Forest Ecology and Management 260 (2010) 915–922

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Mexican wolves, elk, and aspen in Arizona: Is there a trophic cascade?

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ARTICLE INFO

Article history:
Received 26 March 2010
Received in revised form 19 May 2010
Accepted 8 June 2010

Keywords:
Mexican wolves
Rocky Mountain elk
Aspen
Herbivory
Trophic cascades
Apache National Forest
Arizona

ABSTRACT

In 1998, Mexican gray wolves (*Canis lupus baileyi*) were introduced into the Blue Range Wolf Recovery Area (BRWRA) that spans adjacent portions of Arizona and New Mexico. In 2009 we selected three mixed-conifer sites on the Apache National Forest, within the BRWRA of east-central Arizona, to characterize long-term age structure of aspen (*Populus tremuloides*) and to check for the possible occurrence of a tri-trophic cascade involving Mexican wolves, Rocky Mountain elk (*Cervus elaphus nelsoni*), and aspen. These mixed-conifer sites included (a) a refugium site, (b) an old-growth site, and (c) a site thinned in 1991–1992. The refugium site was inaccessible to elk and cattle whereas the old-growth and thinned sites were accessible to elk, but not cattle. Age structure results indicated that aspen recruitment (i.e., the growth of sprouts/seedlings into tall saplings, poles, and eventually trees) at the refugium site had been ongoing over a period of many decades. In contrast, aspen recruitment at the old-growth and thinned sites decreased significantly ($p < 0.05$) during the two most recent decades when elk populations, as indexed by annual harvest levels, were relatively "high". From 2000 to 2008, only 2.9 Mexican wolves per 1000 elk were present on the Apache National Forest compared to 9.3 western gray wolves (*Canis lupus occidentalis*) per 1000 elk in Yellowstone National Park where tri-trophic cascades involving wolves, elk, and aspen have been reported. The low number of Mexican wolves relative to their primary prey (elk) suggests that an ecologically effective density of wolves has not become established in east-central Arizona. Furthermore, the lack of recent aspen recruitment in stands accessible to elk indicates an absence, to date, of a tri-trophic cascade.

1. Introduction

Aspen (*Populus tremuloides*), also known as quaking aspen or trembling aspen, is the most widely distributed deciduous tree species in North America and unusual in reproducing primarily by sprouts (ramets) from a parent root system (Fowells, 1965; Perala, 1990). Areas that support aspen in the western United States (US) commonly contain a variety of woody and herbaceous plants that provide critical habitat and food-web support to many wildlife species (DeByle and Winokur, 1985). Historically, aspen forests occupied nearly 3.9 million hectares in eight western states (Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming) but had declined 60% by the end of the 20th century (Bartos, 2001). At the southern end of aspen's range in the western US losses have been particularly severe with aspen declines of 96% and 88% in Arizona and New Mexico, respectively. Various factors can contribute to the loss of aspen including reduced fire frequency, conifer invasion, disease, a changing climate, intensive browsing by large herbivores, and others (DeByle and Winokur, 1985; Worrall et al., 2007).

The browsing of aspen stands by native large herbivores, such as elk (*Cervus elaphus*) and deer (*Odocoileus* spp.), has likely occurred over many thousands of years in the American West since the leaves and stems of young aspen plants are highly palatable to ungulates. Yet the capability of these stands to persist over long periods of time and to cover large areas indicates that ungulate herbivory may not have seriously limited aspen recruitment (growth of sprouts/seedlings into tall saplings, poles, and eventually trees). However, with the introduction of domestic livestock and reduced populations of large predators across large areas of the West during the late 1800s and early 1900s, followed by enlarged populations of wild ungulates during the latter half of the 20th century, browsing of aspen sprouts/seedlings had become an increasingly important factor affecting recruitment (Mueggler and Bartos, 1977; DeByle and Winokur, 1985; Kay, 1997; Kay and Bartos, 2000).

Recent studies in Yellowstone National Park, an area where domestic livestock grazing has not occurred, point to an additional factor that may contribute to the long-term demise of aspen—the collapse of a tri-trophic cascade involving wolves, elk, and aspen. Following the extirpation of western gray wolves (*Canis lupus occidentalis*) from Yellowstone nearly a century ago, increased browsing by Rocky Mountain elk (*Cervus elaphus nelsoni*) not only suppressed the recruitment of aspen in the park's northern winter ranges but also that of willows (*Salix* spp.), cottonwoods (*Popu-*

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doi:10.1016/j.foreco.2010.06.012

lus spp.), and various species of shrubs (Ripple and Larsen, 2000; Kay, 2001a; Barmore, 2003; Ripple and Beschta, 2004a,b; Beschta, 2005). Increased elk herbivory and decreased aspen recruitment similarly occurred in the Canadian Rockies when wolf populations in Jasper, Yoho, and Kootenay National Parks of Alberta were suppressed during the mid-1900s (White et al., 1998; Beschta and Ripple, 2006). In Rocky Mountain National Park, where elk were reintroduced in the absence of wolves, intensive browsing by elk reduced aspen and willow recruitment (Hess, 1993; Zeigenfuss et al., 2002; Binkley, 2008). Unimpeded browsing by native large herbivores in the absence of apex predators is increasingly recognized as an important factor affecting the biodiversity and ecosystem services of native plant communities that comprise temperate and boreal ecosystems (Ripple et al., 2010).

During the winters of 1995–1996, gray wolves were reintroduced into Yellowstone National Park, thus completing the park's historical predator guild. Soon thereafter studies began observing behavioral responses of elk (e.g., vigilance, use of habitat) due to the presence of wolves (Laundré et al., 2001; Mao et al., 2005; Halofsky and Ripple, 2008a). Altered patterns of browsing and reduced elk densities following wolf reintroduction (White and Garrott, 2005) also appeared to explain the spatially patchy release (increased heights of young woody plants in various locations) currently underway for willow, aspen, and cottonwood in Yellowstone's northern winter ranges (Beyer et al., 2007; Ripple and Beschta, 2007; Halofsky and Ripple, 2008b; Beschta and Ripple, 2010). Similarly, aspen recruitment improved following recovery of wolf populations in Jasper National Park (Beschta and Ripple, 2006).

Like much of the American West, wolves in Arizona and New Mexico were heavily persecuted in the late 1800s and early 1900s. For example, in 1920 alone over 100 wolves were removed from these two states (Brown, 1983). Removals dropped to ~15 wolves/year in the 1930s and by the mid-1940s, or soon thereafter, wolves in Arizona and New Mexico had become functionally extirpated. However, in 1998 Mexican gray wolves (*C. lupus baileyi*) from a captive breeding program were introduced into east-central Arizona and west-central New Mexico, an area designated as the Blue Range Wolf Recovery Area (BRWRA). While these introductions occurred approximately 200 km north of the historical range of Mexican wolves (see Brown, 1983), the BRWRA was thought to have suitable habitat and sufficient prey for maintaining a population of Mexican wolves (USFWS, 1996).

Fig. 1. Location map of Apache National Forest in east-central Arizona. This national forest along with the Gila National Forest in west-central New Mexico comprise the Blue Range Wolf Recovery Area (BRWRA) for the Mexican wolf.

We undertook this study on the Apache National Forest (Fig. 1) where introduced Mexican wolves have been present for a decade. This national forest comprises the portion of the BRWRA that extends into east-central Arizona. It is also adjacent to the White Mountain Apache Reservation where wolves have become protected in recent years. Field reconnaissance of the Apache National Forest in the summer of 2008 indicated that aspen recruitment in recent decades has been generally absent across major portions of the Springerville and Alpine districts. Thus, our overall objective was to assess temporal patterns of aspen recruitment in mixed-conifer stands accessible to elk where we hypothesized that a tri-trophic cascade involving wolves–elk–aspen might again be occurring following the introduction of Mexican wolves, potentially contributing to improved aspen recruitment. The occurrence of such a trophic cascade would suggest recovery of an ecologically effective density of wolves (Soulé et al., 2003).

2. Study area

Our study area was located along the southern portion of the Springerville District, Apache National Forest, approximately 20 km west of Alpine, Arizona. Here, mixed-conifer forests contained varying proportions of Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea englemannii*), blue spruce (*P. pungens*), white fir (*Abies concolor*), subalpine fir (*A. lasiocarpa*), limber pine (*Pinus flexilis*), and ponderosa pine (*P. ponderosa*). Aspen, a desired browse species for elk and deer, commonly occurs within these mixed-conifer stands.

Grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougar (*Puma concolor*), gray wolves, Merriam elk (*C. elaphus merriami*), mule deer (*O. hemionus*), and Coues white-tailed deer (*O. virginianus couesi*) originally inhabited portions of the Mogollon Rim and White Mountains of east-central Arizona (Hoffmeister, 1986). However, the influx of Euro-Americans into this area eventually resulted in the regional extirpation of grizzly bears and wolves as well as extinction of Merriam elk. Rocky Mountain elk from Yellowstone were introduced into east-central Arizona in 1913 and, as previously indicated, Mexican wolves in 1998. The Mexican wolf is the southernmost and smallest subspecies of gray wolf in North America (Mech and Boitani, 2003).

Three aspen sites, at an elevation of ~2700 m, were chosen to represent different treatments to forest stands (Fig. 2). They included (a) a "refugium site" that was inaccessible to wild and domestic ungulates because of topographic barriers (i.e., broken rock, cliff faces), (b) an "old-growth site" that had not experienced logging, and (c) a "thinned site" at which a partial overstory removal of conifers, along with the piling and burning of slash, occurred in 1991–1992. While both the old-growth and thinned sites were easily accessible to wild ungulates, neither had been grazed by domestic livestock. The old-growth site had been fenced to exclude cattle and the thinned site was sufficiently far from the nearest meadow that cattle did not forage at this site.

3. Methods

To help assess potential environmental or land-use factors within the general vicinity of our study sites that might affect aspen recruitment, we assembled annual records of snowpack accumulation, grazing use, timber harvest, and big game harvest within the Apache National Forest for the period 1970–2008. To characterize annual snowpack amounts, we calculated the average January 15 through April 1 snowpack water equivalent for the Beaver Head, Coronado Trail, Hannagan Meadow, Maverick Fork, and Nutrioso snow courses. Domestic livestock grazing was summarized in animal unit months (AUMs, where one AUM represents the foraging