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Trophic cascades from wolves to alders in Yellowstone

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ABSTRACT

We explored possible interactions among gray wolves (*Canis lupus*), Rocky Mountain elk (*Cervus elaphus*), and thinleaf alder (*Alnus incana* spp. *tenuifoli*) in northern Yellowstone National Park. We developed an alder age structure based on annual growth rings for plants growing along six streams in areas accessible to ungulates on the northern range. Alder stems ($n = 412$) along the six streams originated only after wolf reintroduction. By 2013, 80% of the sampled alders along these streams were taller than 2 m, in contrast with a historical pattern of height suppression by ungulate herbivory. This pattern of alder recruitment is consistent with a trophic cascade whereby new alder growth occurred across all study streams within several years after wolf reintroduction. Although declines in elk density since wolf reintroduction likely contributed to the release of alder from herbivory, the immediate onset of new alder recruitment following wolf reintroduction indicates that behavioral responses to predation may also have been an important component in the resulting trophic cascade. These results suggest that predator conservation could play a role in the management and ecological restoration of riparian areas.

1. Introduction

The removal of large carnivores from much of the world has had diverse ecological effects, often revealed through unexpected and complex interactions (Terborgh and Estes, 2010; Ripple et al., 2014b). One example of predator effects occurs in trophic cascades, where the effects of predators on prey are translated downward and across food webs (Estes et al., 2011). Yellowstone National Park (YNP) has been the focus of recent research on trophic cascades involving the extirpation and repatriation of gray wolves (*Canis lupus*) and represents a large-scale natural experiment that provides a unique opportunity to examine the interplay between predators, prey, and plants.

After wolves were extirpated from YNP in the mid-1920s, park biologists became concerned about the effects of increased Rocky Mountain elk (*Cervus elaphus*) browsing on vegetation in the northern and Gallatin ungulate winter ranges (Skinner, 1928; Rush, 1932; Wright et al., 1933; YNP, 1958; Lovaas, 1970; Ripple and Beschta, 2006). Analyses of the annual growth rings of deciduous tree species revealed that recruitment (i.e., growth of seedlings/sprouts into tall saplings or trees) occurred regularly in both of these YNP winter ranges when wolves were present, but declined and became rare after wolf extirpation (Ripple and Larsen, 2000; Beschta, 2005; Halofsky and Ripple, 2008a; Kauffman et al., 2010). These tree-ring study results are consistent with reports of YNP biologists (as cited above) about the decline of woody browse species in the early and middle 20th century. As a result of park service biologists' concerns, a program of elk reductions was initiated in the 1930s and continued through 1968. By the late 1960s, park service culling had reduced the northern range elk population to less than 5000 individuals (Fig. 1a), but with no resulting major recovery in recruitment of woody plants (Houston, 1982; Kay, 1990; Meagher and Houston, 1998; NRC, 2002; Barmore, 2003). After the elk culling program ended in 1968, elk numbers increased dramatically during the 1970s (Fig. 1a). In the 1980s and 1990s, elk numbers fluctuated widely due to winter starvation events (Garrott et al., 2003; Eberhardt et al., 2007). During this period of large population size (>19,000 elk in some years on the northern range), elk were limited by food resources and consumed relatively unpalatable species such as conifers (Kay, 1990; Meagher and Houston, 1998; NRC, 2002).

Wolves were reintroduced into YNP during 1995–96 following approximately seven decades of absence (Fig. 1b). Thirty-one wolves were moved from Canada to the northern range of YNP in January 1995 ($n = 14$) and January 1996 ($n = 17$). By 1996, five wolf pack territories covered nearly all of the northern range within the park (Fig. S1 in supplement, Fig. 1 in Phillips and Smith (1997)). During the fall of 1996, each of three different wolf packs on the northern range killed, on average, 1 elk every 2–3 days (Phillips

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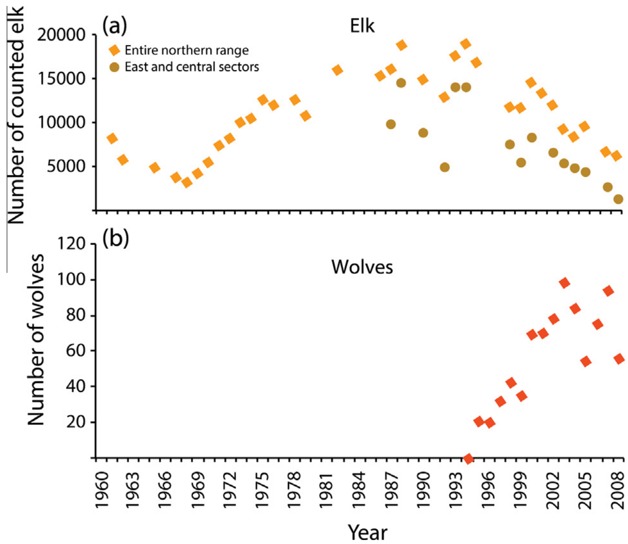

Fig. 1. Number of counted (a) elk and (b) wolves on the northern range. Not shown for elk are poor count years of 1977, 1989, 1991, and 2006. The field sites for this study were all located in the eastern and central sectors of the northern range (as defined by Painter et al. (2015)) and the elk counts for these two sectors were summed and shown with circles as a second series in (a). The eastern and central sectors include the portions of the northern range east of and including the Blacktail Creek drainage. Elk data for the eastern and central sectors were not available prior to 1987.

and Smith, 1997). Following reintroduction, wolf numbers on the northern range increased until 2003 and thereafter declined, while the elk population decreased steadily during this period (Fig. 1a and b). The initial decline in elk numbers in the mid-to-late 1990s was due in part to starvation caused by a degraded winter range and a severe winter in 1996–97; other factors included predation by wolves, bears, and continued hunting by humans of elk that left the park (Eberhardt et al., 2007; White and Garrott, 2013).

Research on the effects of predators, ungulates, and other factors on the establishment and growth of deciduous trees in northern Yellowstone has focused on aspen (*Populus tremuloides*) and cottonwood trees (*Populus* spp.) (reviewed by Ripple and Beschta (2012). Recruitment of these tree species has increased since the reintroduction of wolves, although the magnitude of the recovery is spatially variable (Beschta and Ripple, 2014; Painter et al., 2015). Over the same period, deciduous shrubs in some areas of northern Yellowstone have increased in height, biomass, or cover including willows (*Salix* spp.) (Beyer et al., 2007; Tercek et al., 2010; Baril et al., 2011; Marshall et al., 2014) and various berry-producing shrubs (Beschta and Ripple, 2012; Ripple et al., 2014a).

Herein we report on the first extensive field study of thinleaf alder (*Alnus incana* spp. *tenuifoli*) in Yellowstone's northern range. Thinleaf alder, a small tree or tall shrub, commonly occurs in riparian areas throughout western North America and can grow up to ~12 m tall (Fryer, 2011). Through its nitrogen fixing properties, it enriches soil and facilitates the establishment of other native plants. Thinleaf alder spreads both vegetatively and from small winged seeds, although vegetative reproduction is thought to be more common. It sprouts primarily from root crowns, but can also sprout from roots. Dense alder thickets can provide cover for fish, thermally modify microclimates and stream temperatures via shading, and protect streams from bank erosion. Songbirds eat thinleaf alder seeds, squirrels consume catkins, beaver use stems to build lodges and dams, and various small and large mammals use alder as cover (Fryer, 2011). Thinleaf alder has low palatability as ungulate forage, but it is consumed by ungulates especially when other forage is limited (Gaffney, 1941; Nelson and Leege, 1982; Case and Kauffman, 1997). Northern Yellowstone alders, as well as conifers, were affected by browsing in the 1950s (Jonas, 1955) indicating that elk were using low-quality forage even with densities lower than those of the 1980s–90s. Also, before wolf reintroduction Keigley (1997) observed heavy herbivory effects on various woody browse species on the northern range, including alder.

Because little is known about Yellowstone's thinleaf alder, our main objective was to analyze temporal patterns of thinleaf alder stem establishment on the northern range of Yellowstone National Park. In light of previous research showing changes in cottonwood and aspen recruitment following wolf reintroduction, we hypothesized that thinleaf alder exposed to ungulate browsing would also increase in recruitment over this same time period.

2. Methods

This study took place on the northern ungulate winter range, comprising more than 1500 km^2 of mountainous terrain and open valleys, approximately two-thirds of which occurs within the northeastern portion of YNP in Wyoming (NRC, 2002). Much of the winter range is shrub steppe, with patches of intermixed lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmanni*), and aspen. Thinleaf alder, and various species of willow, cottonwood, and other woody browse plants occur within riparian zones. See Houston (1982) and NRC (2002) for a more detailed description of the northern range study area.

We determined the age structure of alder stems (frequency distribution of number of stems by year of establishment) growing along small streams, and then compared the number of alder stems established before wolf reintroduction versus after wolf reintroduction. This research design provided two predator treatments: (1) wolves absent (pre-1995) followed by (2) wolves present (post-1995).

We located small perennial streams (4th–5th order) on the northern range within the park that intersected the North Entrance road, the Grand Loop, and the Northeast Entrance road. We excluded streams where riparian areas had burned in the large fires of 1988 (i.e., Lava, Lupine, Elk, Lost, and Tower Creeks). For the remaining streams (Glen, Blacktail, Oxbow, Geode, Crystal, Rose, Indian, and Pebble Creeks), we searched for alder 1000 m upstream and downstream of the road. We found alder along six of these streams: Blacktail, Oxbow, Geode, Crystal, Rose, and Pebble Creek representing a west-east gradient across the northern range. All six streams intersect the main west-east road and were within the central and eastern portions of the northern range within the park (Fig. 2).

Within the search area associated with each of the six streams, we measured the diameter at breast height (DBH, cm) of the tallest stem of each alder plant (breast height = 1.4 m). We measured only plants that were accessible to ungulate browsing; this excluded any individuals growing in or adjacent to woody debris that might inhibit ungulate access. From each of the six riparian areas we haphazardly selected four alder stems (24 total stems mostly from the larger size classes) to develop an age/diameter regression equation. The larger size classes were more frequently sampled because, as the first recruits, they would be the most critical in determining when any increase in alder growth began to occur. We cut the selected stems at 1.4 m above the ground level with a hand saw and counted the number of growth rings in the field using a hand lens after sanding the sections. From this set of data we developed an age/diameter relationship equation with 95% confidence intervals (CI). To determine the number of years it took for alder stems to reach breast height, we haphazardly located alder stems ~1.4 m