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Large carnivore extirpation linked to loss of overstory aspen in Yellowstone

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ABSTRACT

The striping of bark on the lower portion of aspen trees (*Populus tremuloides*) by Rocky Mountain elk (*Cervus canadensis*), or "barking", increases entry points for disease organisms such as wood-decaying fungi, thereby increasing aspen tree mortality from heart rot. We hypothesized that this has occurred in Yellowstone's northern range aspen stands as part of a trophic cascade and has contributed to the premature and widespread loss of overstory trees. To evaluate these potential effects, we randomly selected aspen stands along a 60-km traverse across the park's northern range. For overstory trees ≥15 cm in diameter at breast height (*DBH*) within these stands, which were accessible to elk, we measured the height of barking (as indicated by deeply furrowed/blackened bark) and the proportion of increment core lengths with heart rot. Sampled trees had an average barking height of 2.2 m and 93.8% of them had heart rot. In contrast, only 13.3% of aspen trees that had grown in an environment protected from elk had heart rot. Heart rot comprised 45.2% and 2.5% of increment core lengths for the elk-accessible and protected stands, respectively. Results support a multi-level trophic cascade, from predator-to-prey-to-plants-to-fungi, whereby an incomplete large carnivore guild, over a period of seven decades, allowed the widespread barking of aspen by elk to occur. This, in turn, may have increased the prevalence of heart rot and has contributed to an accelerated loss of overstory aspen across the northern range.

1. Introduction

The importance of indirect species interactions that originate with carnivores and spread downward through food webs, or trophic cascades (Ripple et al., 2016), has been increasingly identified in marine, aquatic, and terrestrial ecosystems (Pace et al., 1999; Knight et al., 2005; Terborgh and Estes, 2010; Estes et al., 2011). Trophic cascades have been found for a number of large terrestrial carnivores and their ecological effects increasingly documented. For example, the removal or significant reduction of such carnivores may trigger a cascade of effects that can create a downward spiral toward ecosystem simplification (Ripple et al., 2014). Perhaps nowhere have such effects been more intensively studied than in national parks of the western United States (US) (Beschta and Ripple, 2009).

In the early 1900s, superintendents of Crater Lake, Glacier, Mesa Verde, Mt. Rainier, Rocky Mountain, Sequoia, Wind Cave, Yellowstone, Yosemite, and Zion National Parks often continued or institutionalized predator control efforts directed at the reduction, and sometimes extirpation, of predators such as gray wolves (*Canis lupus*), cougars (*Puma concolor*), bobcats (*Lynx rufus*), lynx (*Felis lynx*), and coyotes (*C. latrans*) (Skinner, 1928). Predator persecution was considered to be within the scope of 1916 legislation that established national parks, even though the legislation was intended "to conserve the scenery and the natural and historic objects and wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations."

Age structure studies (i.e., evaluations of the frequency of tree establishment over time) of deciduous woody species have consistently found that the extirpation or displacement of large carnivores in various western US national parks allowed native ungulates to increase herbivory, thereby affecting plant communities (Baker et al., 1997; White et al., 1998; Beschta and Ripple, 2009). The suppression of sprout and seedling heights, by browsing, of aspen (*Populus tremuloides*) and other woody species became more prevalent and caused a pronounced decline in recruitment (i.e., the growth of young plants above the browse level of native ungulates). Woody plant recruitment in some parks decreased to 10% of expected within 25 years of large carnivore loss/displacement and to only 1% of expected within 50 years, indicating that browsing effects became increasingly severe over time (Beschta and Ripple, 2009). Increased herbivory of young aspen plants was also observed in western Canada national parks, often associated with areas of low predation risk by wolves (White and Feller, 2001) or depleted wolf populations (White et al., 1998; Beschta and Ripple, 2007).

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In Yellowstone National Park (YNP), established in 1872 as the nation's first national park, the persecution of large carnivores continued through the late 1800s and early 1900s (Skinner, 1928), leading to the extirpation of wolves and cougars by the mid-1920s (Weaver, 1978; Ruth, 2004). Following their loss, and with bears (*Ursus* spp.) annually hibernating, Rocky Mountain elk (*Cervus canadensis*) migrating each fall into the valleys of the park's northern ungulate winter range, or "northern range", entered a habitat essentially devoid of large carnivores. Soon thereafter biologists began to note the effects of increased elk herbivory on plants (Smith et al., 1915; Skinner, 1928; Grimm, 1939). Aspen and cottonwood (*P.* spp.) recruitment began to decline in the early 1900s and essentially ceased after the mid-1900s (Beschta and Ripple, 2016). Similarly, a major reduction in willow establishment occurred during the latter half of the 20th century due to intensive elk browsing; berry-producing shrubs were also affected (Kay, 1990; Wolf et al., 2007; Beschta and Ripple, 2012; Ripple et al., 2013).

Overall, the recruitment of aspen, cottonwood, willow (*Salix* spp.), and other woody species in YNP's northern range was greatly reduced throughout most of the 1900s (Wolf et al., 2007; Beschta and Ripple, 2016). Such effects to vegetation occurred even though the park service began a program of elk herd reductions in the 1920s, initially trapping elk for shipment to other areas and later by harvesting them within the park (YNP, 1958; YNP, 1997; NRC, 2002). However, culling of elk in the park stopped after 1968 (Allin, 2000) and the northern range population dramatically increased, from <5000 elk to nearly 20,000 elk by the late 1980s (YNP, 1997).

Many of the aspen that became established in the early 1900s would normally be expected to live beyond 100 years of age (Kay, 1990; DeByle and Winokur, 1985) and thus even with the dramatic downturn in recruitment experienced in the mid-late 1900s, overstory trees today should be prevalent within aspen stands across the northern range. Yet, one of the more perplexing observations in northern Yellowstone has been the widespread loss of overstory aspen trees during the mid-late 1900s (Houston, 1982; Kay, 1990), a loss that continues to date. While high levels of herbivory on young aspen sprouts represents an effective mechanism for preventing the long-term replacement of aspen trees, and eventual loss of the entire stand, such herbivory does not explain the widespread depletion of overstory trees that has been underway.

The stripping or peeling of aspen bark by elk with their teeth, or "barking", became a widespread occurrence in YNP during the 1900s (Kay, 1990; Barmore, 2003). These bark alterations effectively augmented the capability of fungal pathogens to enter aspen trees where they commonly cause wood decay, or "heart rot", and increased tree mortality (DeByle and Winokur, 1985; Hart, 1986). Thus, our underlying hypothesis was that the widespread barking of aspen during the 20th century, when the park's large carnivore guild was incomplete, not only increased the occurrence and severity of heart rot but significantly contributed to the premature mortality of aspen across Yellowstone's northern range.

2. Study area

YNP's northern range comprises approximately 1500 km^2 of mostly valley terrain in the northern Rocky Mountains, of which 1000 km^2 lies within the boundary of YNP. Big sagebrush (*Artemisia tridentata*)-steppe is the predominant vegetation type, grading into mixed-species coniferous forests at higher elevations. Remnant aspen stands are found scattered across the northern range where they may have originally occupied 4–6% of the area (Houston, 1982). Aspen stands typically occur on relatively moist sites in both upland and riparian settings where they normally support a diversity of understory plant species (DeByle and Winokur, 1985).

The northern range provides wintering habitat for elk, as well as smaller populations of mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and moose (*Alces alces*) (NRC, 2002). Bison (*Bison bison*) populations, which utilize the northern range year-round for foraging and other habitat needs, were relatively low throughout the 20th century (YNP, 1997; NRC, 2002). The continued presence of grizzly bears (*U. arctos*) and black bears (*U. americanus*), a recovering cougar population, and the 1995–96 reintroduction of wolves, indicates that the northern range again has a complete guild of large carnivores (Schullery, 1992; Smith et al., 2003). Since the restoration of this predator guild, the density, distribution, and foraging behavior of elk in the northern range have changed, and browsing has decreased as a result (Painter et al., 2015).

3. Methods

We used a stratified-random design for selecting northern range aspen stands that were historically accessible to elk. Between the Gardiner River Bridge and the Thunderer Cutoff Trail parking lot, a distance of nearly 60 km, we delineated nine road segments along Highway 212 which traverses east-west across much of the northern range (Table 1). Road segment 3 was an exception to this general approach; here we utilized the Blacktail Plateau Drive which parallels Highway 212. We randomly selected four aspen stands within each segment that were visible from the road and met the following criteria: (1) each stand occurred between 30 and 500 m from the road and (2) it had one or more overstory aspen trees ≥15 cm in diameter at breast height (*DBH*).

Within each "elk-accessible" stand we selected one of the larger overstory trees for coring at breast height (~1.4 m) with a 12 mm diameter increment corer, to determine bark thickness (cm) and heart rot (%). Heart rot was represented as the proportion of core length with discolored and fragile/crumbly wood relative to the total length of core between inner bark and tree center. In contrast, a pathogen-free portion of a core was typically uncolored and solid. We also measured the height (m) above ground of "furrowed/blackened" bark by averaging measurements from four sides of the bole. Furrowed/blackened

Table 1
Road segment locations and lengths along highway 212 from which elk-accessible aspen sands were selected. Range in site characteristics for sampled stands (i.e., distance from road, elevation, slope gradient) and *DBH*s (diameter at breast height) of sampled trees are also shown.

No.	Road segment location	Road segment length (km)	Distance from road (m)	Elevation (m)	Slope gradient (deg)	*DBH* (cm)
1	Gardiner River to Lava Creek	4.4	50–70	1900–1950	10–25	24.7–44.3
2	Lava Creek to west end of Blacktail Plateau Drive	8.2	30–190	2080–2100	2–22	16.4–43.7
3	Blacktail Plateau Drive	10.8	40–250	2140–2310	1–24	29.4–56.3
4	East end of Blacktail Plateau Drive to Yellowstone River	3.7	50–280	1920–1960	2–20	34.0–61.6
5	Yellowstone River to Lamar River	7.5	30–220	1900–1930	4–12	31.5–63.8
6	Lamar River to east end of Lamar Canyon	4.2	#	#	#	#
7	East end of Lamar Canyon to confluence of Lamar River and Soda Butte Creek	8.7	50–440	2030–2060	9–20	30.9–62.1
8	Confluence of Lamar River and Soda Butte Creek to Trout Lake trailhead	7.2	260–500	2030–2070	2–30	31.4–55.9
9	Trout Lake trailhead to Thunderer Cutoff trailhead	3.5	50–200	2100–2120	6–12	27.2–61.8
	Average =	**6.5**	**186**	**2035**	**12**	**44.4**

aspen stands within 30–500 m of road were not observed along this road segment.

bark represents a typical physiological response of aspen trees to elk barking (DeByle and Winokur, 1985) and its upper height was typically well-defined (Fig. 1) since it distinctly contrasted with the relatively smooth and white/gray surface of unaltered aspen bark occurring immediately above. In each stand we also measured the *DBH* (cm) and barking height (m) of up to four additional live trees ≥15 cm in *DBH*, if present. To generally characterize overstory trees comprising a stand, we counted all live and standing dead aspen trees ≥15 cm in *DBH*. We also determined UTM coordinates (m), distance to a nearest road (m), elevation (m), and slope gradient (deg).

For comparison with the elk-accessible stands along Highway 212, we located six aspen stands that were "protected" from elk use. Within each of these stands, five of the largest aspen trees were cored to determine bark thickness and the amount of heart rot, if any. Four of these stands were located within northern range ungulate exclosures (each ~2 ha in size), including the Mammoth, Junction Butte, Lamar Valley West, and Lamar Valley East exclosures. These exclosures had been established in the late 1950s/early 1960s (Beschta et al., 2016). A fifth stand was found north of the park in the Eagle Creek Campground and a sixth was south of the park in Grand Teton National Park. The Eagle Creek campground is ~6 km north of the park boundary and has been used by elk hunters and other campers for many decades; the largest aspen in this campground exhibited little/no barking from elk. The Grand Teton National Park stand occurred ~14 km south of YNP on a relatively narrow strip of land between Highway 89 and Jackson Lake (~50 m between the highway edge and the lake's shoreline) and within 20 m of a commonly used vehicular pull-out along the highway. The combination of this physically constrained site, next to a major highway on one side and the lake on the other, as well as being immediately adjacent to an often used highway pull-out, appears to have inhibited elk from

Fig. 1. (A) and (B) illustrate barking effects in elk-accessible aspen stands where approximately the lower ~2.2 m of bark on these trees is deeply furrowed/blackened. In (A), young aspen sprouts continue to be suppressed by bison herbivory and when these overstory trees eventually die this stand will likely be lost; note the sparse canopy of the aspen trees. (B) represents a stand where browsing levels have decreased in recent years and young aspen in background exceed the upper browsing level of elk. (C) and (D) illustrate relatively the relatively clear bark of aspen growing on sites where trees have not been barked by elk. For scale, the stadia rod in (B), (C), and (D) is 1.5 m tall.

using this stand and the selected trees had no observable barking. For each of the "protected" aspen stands, we determined UTM coordinates, elevation, and slope gradient.

We utilized linear regression for the elk-accessible stands to determine if barking height, bark thickness, and % heart rot were significantly ($p < 0.05$) associated with distance from road, elevation, or slope gradient. We similarly used linear regression for the protected stands to determine if bark thickness and % heart rot were significantly associated with elevation or slope gradient. Finally, we evaluated for significant differences (*t*-tests, unequal variances) in (a) bark thickness and (b) heart rot between elk-accessible and protected trees.

4. Results

A total of 32 elk-accessible aspen stands were randomly selected along our east-west traverse of the northern range, which consisted of four stands from each of the road segments except for road segment 6 which had no aspen stands meeting the selection criteria (Table 1). Sampled stands averaged 186 m from the road, 2035 m in elevation, and 12 deg. of slope gradient. Cored trees from these stands averaged 44.4 cm in DBH (range = 16.4–63.8 cm) (Table 1). The height of furrowed/blackened bark averaged 2.2 m ($n = 97$ live trees), with 2/3 of these heights occurring between 1.9 and 2.3 m (Fig. 2A). Bark thickness averaged 3.3 cm (Fig. 2B). Heart rot averaged 45.2% of core lengths and was present in 93.8% of the sampled trees (Fig. 2C). There was an average of 6.5 live trees and 2.8 dead trees per stand with the number of dead trees equaling or exceeding live trees in 38% of the stands. Regression results indicated that the height of blackened/furrowed bark, bark thickness, and % heart rot were not significantly associated with any of the site variables (i.e., distance from road, elevation, and slope gradient) as *p*-values were all >0.07.

The six protected aspen stands averaged 1965 m in elevation and 6 deg. of slope gradient (Table 2). The average *DBH* of aspen trees measured within northern range ungulate exclosures (stands #1–4) was 17.2 cm whereas those at Eagle Creek campground (stand #5) and Teton National Park (stand #6) averaged 30.9 cm and 39.5 cm, respectively. Bark thickness averaged 1.0 cm (Fig. 2B). Heart rot averaged 2.5% of core lengths and was present in 13.3% of the sampled trees (Fig. 2C). Regression results indicated that bark thickness and percent heart rot were not significantly associated with any of the site variables; all *p*-values were > 0.09.

Average bark thickness and heart rot percentage were each highly significant ($p < 0.001$) between elk-accessible and protected aspen trees.

Table 2
Stand locations and site characteristics (i.e., elevation, slope gradient) of aspen stands protected from elk, as well as the *DBH* (diameter at breast height) range of sampled trees.

Stand No.	Stand location	Elevation (m)	Slope gradient (deg)	*DBH* (cm)
1	Mammoth exclosure	1825	11	12.5–18.6
2	Junction Butte exclosure	2030	3	15.8–28.0
3	West Lamar exclosure	1900	3	13.6–16.2
4	East Lamar exclosure	2080	13	16.5–19.1
5	Eagle Creek campground	1880	4	26.0–36.6
6	Grand Teton National Park	2070	2	36.1–43.5
	Average =	**1965**	**6**	**23.2**

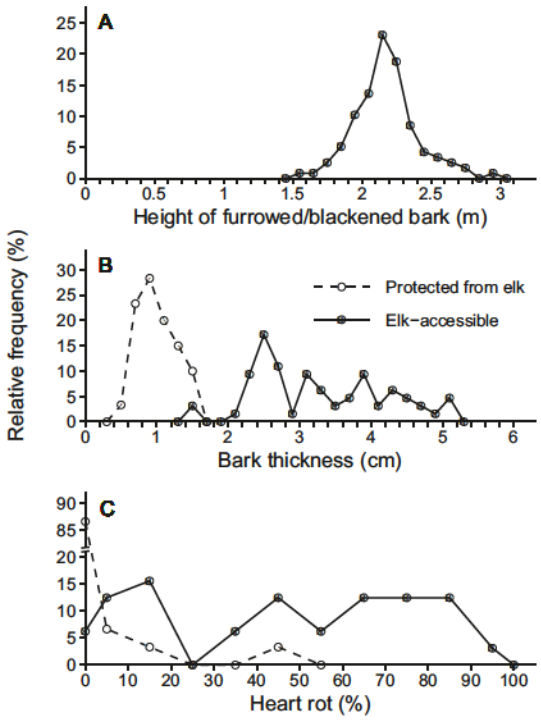

Fig. 2. Relative frequency histograms of (A) upper height (m) above ground of furrowed/blackened bark, (B) bark thickness (cm) at breast height, and (C) the proportion a tree's radius with heart rot (%), for aspen trees protected from elk as well as aspen trees accessible to elk. Simple sizes are $n = 97$ in (A) and $n = 30$ and 32 for protected and elk-accessible trees, respectively, in (B) and (C).

5. Discussion

In this study, we attempted to address a relatively simple question: Can the prevalence of elk barking and the occurrence of heart rot in barked trees represent a mechanism that may explain the early loss of overstory aspen trees across the northern range? Our results indicated heart rot, on average, was more than an order of magnitude greater in barked trees ($\bar{x} = 45.2\%$) than in unbarked trees ($\bar{x} = 2.5\%$). Furthermore, heart rot occurred much more frequently in the barked trees (93.8%) than in the unbarked (13.3%), indicating that many of the remaining overstory aspen may well have an elevated risk of mortality. Overall, the results of this study indicated that heart rot was relatively widespread in barked aspen trees of Yellowstone's northern range. This finding is consistent with the occurrence of a trophic cascade following the dismantling of the park's large predator guild in the early 20th century—a dismantling that extirpated wolves and cougars.

In the late 1980s aspen stands outside the park had 692 and 357 aspen stems/ha that were 11–20 cm and > 20 cm in *DBH*, respectively (Kay, 1990). In contrast, stands in the northern range had 2 and 156 aspen stems/ha that were 11–20 cm and > 20 cm in *DBH*, respectively, confirming that at that time a major deterioration in overstory aspen was well underway in the northern range. Our results, (a) the low number of live trees comprising a stand (84% of sampled stands had 5 or fewer trees ≥15 cm *DBH*), (b) the common presence of dead trees (dead trees equaled or exceeded the number of live trees in approximately 38% of the stands), (c) the widespread occurrence of heart rot in live trees ($\bar{x} = 93.8\%$ of sampled trees), and (d) the prevalence of large diameter trees ($\bar{x} = 44.4$ cm *DBH* for cored trees) in sampled stands, were consistent with Kay's (1990) earlier results and indicated that overstory aspen trees may soon disappear from most northern range aspen stands. Such a conclusion is also consistent with plot data from across the northern range where nearly all overstory aspen trees have died during the last 20 years (E. Larsen, pers. com.).

Where barking of aspen trees by elk is extensive, it represents an important avenue of infection for wood decaying fungi that cause heart rot, such as sooty-bark canker (*Cenangium singular*), black canker (*Ceratocysitis fimbriata*), cytospora canker (*Cystospora chrysosperma*), and others (DeByle and Winokur, 1985). In an assessment of mortality associated with 80–100-yr old aspen trees that had been barked by elk, 64.0% of the trees 2.5–15 cm in *DBH* were dead in stands identified as having "moderately heavy" or "heavy" bark damage from elk in

contrast to 22.5% of the trees where bark damage was "light" or "very light" (Hart, 1986). In addition, larger trees appeared to be less affected by bark damage; 20.5% of those 15–30.4 cm were dead in stands with "moderately heavy" or "heavy" bark damage compared to 17.5% of trees in stands where bark damage was "light" or "very light." These results indicated that the occurrence of barking may be less severe for large diameter trees, perhaps helping to explain the results of this study where overstory trees in sampled stands were predominantly relatively large diameter aspen (Table 1).

A "pattern of declining vigor in aspen stands when elk populations become high" has been common in western US and Canadian national parks (White et al., 1998, p. 452). We often observed sparse crowns and chlorotic leaves within the elk-accessible stands, conditions that are normally an indication of disease, or possibly nutrient deficiency (DeByle and Winokur, 1985). The relatively unhealthy status of northern range aspen was further corroborated by the fact that 84% of measured stands had only five or fewer overstory aspen trees remaining.

Our study emphasized the potential role of increased barking and heart rot as potentially important mechanisms for affecting aspen mortality rates, however other factors may contribute to aspen loss in some areas. For example, Warren's (1926) 1921–23 investigation of northern range beaver found they were beginning to "clean out" aspen adjacent to streams and ponds. Interestingly, Warren (1926, p. 165) only mentioned ungulate browsing once in his extensive report, where he indicated ungulates "… come to the ponds…to feed on the grass or browse on the brush." Approximately three decades later, Jonas (1955) revisited many of Warren's original sites and found that beaver were no longer present due to several factors, of which he considered a lack of food to be the most important. With regard to this factor, Jonas (1955, p. 184) indicated elk herbivory had "destroyed much of the vegetation and prevented regrowth". Even though beaver-elk interactions may have historically affected vegetation dynamics in some of the park's riparian areas, such effects did not influence our results because none of the aspen stands we sampled occurred along streams.

Much of the concern about aspen in YNP's northern range during the early-mid 1900s emphasized the increasingly widespread effects of elk browsing on young aspen sprouts (suckers) (Smith et al., 1915; Packard, 1942; YNP, 1958). In a synthesis of northern range ungulate-vegetation research in the 1960s, Barmore (2003) indicated that deterioration of aspen stands first became apparent in the 1920s and that range reports in late 1930s through the 1950s consistently documented the effects of heavy browsing, primarily by elk. Based on his research on aspen in the northern range, and citing an additional 13 aspen studies published between 1941 and 1977 by other researchers in the western US, Barmore (2003, p. 258) concluded: "That browsing by wild ungulates can cause deterioration and elimination of aspen clones by suppressing sucker growth and by barking older trees has been well documented in the park and in other areas." While intensive browsing of aspen sprouts over time may prevent recruitment and eventually the loss of a stand, barking can increase heart rot and accelerated the loss of established overstory trees. It is this second process that we propose represents a multi-level trophic cascade, from predator-to-prey-to-plants-to-fungi.

When the bark of an aspen tree is stripped by elk, the physiological response of the tree is to produce furrowed/blackened bark that is considerably thicker than the original bark (DeByle and Winokur, 1985). Bark on the elk-accessible aspen trees averaged 3.3 times thicker than that found for trees protected from barking. Furthermore, during our coring of trees, we found this furrowed/blackened bark to be relatively resistant to our coring device indicating that, once formed, it may be relatively resistant to any additional stripping by elk.

Historical photographs of YNP aspen stands from the late1800s indicate there was no evidence that the bark on aspen trees had been damaged by elk (e.g., Fig. 3). Barked trees were also not evident in early photographs of aspen stands in Rocky Mountain National Park (Baker et al., 1997) as well as several Canadian national parks in Alberta and British Columbia (White et al., 1998). In Yellowstone, perhaps the first recognition that barking had begun to affect some aspen stands were the observations by Smith et al. (1915, p. 21) that indicated wintering elk in some areas were capable of peeling bark from young aspen "to such an extent that whole groves of the small trees are killed." A decade later, Heller (1925, p. 437) concluded that "when hard pressed in winter they [elk] commonly resort to the aspen woods where they gnaw the green bark of the trunks to eke out a scanty fare." Early biologists generally considered the eating of aspen bark by elk in winter was primarily an "emergency ration" and only occurred when they were forced to do so by hunger (Skinner, 1928). Later, Packard (1942, p. 478) noted that the barking of aspen "appears to be a habit of elk wherever aspen occur on winter elk range" and further that it had also occurred in the Gros Ventre country of Wyoming, Rocky Mountain National Park, and elsewhere. In Jasper National Park, the lower ~2 m of mature aspen trees had been blackened as a result of elk barking during the mid-1900s (Scharff, 1972), a period when wolf populations had been greatly

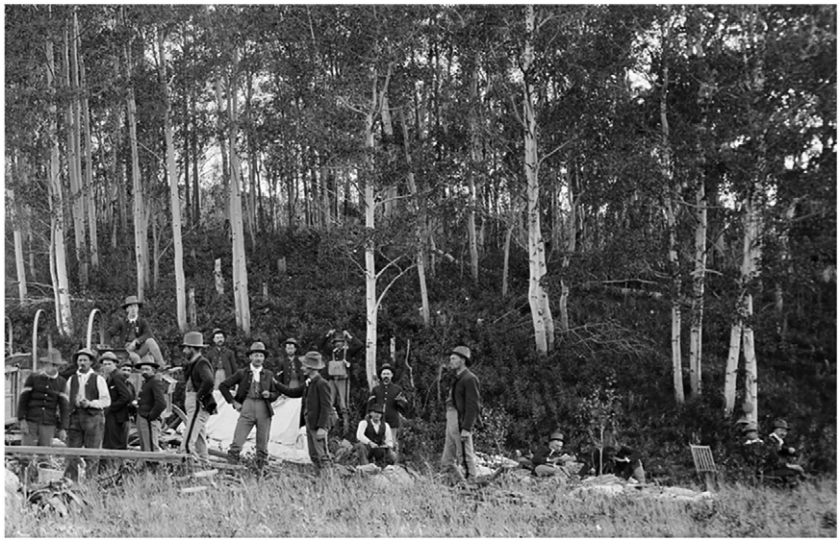

Fig. 3. Aspen grove behind Minnesota National Guard camp at little Blacktail on Yellowstone's northern range in 1893. Barking of the multi-sized aspen trees is not present and the understory is a diverse community of tall forbs and shrubs. Although wolves and cougars were being persecuted at this time, it was several decades later that they were extirpated. Photo by F. Jay Hynes (H-03070), courtesy of Montana Historical Society, Helena, MT.

suppressed. Today, blackened bark typically comprises the lower ~2 m of aspen that occur in elk winter ranges outside of YNP (L. Painter, pers. com.).

The typical height of furrowed/blackened bark associated with elk barking has often been indicated to be ~2 m (Packard, 1942; Hart, 1986; Kay, 1990), whereas we found it to be slightly higher, or 2.2 m. Factors that might contribute to variation in heights include: (a) Altered behavior by elk — When bark stripping first began to occur in northern Yellowstone, elk may have done so to the extent they could reach when standing on all four legs. However, in the general absence of large carnivores and with limited winter forage, elk may have begun to reach higher on a bole by standing on their back legs. (b) Antler rubbing — Elk, and other ungulates, often use aspen trees to rub velvet from their antlers in late summer, thus affecting bark in the process (Altman, 1952). (c) Physical protection — For aspen trees that grow close to each other, this may protect the interior side of adjacent trees thus decreasing the average barking height measured for these trees. (d) Natural pruning — As lower side-branches die-back during normal tree growth, a localized portion of the bark often becomes blackened/furrowed (DeByle and Winokur, 1985; Kay, 1990). (e) Moose — This large ungulate also barks aspen trees and, because of their relatively tall heights, they can reach higher than elk. However, the population of moose in the northern range has remained relatively small compared to that of elk. (f) Tree fall — A conifer or aspen tree that falls against a standing aspen tree may scar the bark the standing tree to various heights, thus contributing to furrowed/blackened bark well above that attributable to elk.

In their synthesis of aspen ecology and management in the western US, DeByle and Winokur (1985) clearly identified the important role elk barking can have on increasing fungal infection and mortality in aspen. Although wildlife species other than ungulates can also affect the bark of aspen, their effects tend to be often localized and less severe. For example rabbits (*Sylvilagus* spp.) and hares (*Lepus* spp.) may remove some bark near the base of a tree for food and, in some instances, may girdle small trees (DeByle and Winokur, 1985). Similarly, mice (*Peromyscus* spp.) and voles (*Microtus* spp.) may eat patches of bark near the base of a tree in winter with damage sometimes extending from ground level up through the entire snowpack depth (DeByle and Winokur, 1985). Porcupines (*Erethizon dorsatum*) may also remove bark from aspen but such effects are typically localized (Graham et al., 1963). Although sapsucker (*Sphyrapicus* spp.) holes influence only small portions of a trees bark, they nevertheless can provide access for microorganisms and fungi to enter a tree (Packard, 1942). However, we are unaware of any studies indicating that the effects of various wildlife species on aspen bark, either individually or collectively, come close to those of elk.

Even though we undertook a major east-west transect for locating elk-accessible aspen stands, our results cannot be construed as necessarily representing the entire population of aspen stands that occur across the northern range. Most aspen stands we sampled were in lower-valley settings and within 500 m of a road, whereas many additional stands occur beyond 500 m and at higher elevations.

6. Concluding remarks

Aspen grow on moist sites and their canopies transmit considerable light. Such sites normally support a diverse understory plant community (grasses, forbs, shrubs) and provide habitat for a large number of vertebrate and invertebrate species (DeByle and Winokur, 1985; Kuhn et al., 2011). For example, relatively high bird richness and diversity is often associated with aspen stands (Finch and Reynolds, 1987; Turchi et al., 1995; Rumble et al., 2001; Hollenbeck and Ripple, 2007). Thus, an accelerated loss of overstory aspen is likely to have serious consequences to understory plant communities as well as the habitat quality for wildlife species that normally frequent aspens stand. While there has been a relative abundance of aspen snags in recent decades in the northern range, an abundance that has generally been beneficial to cavity-nesting birds (Hollenbeck and Ripple, 2008), the paucity of overstory trees in our sampled stands indicates that aspen snag abundance levels in the future are likely to become exceptionally low.

With the return of wolves in 1995–96, completing the park's large predator guild, browsing pressure on young aspen sprouts was reduced in many northern range aspen stands. This ongoing recovery started slowly but has nevertheless increased in strength over time (Painter et al., 2014; Beschta et al., 2018). For example, Painter et al. (2014) found that the 5-tallest young aspen heights, in 87 randomly selected aspen stands from across the northern range, increased from an average height of 35 cm in 2003 to nearly 170 cm in 2012. Similarly, the proportion of stands where the 5-tallest young aspen exceeded 200 cm, the general upper browse level of elk, increased from 0% in 2007 to 25% in 2012. These trends indicate that understory aspen, in an increasing number of stands, are exceeding the upper browse level of elk and will hopefully, over time, lead to the recovery of these stands. However, because overstory trees in many stands have already died, and continue to do so, attaining a full array of age classes will require more than a century even in recovering stands. It thus appears that the trophic-level effects of an altered large carnivore guild, a guild that was incomplete for approximately seven decades due to large predator persecution in the early 1900s, have not only affected aspen age structure during the last 100 years but that such effects are likely to extend well into the 22nd century.

Declaration of competing interest

There are no conflicts of interest concerning our article.

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