitment observed across the landscape are related to spatial variation in the risk of wolf predation on elk. Finally, in a direct test of this BMTC, we used exclosures to experimentally measure the impact of elk browsing on aspen demography across a landscape-level gradient in predation risk.

MATERIALS AND METHODS

History of elk and wolves in Yellowstone

We conducted our study on the 1526-km² Northern Range of Yellowstone, a mid elevation (1500–2000 m), dry landscape (25 cm of annual precipitation) with a mix of grassland, shrub, and conifer habitat that is the primary winter range for the Northern Yellowstone elk herd. The Northern Yellowstone elk herd has a long history of study regarding population dynamics and herbivory, which is relevant to our assessment of wolf-mediated BMTCs in this system.

Prior to the establishment of Yellowstone in 1872, rampant market hunting had drastically reduced the Northern Yellowstone elk population to low numbers, although no formal abundance estimates exist for this time period (Houston 1982, Romme et al. 1995). Under park protection from human hunting, the elk population grew rapidly in the late 1800s and early 1900s, and by 1920–1930, park managers were increasingly concerned about overgrazing of winter range by a putatively overabundant elk population (Schullery 2004). Culling of park elk occurred as early as the 1930s and was particularly aggressive during the early 1960s, with a maximum annual removal of 4619 elk in 1962; in this year the population of elk on the Northern Range was estimated to be <5000 animals (Schullery 2004). In 1969, elk culling ended, and an era of “natural regulation” began where elk were not removed from the park (Houston 1982). From 1967 to 1975, the Northern Range elk population is estimated to have grown at an annual rate of $\lambda = 1.19$, increasing from 6237 to 17410 animals; the population peaked at >25000 animals in 1988 (sightability corrected; Eberhardt et al. 2007). Animals migrating out of the park north to Montana have been subject to human hunting since 1976 (Eberhardt et al. 2007).

In 1995 and 1996, 31 wolves from Canada were reintroduced to the park (Bangs and Fritts 1996). In the first 10 years since reintroduction, the wolf population on the Northern Range increased from 14 wolves in 3 packs to 84 wolves in 6 packs. The wolf population appears to be near saturation, controlled currently by intraspecific competition for limited viable territories as evidenced by increased levels of inter-pack interactions and intraspecific killing (Kauffman et al. 2007). The total Northern Range population peaked at 104 wolves in 2003 and then declined; there were 72 wolves in winter 2006–2007 (Smith et al. 2008). The Northern Range elk population declined from 16791 individuals in 1995 at ~8% annually (White and Garrott 2005), and has held stable at 6000–7000 animals in the last three years (2006–2008).

Predation risk map

In a previous study (Kauffman et al. 2007), we created a landscape-level risk map by evaluating the landscape attributes that influenced the spatial distribution of 774 elk killed by wolves in winter during the first 10 years of wolf recovery (1996–2005). All kills used in the Kauffman et al. (2007) analysis came from two 30-day periods in early and late winter, when wolf packs were intensively monitored by Yellowstone ground and air crews, and sightability bias was minimal with respect to landscape attributes tested (Smith et al. 2004). Several studies have shown that kill distribution is a good indicator of predation risk in nearby wolf–elk systems (Creel and Winnie 2005, Gude et al. 2006). We were concerned that kill locations as the endpoint of the entire predation sequence would misrepresent risk;

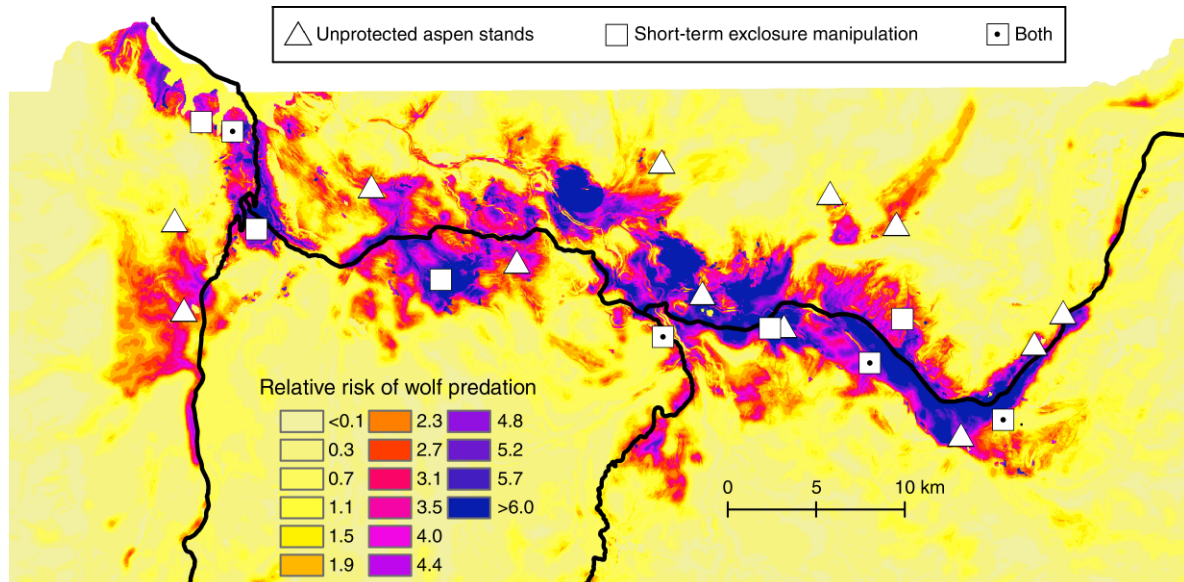


FIG. 1. Map of the relative risk of wolf (*Canis lupus*) predation for elk (*Cervus elaphus*) on Yellowstone's Northern Range, USA. Risk was averaged from 1996 to 2005, with a map value of 1.0 denoting average risk. Site locations for sampled and manipulated aspen stands are shown: open triangles represent unprotected aspen stands, open squares represent aspen stands where short-term enclosure manipulations were conducted, and open squares with a dot represent aspen stands used in both analyses. The figure is modified from Kauffman et al. (2007).

however, we found no differences in landscape attributes between encounter and kill locations for a subset of kills where encounter and chases had been observed ($N = 46$; D. MacNulty, unpublished data).

To generate the predation risk map, we used a logistic regression model with a matched case-control design (Hosmer and Lemeshow 2000), where relative probability of a kill on the landscape was estimated from the differential landscape attributes of kills compared to random locations. Landscape attributes used to build the model included the annual distribution of wolf packs (based on cumulative kernel densities and weighted by pack size), relative elk density (from the habitat model of Mao et al. 2005), and the landscape features of proximity to streams, proximity to roads, habitat openness (forest vs. grassland), slope, and snow depth (see Kauffman et al. 2007 for details). The habitat model of Mao et al. (2005) was based on a resource selection function (RSF; Manly et al. 2002). Such RSF models describe the spatial occurrence of a sample of marked animals as a function of landscape attributes and are assumed to be proportional to the probability of use for a given resource unit such as a pixel in a GIS (Boyce and McDonald 1999). In the risk map (Fig. 1), relative predation risk is standardized to a reference condition of an average set of landscape attributes, denoted by a value of 1. All relative risk values have been rescaled to take account of heterogeneity in elk density. This was done by dividing the risk value at each pixel by the elk RSF score of Mao et al. (2005), which provides an index of relative elk density. Although this method did not

account directly for landscape-level differences in elk group size, it provided an approximation of relative per capita risk of predation for Northern Range elk (Kauffman et al. 2007).

Aspen field sampling

Our first objective was to evaluate the current extent of elk browsing and recruitment failure of Northern Range aspen. To do this, we divided the Northern Range into four geographic strata of approximately equal area running east to west and randomly located four aspen stands per stratum, containing a minimum of 15 adult aspen and located within 3 km of a random location. Aspen were categorized into three size classes: adults (>6 cm diameter at breast height [dbh]), juveniles (>2 m in height <6 cm dbh), and suckers (ramet offspring <2 m tall). In summer 2004, we extracted two increment cores per tree from a random sample of 9–14 adults per stand in each of the 16 natural stands ($N = 182$ trees) and 30 adults in four long-term exclosures created in the 1950s ($N = 120$ trees). We established a variable number of 6 m diameter plots (4 to 8 per stand selected at random from within the boundary of aspen recruits) that summed to $\sim 5\%$ of the total stand area. Within each plot, we counted and measured the base diameter, height, and proportion of twigs browsed on all suckers and juveniles. We randomly selected and aged 60 suckers per stand (plus 60 juveniles in each exclosure) by extracting cross-sectional wedges out of the base of each stem. No individuals in the juvenile class were found in natural stands. Growth–height relationships and age

distributions were compared between natural stands and long-term exclosures.

Tree-ring analyses

Although most authors agree that elk herbivory is the primary cause of historical recruitment failure of aspen (Singer 1996, Kay 2001), several alternative explanations, including climate change and fire suppression, have been proposed and require testing (Romme et al. 1995, 2005). To test alternative explanations of aspen decline, we first prepared our increment cores using standard dendrochronology techniques (Stokes and Smiley 1968). The number of rings from each core were then counted under a stereomicroscope and used to estimate the date of recruitment for each tree. Each adult ring series was measured to 0.001-mm precision using a Velmex measuring device (TA 4030H1-S6 Unislide, Bloomfield, New York, USA). Tree-ring series were omitted if they showed significant physical damage or could not be confidently crossdated using visual assessment or the software COFECHA (Holmes 1983). Of the 302 adult aspen we cored, we used 252 for these analyses (166 from natural stands [mean = 10] and 86 from exclosures [mean = 22]).

To assess aspen growth trends and to provide an independent estimate of site productivity derived from non-browsable individuals, we calculated the annual basal area increment (BAI) for adults. Within each stand, we calculated the mean BAI among individuals for each year and a mean BAI for the last 25 years (1978–2003) as a stand-level measure of productivity. Our measure of productivity was independent of stand age; average BAI was not related to either stand age (origination date; $R^2 = 0.068$, $df = 15$, $P = 0.329$) or average age of individuals within each stand ($R^2 = 0.007$, $df = 15$, $P = 0.758$). Next, we used the software ARSTAN to detrend each ring series into standardized growth sequences (Cook and Kairiukstis 1990). Detrending removes growth trends related solely to age (i.e., diameter change) and helps elucidate climatic patterns in growth. We selected either the negative exponential or linear regression options; ARSTAN also collapses the series into a single chronosequence around an index of 1.0. To assess aspen–climate relationships, we compared these standardized growth sequences to the Palmer Drought Severity Index (PDSI; Wyoming Climate Division 1, National Climate Data Center, data available online),⁶ an index of long-term soil moisture, temperature, precipitation, and evapotranspiration (Palmer 1965). For the years data were available (1896–2003), we indexed winter precipitation by averaging PDSI from November to March. We calculated a Pearson correlation coefficient to assess the relationship between PDSI and the mean standardized growth rate using all stands ($N = 20$). To address whether climate has

influenced aspen recruitment failure, we regressed PDSI on the time period of recruitment failure, 1900–1960. Lastly, to assess whether the cessation of aspen recruitment was related to other natural causes, such as stand age or site factors, we conducted two multiple regressions. In the first, we used the date of last recruitment in each stand as our response variable and slope, aspect, elevation, BAI (site productivity), and the date of first recruitment (an estimate of stand age) as explanatory variables. In the second test we used the average date of the last three recruitment events in each stand (perhaps a more generalized measure of cessation) as the dependent variable and the same set of explanatory variables.

Predation risk effects on sucker age distributions

Because our inspection of sucker age structures indicated considerable variability in the demography of young aspen among our 16 natural stands, we designed an analysis to ask if aspen sucker survival was higher in risky sites than in safe sites. Assuming constant annual production of new suckers, we modeled the survivorship curve of each aspen stand ($i = 1$ to 16) as a logistic function where the probability of sucker s surviving to age t is given by

$$s_s(t) = \frac{\exp(b_i \times \text{age}_s)}{1 + \exp(b_i \times \text{age}_s)} \quad (1)$$

where age_s is the age (in years) of sucker s , and b_i is the slope parameter of survival in stand i . We fit b_i to each age distribution by maximizing the likelihood of the age distribution data given the survivorship model (Doak and Morris 1999) for each stand as follows:

$$L(\text{data}_i | \text{model}_i) = \frac{N!}{d(0)!d(1)! \dots d(s)!} p_i(0)^{d(0)} p_i(1)^{d(1)} \dots p_i(s)^{d(s)} \quad (2)$$

where L is the likelihood of the data from the aspen stand i , given model i , N is the total number of suckers, d is the number in each age class (0, 1, ..., s), and p is the proportion in each age class.

We used the fitted b_i for each stand as the response variable in an evaluation of the landscape factors influencing variation in survivorship among stands. Landscape factors included stand productivity, relative elk habitat use, relative wolf habitat use, and relative predation risk. Stand productivity was indexed as the average BAI for the last 25 years (described in the previous section). Relative elk habitat use was included as a general index of elk density and was estimated from the previous elk RSF based on telemetry locations of Northern Range cow elk (Mao et al. 2005). Sampling of scat within study plots indicated that elk were by far the most abundant ungulate using our natural stands. We included two measures of predation risk, both of which were previously derived for the Northern Range (Kauffman et al. 2007). To allow comparison with previous

⁶ (<http://lwf.ncdc.noaa.gov/oa/ncdc.html>)

analyses of wolf–elk–aspen interactions, we included a kernel-based index of wolf use of the landscape that accounted for the territory usage of each wolf pack, overlap among packs, and pack size. Secondly, we used the predation risk map (Fig. 1) derived from wolf-killed elk on the Northern Range. The vast majority of elk browsing on aspen occurs during winter (Romme et al. 1995, 2005), and thus, these estimates of risk are most appropriate for testing the BMTC. We used multiple regression to evaluate the influence of landscape variables on the fitted survival coefficients from each stand. Correlation of explanatory variables indicated r values < 0.55 for all variables (highest r values were for correlations of wolves vs. risk [0.55] and elk vs. risk [0.55]). Explanatory variables were transformed where appropriate; inspection of the residual plots led us to include a squared term for the BAI variable in the analysis.

Experimental test of the BMTC hypothesis

If wolves protect aspen, as predicted by the BMTC hypothesis, the effect of elk exclosures should be diminished or nonexistent in areas of high predation risk. Using the Northern Range risk map (Fig. 1), we selected nine aspen stands that spanned a wide range of variation in predation risk, including some of the riskiest places on the Northern Range. Site selection was done with the goal of including aspen stands ranging from the extremes of very low to very high predation risk. To assure that sites occurred in elk habitat, we constrained our selection to sites predicted to receive an intermediate level of use by elk, based on the Northern Yellowstone elk habitat model of Mao et al. (2005). In the fall of 2004, we selected six Northern Range aspen stands; three additional sites were added in the spring of 2005 (Fig. 1). At each stand, we randomly located six exclosure and control plots (~ 1.5 m in diameter) and tagged five randomly selected suckers in each plot. To protect exclosure plots from browsing, we constructed wire exclosures consisting of a circular tube of wire fencing (15.2×15.2 cm mesh) anchored to the ground with three rebar stakes. Exclosures were removed and re-deployed during the summer 2005 (June–September) at the request of park administration. Each spring and fall (2004–2007) we located tagged plants in both exclosure and control plots, determined whether they were alive or dead, and measured the height of the tallest leader. Dead plants were replaced with newly-marked individuals at each survey. Average annual growth was estimated for each plant as the average growth increment between each fall survey period. Average survival was similarly estimated across years as the total cumulative number of plants remaining, divided by the total cumulative number of plants alive at each subsequent fall census period. Growth and survival rates were compared between exclosure and control plots using paired t tests, and demographic differences ($N = 9$) were regressed against stand-level predation risk

from Fig. 1 to evaluate whether the benefits of exclosures were diminished in risky sites. Elk use of our experimental stands was confirmed via snow track sampling and remote video surveillance; American bison (*Bos bison*) were occasionally detected at aspen stands, though their foraging on aspen was extremely rare.

RESULTS

All 16 unprotected stands indicated a complete failure of individuals to survive past the sucker stage class, regardless of their location on the landscape (Figs. 2 and 3). We found no juveniles in sample plots, indicating that individual suckers are not surviving to the juvenile (or unbrowsable) stage. In addition, the time period when aspen recruitment failed across the 16 stands lasted >60 years (1892–1956) and spanned periods with and without wolves by several decades (Fig. 2).

Fire suppression often leads to encroachment by conifers, which can outcompete aspen and reduce recruitment (Gallant et al. 2003). However, none of the aspen stands that we studied were encroached by conifers, ruling out fire suppression as a proximate cause. Visual inspection of a plot of BAI through time (Fig. 2) indicated a clear increase in growth rates as the stands aged. In addition, standardized aspen growth was tightly correlated with the PDSI measure of climate ($r = 0.2665$, $df = 107$, $P = 0.005$); however, PDSI did not change across the time period of aspen recruitment failure ($R^2 = 0.026$, $df = 59$, $P = 0.216$). Neither climate nor reduced vigor of adults can explain the historical cessation of aspen recruitment on Yellowstone's Northern Range (Fig. 2). In addition, the dates when aspen ceased recruiting into particular sites could not be explained by any site factor or our estimate of stand age. For instance, multiple regression demonstrated that the year in which aspen was estimated to last recruit was not related to aspect ($t = 0.647$, $df = 15$, $P = 0.534$), elevation ($t = 0.760$, $df = 15$, $P = 0.467$), slope ($t = -0.148$, $df = 15$, $P = 0.886$), BAI ($t = 1.559$, $df = 15$, $P = 0.154$), or our stand origination estimate (i.e., age of the oldest individual in the stand; $t = 0.104$, $df = 15$, $P = 0.920$). The lack of evidence for site characteristics or stand age explaining recruitment failure was also found when we used the average date of the last three recruitment events. No significant correlations were found among any of the explanatory variables, except a significant, negative correlation between BAI and slope ($r = -0.507$, $P = 0.045$).

In contrast to the complete recruitment failure of the natural stands, aspen growing within the long-term exclosures have continually recruited young individuals to the juvenile and adult age classes (Fig. 2). Exclosures had proportionately more old-aged aspen than natural stands (Kolmogorov-Smirnov test; $D_{21,794} = 193.4$, $df = 17$, $P = 0.013$). Average sucker height for a given age was higher in exclosures than in unprotected stands ($F_{1,1029} = 234.29$, $P < 0.001$), demonstrating a clear growth advantage to protected suckers (Fig. 3).

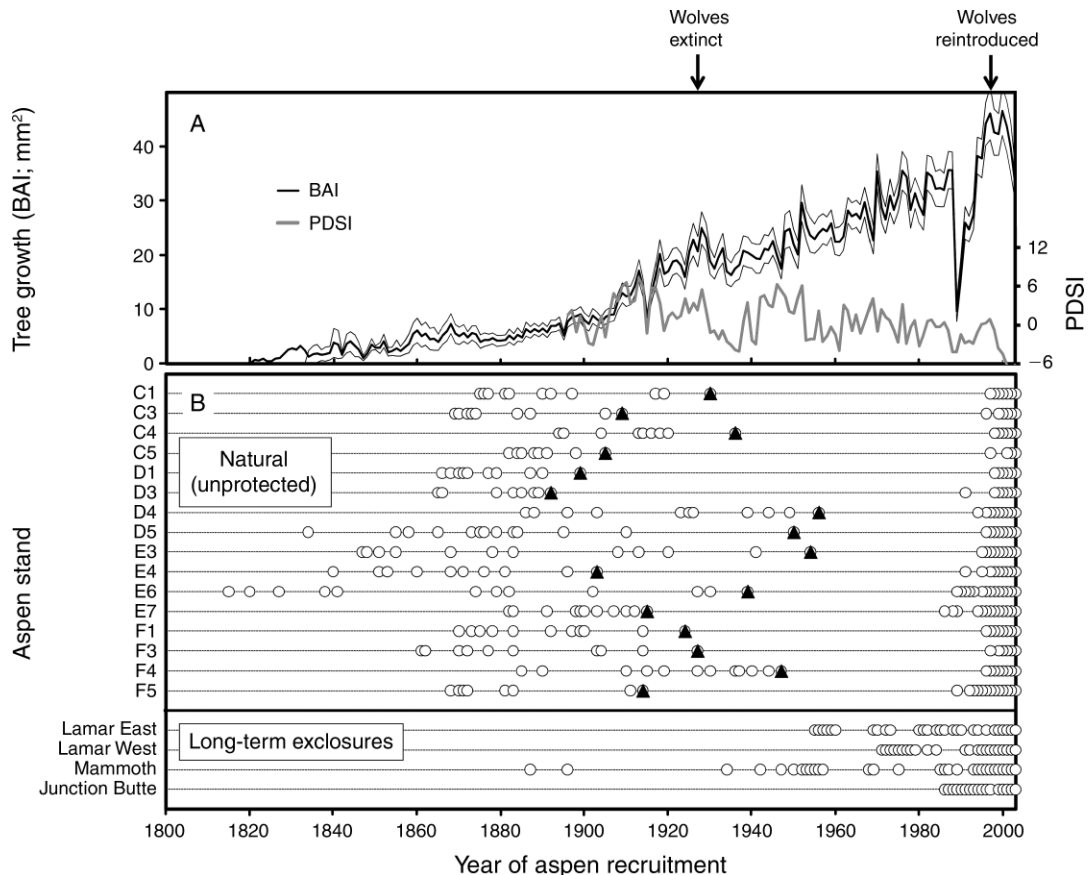


FIG. 2. Recruitment failure of aspens (*Populus tremuloides*) on Yellowstone's Northern Range in relation to trends in climate and growth rates from tree rings. (A) Basal area increment (mean \pm SEM; thick and thin lines, respectively), the area of wood produced each year, increases through time as trees grow in diameter and no new trees enter the stand. Note the dramatic reduction in BAI occurred the year following the Yellowstone fires of 1988. Palmer Drought Severity Index (PDSI) averaged for November to March shows no decline during the time period of recruitment failure (1900–1960). PDSI values near 0 indicate normal years, while larger values indicate high soil moisture, and lower values indicate low soil moisture. (B) All 16 natural aspen stands have ceased to recruit new adults into the population (solid triangles show last recruitment event in stand among adult trees, and open circles denote aspen trees of all ages sampled within each population), whereas successful recruitment of adults has continued in the long-term exclosures since their establishment. Sucker regeneration is vigorous in both natural stands and exclosures (young suckers recruited recently are on the right-hand side of the panel); however, suckers do not survive beyond the browsable class in natural stands (see also Fig. 3). Exclosures were erected in 1957 (Lamar East and Mammoth) and 1962 (Lamar West and Junction Butte). The Junction Butte exclosure experienced a stand-replacing prescribed burn in 1987.

Our evaluation of the influence of landscape factors on aspen browsing and sucker survivorship indicated that aspen stands were not experiencing lower browsing rates or higher sucker survival in risky areas. Contrary to the BMTC hypothesis, the average proportion of browsed shoots was positively related to predation risk (linear regression; $\beta = 0.039$, $R^2 = 0.266$, $df = 16$, $P = 0.041$) and was unrelated to other landscape variables (Fig. 4). Survivorship models fitted to age distributions varied considerably across the 16 aspen stands (Fig. 3), with beta coefficients ranging from -1.06 to -0.25 (mean beta = -0.52). Aspen sucker survivorship was not related to predation risk (multiple regression; $t = 0.71$, $df = 15$, $P = 0.492$) or relative elk habitat use ($t = 2.03$, $df = 15$, $P = 0.069$). Instead, much of the variation in sucker demography was explained by site productivity, mea-

sured as average BAI of adults at the site ($t = 3.27$, $df = 15$, $P = 0.008$). Rather than wolves benefiting aspen, sucker survival was lower near core wolf areas ($t = -3.20$, $df = 15$, $P = 0.009$). This analysis, which integrates aspen survival rates over the last 15 years, shows no indication that suckers have higher survival in risky areas (Fig. 5).

When we experimentally assessed whether wolves provide protection to aspen in risky sites we found very consistent results, indicating that the risk of wolf predation does not confer protection to young browsable aspen. Neither survival ($R^2 = 0.241$, $df = 8$, $P = 0.180$) nor growth ($R^2 = 0.146$, $df = 8$, $P = 0.310$) differences between control and exclosure pairs were diminished in stands with greater predation risk (Fig. 6). Exclosures at aspen stands spanning a wide range of

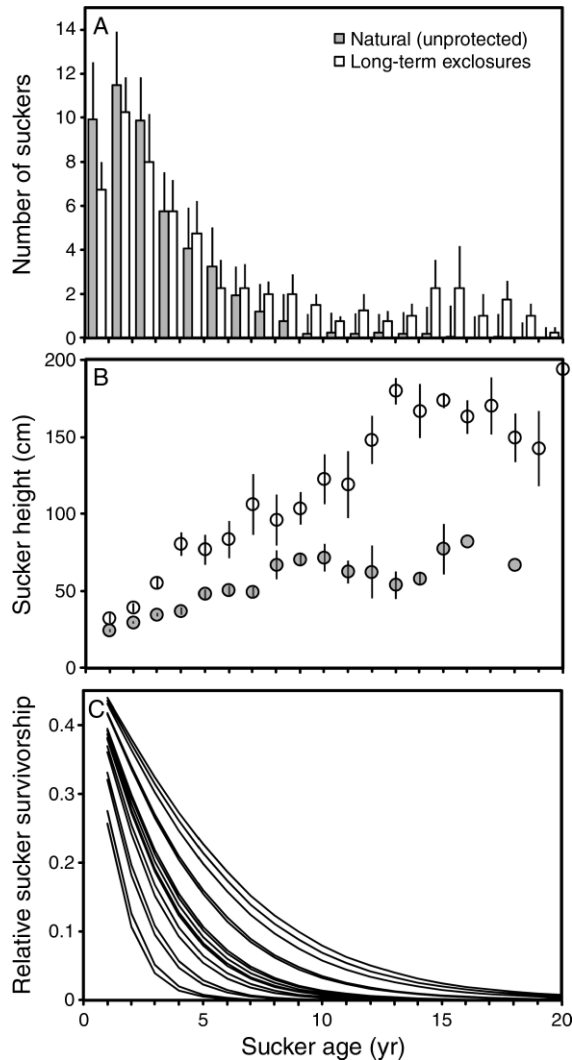


FIG. 3. Comparison of age distribution and growth rates of aspen suckers growing in natural stands vs. long-term exclosures. (A) The age distribution of suckers (mean \pm SEM) growing in four long-term exclosures shows more individuals in the older age classes than the age distributions from 16 natural stands. (B) Sucker height (mean \pm SEM) for a given age was higher in long-term exclosures (open circles) than in natural stands (gray circles). (C) Fitted survivorship curves (from the 16 natural stands only) show considerable variability in the survivorship of aspen across the study area.

predation risk improved annual average survival (one-tailed paired t test; $t = -3.97$, $df = 8$, $P = 0.004$) and growth ($t = -20.42$, $df = 8$, $P < 0.001$) over three years. By contrast, aspen plots exposed to herbivory failed to increase in height [rate of growth = -6.05 ± 1.46 cm/yr (mean \pm SE; $t = -4.15$, $df = 8$, $P < 0.002$)], indicating continued suppression by elk herbivory (Fig. 6).

DISCUSSION

The results of our work confirm that elk are indeed responsible for aspen decline on the Northern Range of

Yellowstone (Singer 1996, Kay 2001). However, our detailed demographic data indicate that claims of a landscape-level aspen recovery are premature, and we did not find any support for the BMTC hypothesis involving wolves, elk, and aspen. Several main lines of evidence lead us to these conclusions. First, our tree-ring sampling showed that aspen stands continued to recruit new individuals across the Northern Range for at least several decades before and after wolf extirpation (Fig. 2), and we did not find the abrupt cessation of aspen recruitment noted by previous authors (e.g., Romme et

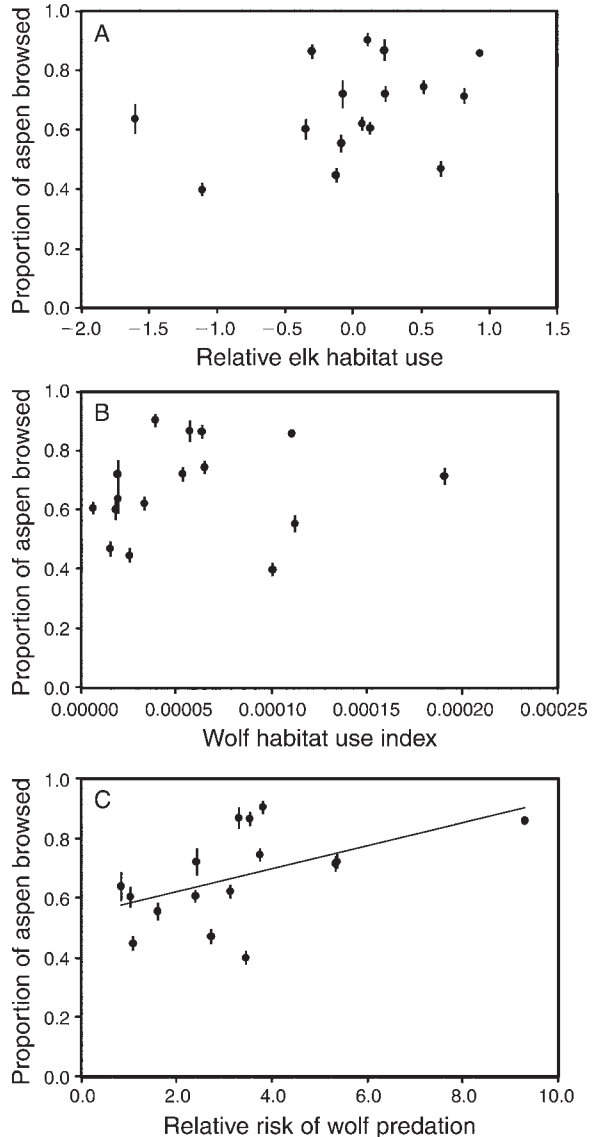


FIG. 4. Relationship between elk browsing intensity and landscape variables at 16 aspen stands on the Yellowstone's Northern Range. Stand-level browsing rates are shown in relation to (A) elk habitat use, (B) wolf habitat use, and (C) wolf predation risk. See subsection *Predation risk effects on sucker age distributions* for an explanation of the calculation of elk and wolf habitat use. Results are shown as mean \pm SEM.

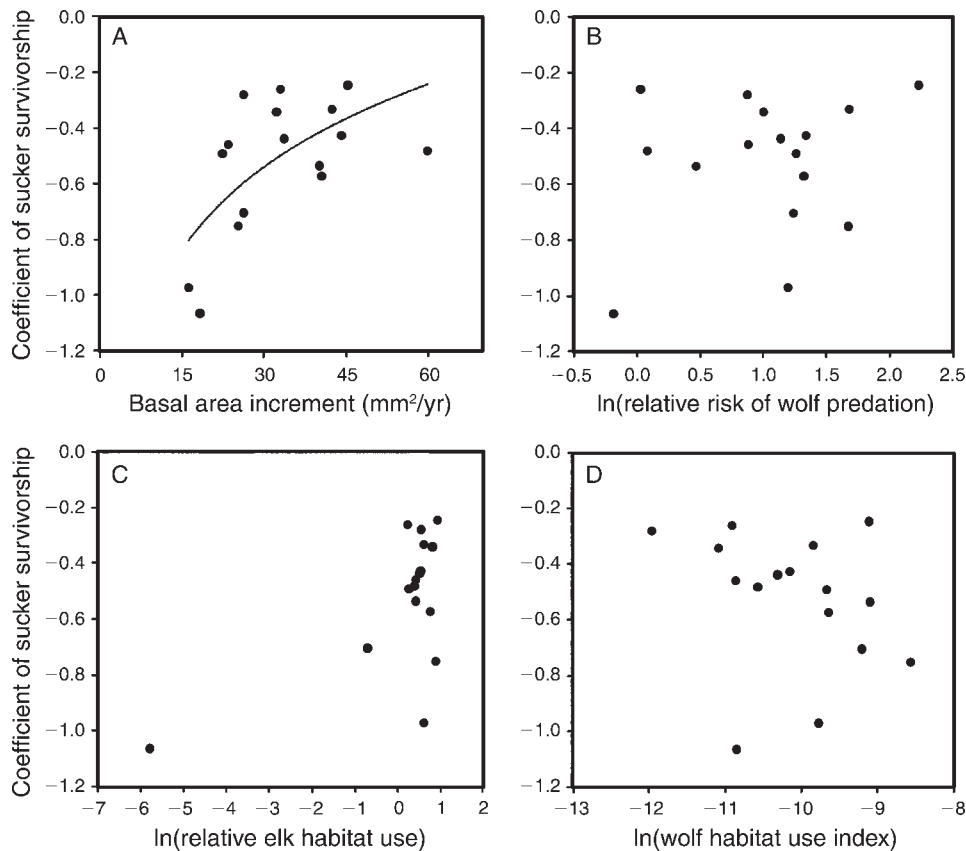


FIG. 5. Relationship of aspen sucker survivorship with (A) site productivity, measured as adult aspen basal area increment (BAI, a measure of growth rate), and log-transformed (B) predation risk, (C) relative elk habitat use, and (D) relative wolf habitat use. Most of the variation in sucker survivorship is explained by variation in site productivity.

al. 1995, Ripple and Larsen 2000). Regardless of the rate at which recruitment ended, we do not believe our study, nor any of Yellowstone's previous aspen tree-ring studies, can be interpreted as evidence for rapid behavioral changes of elk foraging (Ripple and Larsen 2000, Ripple and Beschta 2004). These patterns of recruitment cessation are more consistent with the numerical effect of a slow, steady increase in elk abundance, which is known to have occurred following the end of market hunting (in the late 1800s) and wolf extirpation (in the 1920s) (Schullery 2004). Second, although there is currently variation among aspen stands in the survival of young browsable aspen, much of this variation is attributable to differences in stand productivity and none was attributable to predation risk gradients (Fig. 5). Finally, in our most direct test of the BMTC hypothesis, we found that elk browsing had strong impacts on aspen demography that were not diminished by predation risk (Fig. 6). These results have broad implications for the mechanisms by which the restoration of top predators can indirectly benefit plant communities and biodiversity.

Our results differ from those of previous Yellowstone studies primarily because (1) we used an empirical

measure of predation risk derived a priori (Kauffman et al. 2007), (2) we simultaneously evaluated the influence of abiotic factors on aspen demography, and (3) we used a multi-year manipulative experiment with a paired study design to control for confounding site differences. Previous studies (e.g., Ripple et al. 2001, Ripple and Beschta 2004, 2007) selected aspen sites based on untested assumptions regarding predation risk gradients, which differ from the risk map we used that was based on actual predation events (Kauffman et al. 2007). For example, the first study to suggest a BMTC among wolves, elk, and aspen (Ripple et al. 2001) used wolf territory core and periphery areas as the risk treatment. In contrast, Kauffman et al. (2007) showed that actual predation events became decoupled from wolf territories as the number of wolf packs increased on the Northern Range; landscape-level differences in habitat more strongly determined where wolves killed elk (see Fig. 1). Similarly, earlier work (Ripple and Beschta 2003) suggesting a wolf-induced BMTC on cottonwood (*Populus* spp.) assumed that large open grasslands were safe habitat for elk. Since then, more detailed studies have revealed that such sites are actually highly risky; elk are both more vigilant (Liley and Creel

2007) and more likely to be killed in such areas (Creel and Winnie 2005, Kauffman et al. 2007), and they tend to avoid them when wolves are present (Creel et al. 2005). Previous studies have found differences in aspen growth attributable to putative risk gradients, such as riparian vs. upland sites (Ripple and Beschta 2007). We suspect that these growth differences are actually due to the confounding effects of abiotic gradients such as soil moisture, mineral content, or patterns of snow accumulation. Quantifying risk effects on plants across large landscapes requires independent quantification of predation risk and an explicit accounting of the influence of abiotic conditions on primary production.

Our study differs from previous studies that have used tree-ring data to reconstruct the historical failure of aspen in YNP, and these differences are due primarily to how individual aspen stands were sampled. For instance, Ripple and Larsen (2000) extracted increment cores from the single largest aspen from each of 20 stands, and, separately, from 98 trees across 57 other stands. Similarly, Larsen and Ripple (2003) sampled two trees per three size categories in each of 210 stands. While the total number of trees sampled among these studies is large, the number of trees sampled per stand is low. Thus, the information they represent is more descriptive of stand origination (i.e., the age of the oldest individuals) than about recruitment, which may continue long after origination and be reflected in smaller diameter trees. Romme et al. (1995) used a greater number of aspens per stand; they extracted cores from 5 to 10 dominant canopy trees from 15 Northern Range stands. Nevertheless, Romme et al. (1995) interpreted their data as indicative of a notable lack of recruitment after ~1900, a pattern that is not evident in our data. Our study found recruitment occurring well into the 1950s (Fig. 2; see also Halofsky and Ripple 2008b), and we did not observe any abrupt change in recruitment noted in earlier studies. Unlike previous authors (Ripple and Larsen 2000, Ripple and Beschta 2004), we do not believe one can infer an historical change in foraging behavior of elk from the historical patterns of aspen recruitment (Fig. 2).

Although we did not find that the effects of wolf predation risk translate down to the aspen stands foraged by elk, our results are nonetheless consistent with recent work evaluating elk behavioral responses to wolves. Elk responded initially to the reintroduction of wolves by increasing vigilance levels (Laundré et al. 2001), and elk respond currently to wolf presence in similar fashion (Liley and Creel 2007, Winnie and Creel 2007). Elk behavioral observations (i.e., patterns of vigilance, antipredator movement, and risk of death) are consistent with the gradient of predation risk that we have used (Fig. 1). For example, in response to wolf presence, elk have been shown to make short-term shifts away from habitat types that we classified as risky (Creel et al. 2005, Gude et al. 2006). But these antipredator behaviors have not resulted in detectable shifts in broad-

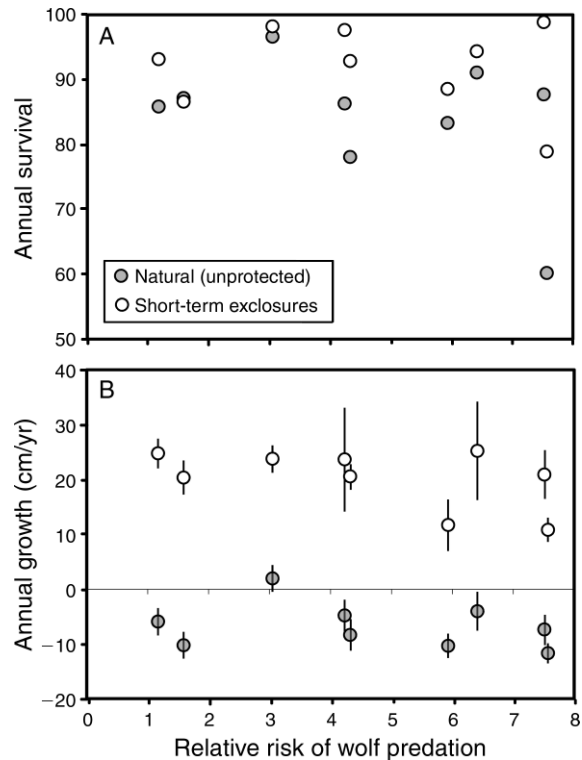


FIG. 6. Effect of elk browsing on aspen sucker (A) survival and (B) growth across a predation risk gradient (mean \pm SEM). Protection from browsing significantly enhanced rates of sucker survival and growth. Predation risk did not diminish the demographic benefit of protecting aspen from browsing, because neither survival nor growth differences between control (solid circles) and enclosure (open circles) pairs were lowered in stands with greater predation risk. Units of relative predation risk follow Fig. 1.

scale, winter habitat use across the Northern Range as estimated from analyses of radio-collared elk before and after wolf reintroduction (Mao et al. 2005). In our work, aspen sucker survivorship was actually lower near the cores of wolf territories, likely due to wolves maintaining territories in areas of high elk density (Mao et al. 2005). In an analysis of elk movement paths, Fortin et al. (2005) found no evidence that elk avoid core wolf-use areas. The picture that emerges from behavioral studies of elk and wolves is that, while elk do respond to the predation risk posed by wolves, their responses are subtle and, over the course of an entire winter, do not result in meaningful cumulative changes in habitat use. Annual variation in other factors such as wolf territory locations and pack sizes, snow levels, and elk distribution will further act to erode the spatial consistency in wolf predation risk and thus limit cascading impacts of predation risk (Fortin et al. 2005). Our work highlights the need for studies of BMTCs to integrate antipredator behavior over time frames that are relevant to prey animals and their herbivory pressure on plant communities.

The spatial scale of predation risk and temporal consistency of elk antipredator behavior are key issues in reconciling our work with studies conducted by previous researchers in the Greater Yellowstone Ecosystem. For example, Ripple and Beschta (2003) suggested that elk behavioral decisions made on the scale of a few meters were responsible for increased cottonwood growth on the Northern Range. They suggested that a "terrain fear factor," whereby high terraces, cut banks, and downed logs act as barriers to elk escape, was responsible for reduced browsing. Our analysis was based on a predation risk map with a 30-m resolution, which would not have captured many such terrain features. If elk avoid such types of terrain now that wolves are present, it is conceivable that fine-scale alteration of aspen foraging is occurring and was not captured by our analysis. However, Ripple and Beschta (2003) did not relate their measure of predation risk to any direct measure of elk behavior and, to our knowledge, no study in Yellowstone or elsewhere has documented elk behavioral response to wolves at a spatial scale <30 m during winter when elk herbivory on woody plants occurs. One exception is Halofsky and Ripple (2008a), who observed elk behavior in winter and found some limited support for elk responding to escape impediments. We caution, however, that this study had extremely low sample sizes of observed elk compared to other studies of elk vigilance. Liley and Creel (2007) evaluated the relative influence of prey conditions, wolf presence, and environmental conditions on elk vigilance in the Northern Range study area. Although they found that vigilance increased as a function of distance to forest edge, they concluded that "environmental variables acted more as modifiers rather than drivers of elk vigilance" (Liley and Creel 2007:9). To our knowledge, studies that have evaluated wolf effects on elk vigilance or antipredator movement have done so at fairly large spatial scales, such as different regions of Yellowstone with and without wolves (Laundré et al. 2001, Lung and Childress 2007), the presence or absence of wolves within (3.5 km wide) drainages (Creel et al. 2005), or elk movement at the core and periphery of wolf territories (Fortin et al. 2005). There appear to be no direct behavioral data that would support the notion that elk make antipredator decisions at very fine (i.e., 5–10 m) spatial scales.

Our results fit well with the notion that predators with an active hunting mode are unlikely to produce BMTCS (Schmitz 2005). Studies have shown that elk respond to wolves by altering behavior (Laundré et al. 2001, Liley and Creel 2007, Winnie and Creel 2007) and habitat selection (Creel et al. 2005, Gude et al. 2006). We suggest, however, that such predation risk responses, while detectable, primarily occur only as a response to the near-imminent threat of wolf predation. Wolves are such highly mobile predators that true (i.e., spatially and temporally consistent) refuge habitat is unlikely to exist

for elk. Indeed, Creel et al. (2008) showed that elk (in Yellowstone and in habitats adjacent to the park) responded to "risky times" but not "risky places," a pattern the authors attributed to risk allocation strategies (Lima and Bednekoff 1999) of elk. Because elk antipredator responses (habitat avoidance, foraging reductions) are not consistent in space or time, the benefits of reduced plant consumption are likely to occur only rarely, and not at the frequency and consistency necessary to produce meaningful benefits to plant communities.

Other constraints exist that influence the strength of elk antipredator response. The recent predation risk map created from wolf-killed elk (Kauffman et al. 2007) makes clear that these prey face a stark trade-off during winter, when they must balance the risk of predation with the risk of starvation. In this large mammal system, prey face diminishing fat reserves during winter (Parker et al. 2009), which likely shifts the optimal behavior away from antipredator activities in favor of increased foraging, especially for elk in poor condition. Observed differences in the antipredator behavior between male and female elk provide evidence that nutritional condition lessens the antipredator response. In temperate ungulates with polygynous breeding systems, breeding males are in much poorer condition in winter than females because of the fasting that occurs during the autumn rut (Toigo and Gaillard 2003). In elk, behavioral studies have shown that bulls are less responsive to the presence of wolves (Winnie and Creel 2007), even though they are >6 times more likely to be killed based on their relative abundance in the herd (Creel et al. 2005). Analogous results were found in a model spider-grasshopper system, where trait-mediated effects detected over a short time period disappeared across longer time frames due to behavioral compensation by prey (Luttbeg et al. 2003). Given the strong influence of winter severity on mortality of temperate ungulates, a large proportion of individuals may be in such poor condition by the end of winter that their antipredator behavior is greatly diminished.

Several studies have shown that wolves can cause trophic cascades (McLaren and Peterson 1994), and that their restoration is likely to benefit biodiversity (Hebblewhite et al. 2005), especially in areas where ungulate prey are overabundant. However, these recorded cascades have been mediated by wolf-induced reductions in prey density, not alteration of prey behavior. There were roughly 10 000 fewer elk on the Northern Range when our study was conducted compared to before wolf reintroduction, a reduction that is at least partially due to direct predation by wolves (Eberhardt et al. 2007). Based on this reduction in elk numbers alone, browsing pressure throughout the Northern Range is ~40% of pre-wolf levels (based on winter counts of 6738 in 2007 and 16 791 in 1995; White and Garrott 2005). A likely explanation of some of the patchy releases suggested for

willow, cottonwood, and aspen in Yellowstone is that the range-wide decline in elk browsing pressure has reduced herbivory levels on some woody-plant communities below site-specific thresholds required for positive growth. For example, the apparent height increases of some riparian aspen in Yellowstone (Ripple and Beschta 2007) are likely a result of an overall reduction in browsing, coupled with high site productivity. The strong abiotic gradient in aspen sucker survival that we found suggests that such threshold levels of herbivory vary widely (and patchily) across the Northern Range. This notion is supported by Bilyeu et al. (2008), who found that water availability strongly controlled the response of willow species to experimental exclusion of ungulate browsing on the Northern Range. The lack of antipredator behavior strong enough to alter elk herbivory of aspen in the Yellowstone system suggests that TMIs are not ubiquitous in systems involving large, coursing predators, and that ecologists need to further explore the conditions, across taxa and ecosystems, in which fear can structure ecosystems. This need is especially apparent in cases where the conservation goal is to restore ecosystem function via the reintroduction of top predators. In addition to the effects of hunting mode (Schmitz and Suttle 2001), our understanding of these effects will benefit from future studies that evaluate how the strength of TMIs are mediated by predator efficiency (i.e., success rate and lethality), prey vulnerability, food limitation, and the heterogeneous landscapes over which predator and prey interact.

The decline of Yellowstone aspen is a striking example of population- and distributional-level impacts of a generalist terrestrial herbivore. There has been considerable debate regarding the extent to which Yellowstone aspen decline is caused by elk browsing, fire suppression, or drought (Romme et al. 1995, Huff and Varley 1999). While conifer encroachment (due to fire suppression) and drought can certainly influence aspen regeneration, our work indicates that elk browsing as a single factor is controlling the regeneration of Northern Range aspen. When elk browsing is reduced or precluded experimentally, aspen stands successfully regenerate. This result is not new. Several researchers have evaluated aspen enclosure experiments on the Northern Range and have also concluded that elk herbivory is the primary factors controlling aspen recruitment (Singer 1996, Kay 2001). Our work suggests, however, that the risk of wolf predation alone is unlikely to alter the degree to which aspen are limited by elk herbivory. Our findings lead us to suggest that a landscape-level aspen recovery in Yellowstone will only occur if wolves (in combination with other predators and climate factors) further reduce the elk population. If the Northern Range elk population does not decline to levels considerably lower than current numbers, many of Yellowstone's aspen stands will likely continue to decline in the coming decades.

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