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Wolf, Elk, and Aspen Food Web Relationships: Context and Complexity

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Abstract

Like most ecological communities, aspen (*Populus tremuloides*) forests are influenced by a synergy of bottom-up (resources-driven) and top-down (predator-driven) processes. Since the 1920s, ecologists have observed the decline of many aspen communities throughout the Intermountain West. The extent and possible drivers of this decline are topics of much recent scientific study. In addition to bottom-up effects, which include drought, fire suppression, and disease, ungulate herbivory is a contributing factor. Trophic cascades are ecological relationships in which an apex predator produces strong top-down, direct effects on its prey and indirect changes in faunal and floral communities at lower trophic levels. Apex predators, such as the gray wolf (*Canis lupus*), have been linked to aspen vigor and recruitment, via trophic cascades mechanisms. Scientists have hypothesized that returning wolves to the landscape enables aspen to recruit into the forest overstory, via the density-mediated and behaviorally-mediated effects of wolves on their ungulate prey, primarily elk (*Cervus elaphus*). We present a synthesis of scientific findings on this topic, identify trends in the ecological impacts of wolves in aspen communities in a variety of ecosystems, and suggest areas for further investigation. Knowledge gaps include the interaction of top-down (e.g., predators) and bottom-up (e.g., drought, fire, hydrology, logging) effects, and how the ecological context of the interaction affects the outcome. Future horizons involve exploring these food web relationships as a complex of inter-level interactions in a more integrated, empirical manner. We suggest adopting a new standard for the aspen/wolf ecology literature by shifting its emphasis and lexicon from trophic cascades

to food web studies. Such an integrated approach can help managers create more resilient aspen communities.

1. Introduction

Aspen (*Populus tremuloides*), the most widely distributed tree species in North America (DeByle and Winokur 1985), has been declining in large portions of the Intermountain West since the 1920s (Murie 1926-1954; Leopold 1943). The extent and possible drivers of this decline have become topics of much scientific investigation (Romme et al., 1995; White et al., 1998; Kulakowski et al., 2006; Hogg et al., 2008; Worrall et al., 2008). This decline is of conservation concern for many reasons, including the fact that aspen provides important habitat for elk (*Cervus elaphus*), songbirds, and other species (DeByle 1985; Romme et al., 2001; Hollenbeck and Ripple 2008; Oaten and Larsen 2008).

A prominent ecological debate in the past fifty years concerns whether resources have a stronger influence on plant communities than predation (Murdoch 1966; Sinclair 2003). Resources, such as moisture and sunlight, are necessary for plant growth. Predation controls herbivore pressure on plants (Hairston et al., 1960), thereby driving sometimes strong trophic effects throughout communities. Additionally, competition and omnivory create complex trophic linkages among community members (Menge and Sutherland 1976; Polis and Strong 1996). In the 1920s, ecologist Charles Elton linked wolf (*Canis lupus*) presence to food web effects that can release plants from ungulate herbivory (Elton 1926). More recently, these food web relationships have been linked to aspen conservation (Ripple et al., 2001; White et al., 2003). However, resources available to aspen provide the energetic foundation to sustain this species, and so also may be strong regulators of aspen dynamics.

In this paper, we review the food web research that has examined the ecological factors that influence aspen growth and stand dynamics. Factors such as moisture, disturbance,

24 herbivory, and human natural resources use create diverse, multi-causal aspen responses

25 (Eisenberg 2012). All may be as important drivers of aspen overstory recruitment as wolf

26 presence, depending on context (White et al., 2003). As managers strive to create more

27 ecologically resilient aspen communities, all of these factors have become key elements to

28 consider in aspen forest management.

29

30 **2. Trophic Cascades Theoretical Background**

31

32 2.1 *Trophic cascades components and top-down effects*

33   A food web is a theoretical construct that depicts trophic relationships in a community

34 (Elton 1926). Ecologists have identified the fundamental components of a food web as primary

35 producers (plants), primary consumers (herbivores), and secondary consumers (predators)

36 (Darwin 1859; Elton 1926; Hairston et al., 1960). Predators can include apex predators, defined

37 as a carnivore species that dominates its trophic class (Terborgh et al., 2010) and can have strong

38 effects on other food web components (Navarrete and Menge 1996; Soulé et al., 2005).

39   Trophic cascades are ecological relationships in which an apex predator produces a

40 strong direct effect on its prey and strong indirect changes in faunal and floral communities at

41 other trophic levels (Paine 1980; Crooks and Soulé 1999). Trophic cascades can be stronger at

42 the lower end of the productivity gradient, such as in Arctic or arid ecosystems (Oksanen and

43 Oksanen 2000). Ecologists have observed that when apex predators such as wolves are removed,

44 the species that was their primary prey increases significantly in number (Hairston et al., 1960;

45 Paine 1969). This increase is termed an irruption (Leopold et al., 1947). An irruption leads to

46 intensive consumption of food resources and indirectly affects other species dependent on those

47 plant communities (Berger et al., 2001; Bailey and Witham 2002; Hebblewhite et al., 2005a).

48   While the density-mediated effects (reduced prey numbers) of predation have long been

49 documented (Lotka 1907), behaviorally-mediated effects (altered prey feeding behavior) are a

50 more recent discovery. Apex predator presence changes prey feeding behavior (Schmitz et al.,

51 1997; Laundré et al., 2001; Fortin et al., 2005), by making prey more vigilant (Lima and Dill

52 1990). This top-down mechanism (Polis and Strong 1996) reduces the time prey spend eating

53 (Brown et al., 1999) and can enable vegetation to regrow (White et al., 1998). For example, in an

54 old-field experiment, Schmitz et al. (1997) found behaviorally-mediated effects of arthropod

55 presence on grasshoppers. However, several experimental studies have attributed reduced prey

56 vigilance in systems with a high predator population to prey differential response to complex

57 cues. Ferrari et al. (2010) causally linked a reduction in anti-predator response by fish to adaptive

58 decision making.

59   Both density-mediated and behaviorally-mediated mechanisms have the potential to

60 create trophic cascades. Nevertheless, the existence of behaviorally-mediated effects remains a

61 debated topic in the wolf→elk→aspen trophic cascades literature (Ripple and Beschta 2004;

62 Halofsky and Ripple 2008; Kauffman et al., 2010). The fact that behaviorally-mediated

63 responses are not simple (Brown and Kotler 2004) has fueled this debate. For example, Creel et

64 al. (2008) found lower elk vigilance at a site with a higher proportion of time spent at risk

65 (higher number of wolves), and higher vigilance at a site with fewer wolves.

66   Simple apex predator presence does not ensure that trophic cascades will occur. In low

67 densities, apex predators may not be ecologically effective (Soulé et al., 2003). An ecologically

68   effective population of an apex predator is defined as one sufficient to produce trophic cascades.

69   (Soulé et al., 2003; Estes et al., 2010).

70

71   2.2 *Bottom-up effects and trophic trickles*

72   Bottom-up effects may stimulate or reduce vegetation growth (Borer et al., 2005).

73   Lindeman (1942) described energy passing upward through trophic levels, which he envisioned

74   as distinct and functionally homogeneous sets of green plants, herbivores, and primary

75   carnivores. He referred to this as bottom-up control of ecological communities. Soil moisture

76   influences plant growth (Bassett 1963). Nutrient (e.g., nitrogen, phosphorus) availability may

77   increase after fire, also stimulating growth (Belleau et al. 2006). Bottom-up effects include

78   vegetation effects on herbivores, such as food resource availability (Murdoch 1966).

79   Anthropogenic modifications of plant communities also can cause bottom-up effects. For

80   example, timber harvest creates early-seral forest communities (Swanson et al., 2010).

81   Hunter and Price (1992) suggested that strong bottom-up effects prevail in all systems.

82   They observed that " . . . the removal of upper trophic levels leaves lower levels intact, whereas

83   the removal of lower trophic levels leaves no system at all." The bottom-up effects present in all

84   food webs may buffer top-down effects (Power 1992). Studies in a variety of settings and

85   systems have documented weak top-down effects, termed trophic trickles (Power 1990; Hunter

86   and Price 1992; McAnn et al., 1998; Halaj and Wise 2001; Dawes-Gromadski 2002; Menge

87   2005; Kauffman et al., 2010). A trophic trickle is defined as a situation where an apex predator is

88   present, but has limited indirect effects on vegetation (Strong 1992). Highly speciose systems

89   can demonstrate trophic trickles (Strong 1992).

90   Like most ecological communities, aspen forests are structured by a synergy of bottom-

91 up (resources-driven) and top-down (predator-driven) effects (Schmitz et al., 2006; Eisenberg

92 2012). Ecological context (e.g. spatial landscape heterogeneity and climate patterns) influences

93 the relative importance of these effects. Such context may cause woody species recruitment to be

94 more strongly influenced by bottom-up than top-down effects (Marshall 2012). In a

95 wolf→elk→aspen food web, for trophic cascades to occur, wolves must have a strong effect on

96 elk, and elk must have a strong effect on aspen. If both effects do not occur simultaneously, then

97 the result could be a trophic trickle or a system dominated by bottom-up effects.

98

99 **3. Aspen Conservation Status and Associated Factors**

100

101 3.1 *Aspen conservation status and recruitment*

102   A forest's ability to persist over time depends in part on successful growth of young trees

103 into the canopy (van der Valk 2009). A variety of environmental factors influence this

104 recruitment, including nutrient and moisture availability, disturbance, and herbivory (Franklin et

105 al., 2002; Horsley et al., 2003; Littell et al., 2008).

106   In the Intermountain West, from the mid-1920s until recently, researchers have been

107 finding predominately even-aged, single-storied aspen stands. Composed largely of trees >80

108 years old (Mueggler 1989), these stands arose after stand-replacing wildfires (Kulakowski et al.,

109 2004). This even-aged structure is not an historic condition, largely being the result of

110 unsuccessful recruitment over the past 80 years (Romme et al., 1995). In addition to lack of fire

111 and chronic herbivory (Singer 1996; Baker et al., 1997; Johnston 2001; Vavra et al., 2005),

112 ecologists have linked low recruitment to predator extirpation (Romme et al., 1995; Naiman and

113   Rogers 1997; White et al., 1998; Ripple and Larsen 2000). However, some of this measured

114   aspen decline may simply be the result of normal forest community succession toward conifer

115   dominance in the absence of fire (Shepperd et al., 2001a). Multiple interacting ecological factors

116   influence aspen population dynamics (Brown et al., 2006; Worrall et al., 2008). These factors

117   operate on a sub-continental scale, and sometimes may be related to trophic cascades (Kashian et

118   al., 2007; Kaye 2011).

119

120   *3.2 Effects of predator removal and herbivory on aspen recruitment*

121   Ecologists long have observed the relationship between apex predators and recruitment of

122   young trees into the forest canopy. Many of these observations have been associated with wolf

123   removal. In 1925, in Grand Teton and Yellowstone (YNP) National Parks, Wyoming, Olaus

124   Murie observed intense herbivory, which he attributed to the elk irruptions caused by wolf

125   removal (Murie 1925-1954). Fifty years later, in Isle Royale National Park, Michigan, McLaren

126   and Peterson (1994) discovered that wolves produced density-mediated effects on moose (*Alces*

127   *alces*). This released balsam fir (*Abies balsamea*) from moose herbivory and led to recruitment

128   of this previously suppressed tree species. These effects were more pronounced in areas with a

129   higher number of wolves, which suggested trophic cascades (Mclaren and Peterson 1994).

130   Similar effects have been observed in many boreal and temperate forest ecosystems (Beschta and

131   Ripple 2009; Ripple et al. 2010). Intensive browse by ungulates has been identified as a factor

132   degrading forests worldwide (Oksanen and Oksanen 2000; Soulé et al., 2003). Tree sprouts in

133   general subjected to repeated browse develop a stunted, shrubby growth form and ultimately fail

134   to recruit into the canopy (Keigley and Frisina 1998).

135 Elk, deer (*Odocoileus spp.*), and domestic ungulates can suppress aspen sprouts and keep

136 them from reaching the overstory. Among the suite of herbivores present in Rocky Mountain elk

137 winter range (low-elevation grasslands with patches of aspen), elk have the strongest impacts on

138 aspen, (Houston 1982; Debyle 1985; Barmore 2003). Aspen is considered to be high-quality

139 browse and can provide up to 60% of elk diet during winter months (Hobbs et al., 1981; Canon

140 et al., 1987). Outside of elk winter range and beyond the Intermountain West, deer and domestic

141 ungulate impacts on aspen can be significant (Alverson et al., 2003; Tortenson 2006; Seager et

142 al., this issue). In systems without elk, deer can suppress aspen (Leopold 1943; Binkley et al,.

143 2006). Bison (*Bison bison*) impacts on woody species [e.g., willow (*Salix spp.*)] have been

144 documented (Painter and Ripple 2012), but have not been measured in aspen communities.

145 Moderate browsing can stimulate production of new shoots by releasing apical dominance

146 (Bilyeu 2007; Johnston 2007).

147 A variety of factors influence ungulate use of woody species. Resource quality and

148 position on the landscape (e.g., aspect, elevation) (White et al., 2003), time of year, and

149 snowpack influence browse (Brodie et al., 2012). Elk tend to use south-facing slopes in winter,

150 because these retain more heat and are the first to become snow free, which increases plant

151 availability (Chen et al., 2002). Some research suggests that avoidance of wolf predation can also

152 reduce browse (Ripple et al., 2001; White et al., 2003). However, more recent, studies have

153 failed to find such an avoidance effect (Creel et al., 2008; Creel and Christianson 2009;

154 Kauffman et al., 2010). The need to conserve energy also can influence ungulate use of woody

155 species. In Oregon, Seager (2010) found that wild ungulates avoided utilizing aspen in areas with

156 significant amounts of down wood. Since wolves were not part of this system, he attributed this

157 effect to ungulate energy conservation. In Glacier National Park (GNP), Montana, and Waterton

158   Lakes National Park (WLNP), Alberta, Eisenberg (2012) found elk avoiding the interior of aspen

159   stands, regardless of wolf population size. Elk co-evolved with wolves, so this could be an

160   instinctive energy-conserving behavior (Geist 2002).

161

162   3.3 *Additional factors associated with aspen decline*

163   Large-scale, stand-replacing wildfire plays a key role in regenerating and perpetuating

164   aspen stands and enhancing elk habitat (Cook 2002). A fire of sufficient intensity and severity to

165   kill the aspen forest overstory stimulates abundant suckering. However, some suckers arise after

166   a light fire, or even in its absence (Bartos and Mueggler 1981). Conifer invasion, a by-product of

167   fire suppression, can reduce aspen stand size. Many aspen stands are seral communities that give

168   way to conifers (Rogers 2002; Morelli and Carr 2011). Conifers have longer lifespans than

169   individual aspen ramets and can overtop aspen. Fire eliminates young conifers from the

170   understory, while stimulating aspen sprouting (Smith and Smith 2005). The longer fire return

171   intervals found at high elevations enable conifers to reach the overstory and replace aspen

172   (Kulakowski et al., 2004).

173   In the absence of fire and with chronic elk herbivory, aspen stands fail to successfully

174   recruit new stems, leading to senescent, even-aged stands (White et al., 1998). In GNP, Singer

175   (1979) attributed aspen decline to decades of fire suppression combined with elk browse. But,

176   fire alone may be insufficient to restore aspen. Throughout the Intermountain West, research in

177   aspen stands in elk winter range that burned and did not have wolves has found abundant post-

178   fire suckering, heavy elk browse, and lack of aspen recruitment (Romme et al., 1995; Baker et

179   al., 1997; Barnett and Stohlgren, 2001; Kay 2001; Bailey and Witham 2002; Hessl and

180 Graumlich 2002). Aspen sprout density and elk herbivory intensity are positively linked to fire

181 severity (Bailey and Witham 2002; Smith et al., 2011).

182   Additional factors associated with aspen decline include disease, insect outbreaks, and

183 drought (Worrall et al., 2008). In the southern Rocky Mountains, drought is the strongest driver

184 of recent aspen decline (Worrall et al., 2010; Hannah and Kulakowski 2012). Conifer

185 encroachment and ungulate herbivory can exacerbate drought effects (Shepperd et al., 2001b;

186 Lamalfa and Ryel 2008; Worrall et al., 2008). Conversely, excessive moisture may increase

187 disease occurrence in sprouts, thereby reducing their ability to recruit into the canopy (Jacobi et

188 al., 1998). In a variety of scenarios and landscapes, from Canada to the southern Rocky

189 Mountains, all of the above factors can cause aspen overstory death and failure of the understory

190 to sprout and recruit (Hogg et al., 2008; Worrall et al., this issue). Aspen functional type (e.g.,

191 seral, stable) may further influence aspen response to stressors (Rogers et al., 2012).

192

193 **4.   Trophic Cascades Hypotheses Involving Wolves, Elk, and Aspen**

194

195 4.1 *Trophic cascades hypotheses*

196   Prior to the 1995 and 1996 YNP wolf reintroduction, ecologists speculated about the

197 potential effects of wolf removal on elk over-consumption of woody browse species (Leopold et

198 al., 1947). In YNP, these species include aspen, cottonwood (*Populus spp.*), and willow (Romme

199 et al., 1995; Naiman and Rogers 1997). Returning wolves to this system could reduce the number

200 of elk via predation. Fewer elk could release woody browse species from herbivory and stimulate

201 trophic cascades. Such primary effects could have beneficial secondary effects on other taxa,

202 such as songbirds, beavers, and fish (Naiman and Rogers 1997).

203   The YNP wolf reintroduction inspired trophic cascades research that has linked wolves to

204   elk to aspen recruitment (Smith et al., 2003; Ripple and Beschta 2007; Ripple and Beschta 2010).

205   Ecologists have hypothesized that wolves are enabling aspen to recruit above the browse height

206   of elk and that this provides evidence of trophic cascades (White et al., 2003). This notion has

207   gained popularity in the media; documentaries and magazine articles have promoted the idea that

208   wolves are "saving" aspen (Bass 2005; Robbins 2005). Yet some consider these claims to be

209   possibly premature or spurious (Kauffman et al., 2010; Mech 2012). Still others assert that while

210   the wolf is an apex predator that exerts important ecological effects in food webs, it is but one of

211   the many factors that influence aspen ecology at the landscape scale (Kimble et al., 2011;

212   Eisenberg 2012).

213

214   4.2 *Trophic cascades conceptual models*

215   Ecologists use conceptual models to characterize food webs and provide a framework to

216   explore interaction directions and strengths. Such simplified models allow examination of

217   bottom-up and top-down effects (Menge and Sutherland 1976; Carpenter et al., 1985) and can

218   help quantify these effects (Grace 2006; Reisner 2010). Conceptual models are used to study the

219   effects of wolves on aspen communities (e.g., White et al., 1998; Ripple and Beschta 2004;

220   Hebblewhite et al., 2005a; Eisenberg 2012).

221   We created a series of conceptual models to depict the functional components of the

222   wolf→elk→aspen food web (Figure 1). Many more food web components would be possible, if

223   one were to build an interaction web model for this system (Lavigne 1995). To represent bottom-

224   up forces, we included Environment (e.g., moisture) and Disturbance (e.g., fire, flooding, and

225   insect outbreaks). For the purposes of this review, we focus on fire, as other disturbance factors

226 (e.g., flooding) have not been addressed in aspen trophic cascades studies. We structured each

227 model horizontally, rather than vertically, to emphasize a less hierarchical structure (Hunter and

228 Price, 1992; Polis 1994; Menge et al., 1994).

229   The bottom-up model (figure 1-a) depicts a case where ecological resources and fire are

230 the strongest drivers of aspen recruitment. In this model, wolves are relatively unimportant

231 members of an aspen community. Sunlight, moisture, and disturbances such as fire sustain

232 vigorous aspen recruitment. Aspen provide improved food resources for elk, which support

233 wolves. Regardless of wolf density, this model represents a system driven via bottom-up energy

234 flow.

235   Conversely, the top-down model (Figure 1-b) depicts a case where wolf predation is the

236 strongest driver of aspen recruitment. In this model, wolves suppress elk, which releases aspen

237 from herbivory, and consequently improves food resources for elk. This indirectly creates food

238 resources for wolves, via a positive feedback loop. Both density-mediated and behaviorally-

239 mediated mechanisms result in top-down indirect effects on aspen.

240   The trophic trickles model (Figure 1-c) illustrates a case where in the absence of bottom-

241 up effects (e.g., disturbance), even at a high density, wolves are unable to indirectly stimulate

242 aspen recruitment. In this model, elk intensely browse aspen. Lack of fire additionally reduces

243 aspen vigor. This combination of factors creates a negative feedback loop in which elk have

244 degraded food resources, and in turn provide diminished food resources for wolves. Thus,

245 wolves are present, but not ecologically effective in driving top-down trophic cascades via

246 density-mediated and/or behaviorally-mediated mechanisms.

247

248 **5. Synthesis of Food Web Relationships in Aspen Science**

249

250 5.1 *Early conceptual studies*

251   Landscape-scale trophic cascade studies in general, and wolf→elk→aspen food web

252 studies specifically, represent a fairly new field. Three early studies conceptually examined

253 factors that could be influencing aspen recruitment and discussed the potential role of wolves

254 (Romme et al., 1995; White et al., 1998; Ripple and Larsen 2000).

255   In the aftermath of the 1988 YNP fire, Romme et al. (1995) measured aspen regeneration

256 and recruitment, and identified elk as the dominant herbivore impacting the aspen in the park.

257 This study provided a comprehensive summary of the linkages evaluated in YNP (e.g., fire,

258 weather, elk market hunting) and found to be important to aspen recruitment. In the discussion of

259 their findings, the authors speculated about wolf absence as a factor that had allowed the elk

260 population to grow. However, the focus and main conclusions of this study did not link wolves to

261 aspen recruitment. Most notably, the authors concluded that "a single-factor approach to

262 managing and understanding aspen dynamics in YNP is insufficient." While they did not test this

263 conclusion experimentally, this early observation has been confirmed by later studies.

264   White et al. (1998) conducted a literature review, focusing on six Rocky Mountain

265 National Parks in Canada and the US. They linked aspen decline to predator extirpation, a top-

266 down, density-mediated effect. The authors further found that fire was failing to stimulate aspen

267 recruitment, which they attributed to intense elk herbivory in the absence of wolves. White et al.

268 (1998) proposed a four-level trophic model that included humans as the apex predator.

269   Ripple and Larsen (2000) conducted an analysis of aspen overstory recruitment on the

270 YNP northern range. They concluded that successful aspen recruitment occurred from the mid-

271 1700s until the 1920s and then ceased. They hypothesized that the main factor associated with

272   this decline was wolf extirpation. They speculated that wolves may influence aspen recruitment

273   via trophic cascades mechanisms, including the behaviorally-mediated effects of predation risk.

274

275   *5.2 Wolf→elk→aspen studies*

276   In the past twelve years, approximately eleven wolf→elk→aspen studies have occurred

277   (Table 1), inspired by Romme et al. (1995); White et al. (1998); and Ripple and Larsen (2000).

278   Study findings range from strong top-down effects linked to wolves, to strong bottom-up effects

279   prevailing, to a combination of top-down and bottom-up effects driving aspen recruitment, with

280   potential trophic trickles. Taken as a body, these studies furnish evidence that, as in other

281   systems (e.g., aquatic), it is difficult to cast aspen food web ecology as simple top-down or

282   bottom-up scenarios.

283   Ripple et al. (2001) conducted some of the earliest correlational research on trophic

284   cascades in aspen on the YNP Northern Range. This important study investigated the effects of

285   wolves on elk behavior. The authors wanted to determine whether reintroduced wolves were

286   influencing elk browse patterns and aspen regeneration via trophic cascades mechanisms. They

287   used elk pellet groups, aspen sucker heights, and the percentage of browsed suckers to measure

288   differences in aspen stands in high and low wolf-use areas. They used wolf telemetry data (VHF

289   radio-collars) to determine high and low wolf-use areas. High-use areas included territories

290   occupied by wolf packs (Ripple et al., 2001). The authors found that wolves had apparently

291   altered elk foraging behavior, with fewer elk pellets in riparian sites that may have had greater

292   predation risk by wolves. Aspen suckers in riparian high wolf-use areas were taller than in other

293   areas measured. They found no significant effect of fire on aspen density or height. This early

294   observational study supports the top-down model (Figure 1-b). It was among the earliest studies

295 to evaluate the behavioral effect of wolves on elk (e.g., Laundré et al., 2001). It did not fully

296 examine bottom-up effects (e.g., moisture, snow pack), which may have been important, too.

297 More recent research has attempted to address bottom-up effects.

298   Several subsequent observational studies examined the effect of wolf presence/absence

299 on Rocky Mountain aspen communities. All hypothesized that behaviorally-mediated effects

300 would be linked to aspen recruitment. The methods used in these studies differed, but all found

301 top-down effects (Larsen and Ripple 2003; White et al., 2003; Beschta and Ripple 2007; Ripple

302 and Beschta 2007; Halofsky and Ripple 2008), indicated by aspen recruitment above browse

303 height (Table 1). The top-down model (Figure 1-b) depicts the food web dynamics identified by

304 these researchers, where wolf presence was the strongest driver of aspen recruitment. These

305 studies all considered top-down and bottom-up factors and their interaction. For example, Larsen

306 and Ripple (2003) found no aspen recruitment after a 1988 fire in the Sunlight Basin, Wyoming,

307 during a period when there were no wolves. They also found no relationship between moisture

308 (e.g., xeric or mesic aspen stand types) and recruitment. In YNP, Halofsky and Ripple (2008)

309 linked the combined effects of fire, changes in elk density and predation risk, and decreased

310 herbivory after wolf reintroduction to facilitated growth of young aspen. However, these studies

311 did not empirically quantify bottom-up effects on aspen regeneration and growth so cannot

312 conclude that bottom-up processes are unimportant. They defined predation risk via an

313 unvalidated model (e.g., more hypothesized impediments to predator detection and escape result

314 in less elk use of site, an indirect measure of risk), rather than directly (e.g., measurement of wolf

315 locations with telemetry data). Therefore, the indirect, unvalidated model for predation risk may

316 be wrong (Kauffman et al., 2010).

317   Hebblewhite et al. (2005a) investigated the effects of wolf recolonization in Banff

318   National Park, Alberta. In this observational study, the authors hypothesized that variations in

319   wolf presence, would correlate positively to the strength of top-down effects. They measured

320   variations in wolf presence using telemetry data (Hebblewhite et al. 2002) and included a site

321   from which wolves had been partially excluded (the Banff townsite). Additionally, Hebblewhite

322   et al. (2005a) tested for density-mediated and behaviorally-mediated effects of wolves on elk and

323   evaluated trophic cascades in aspen and willow communities. The authors found no significant

324   effects of wolf presence on aspen, as measured by recruitment of young trees into the forest

325   canopy. Aspen sapling densities and recruitment were higher in sites that had been disturbed

326   recently (<25 years) by fire. Willow sites showed a release from elk herbivory correlated

327   positively to wolf presence. The density-mediated effects of wolves on elk were more important

328   than behaviorally-mediated effects. The authors concluded that in an aspen system, bottom-up

329   effects (e.g., disturbance) and other contextual factors interact with and influence top-down (e.g.,

330   wolf predation) effects (Hebblewhite et al., 2005a). In this study, the trophic trickles model

331   (Figure 1-c) characterizes aspen findings, and the top-down model (Figure 1-b) represents

332   willow findings.

333   Binkley et al. (2006) evaluated the density-mediated effects of wolves on deer on the

334   Kaibab Plateau. This study occurred in a system without elk, in which white-tailed deer (*O.*

335   *virginianus*) are the primary herbivore. The authors revisited a classic case study first presented

336   by Elton (1926), subsequently chronicled in greater depth by Leopold (1943; 1949), and

337   critiqued by Caughley (1970). The Kaibab Plateau lies within both the Kaibab National Forest

338   and Grand Canyon National Park (GCNP), which have different resource management strategies

339   (resource extraction vs. resource protection). Wolves and other predators were removed by the

340   1920s; deer subsequently irrupted.

341   This study found lack of aspen recruitment after predator removal. Climate, a bottom-up

342   effect, did not influence aspen recruitment. However, the authors also found complex effects

343   driven by factors such as logging (Binkley et al., 2006). Logging creates early-seral communities

344   (Swanson et al., 2010), an effect that in this study may have attenuated the top-down signature of

345   predation. Early seral-communities offer enhanced food sources for deer via the conifer removal

346   and soil disturbance associated with logging, which release aspen (Shepperd 2001b; Jones et al.,

347   2005). In the absence of wolves on the Kaibab National Forest, during a thirty-year period

348   beginning in 1963, Binkley et al. (2006) observed recruiting aspen numbers more than one order

349   of magnitude above the long-term trend. However, this response was not observed within GCNP,

350   which was not logged. Natural resources management factors (e.g., cattle grazing, deer hunting

351   by humans) increased contextual complexity. This study was among the first to document a

352   complex of inter-level interactions in a more integrated manner. The top-down model (Figure 1-

353   b) represents the general study findings. However, the bottom-up model can be used to depict the

354   effects of timber harvest (Figure 1-a).

355   More recent research has taken a closer look at some of the contextual relationships

356   implicit in trophic responses and has also increased the rigor of such studies. Kauffman et al.

357   (2010) were the first to employ an experimental approach to measure top-down effects in a

358   wolf→elk→aspen food web. This built on an earlier study (Kauffman et al., 2007), in which the

359   authors identified high predation risk sites via telemetry and kill-site data to quantify predation

360   risk directly. Kauffman et al. (2010) investigated behaviorally-mediated trophic cascades. To

361   determine whether landscape-scale differences in aspen recruitment were related to spatial

362 variation in wolf predation risk, the authors randomly placed small ungulate exclosures on the

363 YNP Northern Range in areas of high, moderate, and low predation risk. High predation risk

364 sites included riparian areas. Contrary to what Ripple and Beschta (2007) found, Kauffman et al.

365 (2010) determined that aspen were not recruiting and that wolves were not modifying elk

366 browsing behavior. Kauffman et al. (2010) incorporated the effects of climate into their analysis,

367 but did not examine fire as a factor in aspen recruitment. Because Kauffman et al. (2010) did not

368 focus on bottom-up effects, the bottom-up model does not strictly represent their findings (Figure

369 1-a). Using an experimental approach, they tested for a behaviorally-mediated wolf effect on elk

370 and did not find one. Therefore, the trophic trickles model, which suggests that wolves may not

371 be the only or primary drivers of aspen recruitment in a tri-trophic system, represents their

372 findings (Figure 1-c).

373   Kimble et al. (2011) conducted research in the Northern Range, in the Gallatin National

374 Forest just north of the YNP border. Resource extraction in the form of hunting by humans and

375 timber harvest occurs in this mixed-use landscape. The authors wanted to find evidence of wolf-

376 driven trophic cascades. They re-measured permanent, long-term study sites within this forest,

377 originally measured in 1991 before wolves were present. This study took place in the same

378 general area studied by Larsen and Ripple (2005). Kimble et al. (2011) evaluated both density-

379 mediated and behaviorally-mediated wolf effects on elk. Despite wolf presence, the authors

380 found a lack of top-down effects in the aspen (e.g., recruitment). They did not find that wolf

381 presence caused elk to avoid high predation risk sites (e.g., riparian areas).The trophic trickles

382 model (Figure 1-c) represents their findings.

383   Eisenberg (2012) investigated food web relationships between wolf predation, elk

384 herbivory, aspen recruitment, and fire. The study setting, in the central portion of the Crown of

385 the Continent Ecosystem, spans the US/Canada border and encompasses GNP, Montana, and

386 WLNP, Alberta. The observations were stratified across three spatially distinct areas: the North

387 Fork Valley, in the western portion of GNP; the Waterton Valley, in the eastern portion of

388 WLNP; and the Saint Mary Valley, in the eastern portion of GNP. All valleys are elk winter

389 range. The valleys have three different observed wolf population levels (Saint Mary: low;

390 Waterton: moderate; North Fork: high), which represent three corresponding levels of long-term

391 predation risk (the probability of an elk encountering a wolf). Ecological characteristics (e.g.,

392 climate, soils, elevation, plant associations) are comparable among valleys. Recent fire has

393 occurred in 90% of the North Fork.

394   The study objective was to examine the relative influence of bottom-up (fire) and top-

395 down (predation risk) factors and the context-dependence of these relationships. Density-

396 mediated and behaviorally-mediated wolf effects on elk were evaluated. Browse on aspen was

397 lower in the North Fork, where there was a high wolf population, suggesting a top-down effect.

398 However, the low aspen recruitment in the absence of fire in all valleys indicates a bottom-up

399 effect. In sum, the risk of wolf predation alone did not drive the food web relationships observed

400 in this study. Bottom-up and top-down forces worked together in valleys that contained well-

401 established wolf populations, and to a lesser degree in a valley with a low wolf population. Both

402 density-mediated and behaviorally-mediated wolf effects on elk were found, but these

403 relationships were complex. Eisenberg (2012) used wolf density to represent predation risk, in a

404 broad-scale, qualitative way (e.g., wolf population data). The trophic trickles model (Figure 1-c)

405 best characterizes the Eisenberg (2012) study. However, because this was an observational study,

406 trophic trickles could not be empirically documented.

407

408   *5.4 Top-down or bottom up: is this a false dichotomy?*

409   The studies reviewed above provide evidence of a wide range of effects that can drive

410   aspen recruitment. Differences in findings are attributable to differences in scale (spatial and

411   temporal), location, consideration of bottom-up effects, research design (e.g., correlational vs.

412   experimental work), and methodologies. For example, some landscape-scale studies have found

413   great variation in aspen indirect responses to wolf presence (Table 1). Additionally, detectability

414   of top-down effects may have been influenced by the plant-response variable measured. In a

415   meta-analysis, Schmitz et al. (2000) found trophic cascades stronger when plant damage was the

416   measured response, versus plant biomass or reproductive output.

417   Some of the contradictory findings of these studies may be due to the increase in

418   scientific knowledge as researchers have come to better understand wolf→elk→aspen food

419   webs, YNP in particular. For example, three studies now disagree with earlier findings about

420   simple behaviorally-mediated trophic cascades (Creel et al., 2008; Creel and Christianson 2009;

421   Kauffman et al., 2010). In YNP, early studies took necessary first steps at assessing the impacts

422   of behaviorally-mediated trophic cascades (Ripple et al., 2001). Subsequent work held that

423   hypothesis to more rigorous testing and found some top-down effects (Hebblewhite et al.,

424   2005a). More recently, some studies have found nuanced behavioral responses by elk to

425   predation risk by wolves and context-dependence of top-down effects (Eisenberg 2012). It bears

426   noting that some of the earliest work that examined wolf effects on forest communities other

427   than aspen (e.g., balsam fir) found that bottom-up effects such as fire could attenuate the top-

428   down effects of wolves (McLaren and Peterson 1994). Significant breakthroughs in soil and fire

429   ecology also have increased our awareness of the complexity of aspen food web relationships

430   (St. Clair et al., 2010; Smith et al.; 2011).

431   A key difference in findings pertains to how predation risk was measured (e.g., indirectly

432   vs. directly). Ripple and Beschta (2007) used topography to define predation risk. Eisenberg

433   (2012) used wolf density to represent predation risk, in a broad-scale, qualitative way (e.g., wolf

434   population data). Hebblewhite et al. (2005b) and Kauffman et al. (2007) also used wolf density

435   to represent predation risk, but in a more quantitative manner (e.g., wolf telemetry data) than

436   Ripple and Beschta (2007) or Eisenberg (2012). These three different approaches to quantifying

437   predation risk may yield divergent results. Some authors have noted that risk of predation by

438   wolves defies a simple definition, and has yet to be fully defined (Hebblewhite et al., 2005b;

439   Eisenberg 2010).

440   A deeper look at some tri-trophic components could have changed the results of the

441   studies we reviewed. Elk population dynamics and distribution are complex (Vucetich et al.,

442   2005), as is also the case with most predator species (Lotka 1907; Taylor 1994). When designing

443   research that evaluates wolf impacts on elk, we suggest empirically accounting for elk population

444   dynamics. Decreases in elk abundance, distribution, and group sizes driven by circumstances

445   beyond wolf predation (e.g., climate, food availability, hunting by humans) could contribute to

446   trophic cascades related to wolves (White et al., 2012) and potentially could make wolves more,

447   or less, ecologically effective. Many of the studies we evaluate have not fully incorporated the

448   effects of snowpack. The amount of snow on the ground, a bottom-up effect, can significantly

449   alter elk behavior and aspen growth. During low snow years, elk have easier access to sprouts for

450   browsing (Brodie et al., 2012).

451   The diverse findings discussed here vividly illustrate that aspen food web relationships,

452   including trophic cascades, cannot be neatly described as top-down or bottom-up scenarios. Like

453   the models we present, many variations of these relationships are likely, depending on context.

454   Hunter and Price (1992) suggested that the dichotomy between top-down and bottom-up effects

455   may be false. They observed that a more interesting question would be to what extent context

456   can influence the relative strength of top-down and bottom-up forces in a community. Over two

457   decades ago, ecologists argued for a more integrated approach to studying community dynamics

458   (e.g., Menge et al., 1994; Power 1992). More such research continues to be needed.

459

460   **6.   Knowledge gaps**

461   Trophic cascades science in aspen communities is relatively new. The majority of studies

462   on this topic have been done by a handful of researchers working over a period of less than one

463   and a half decades. Consequently, the knowledge gaps in this area are enormous. For example,

464   we have learned that wolves can sometimes exert strong direct and indirect effects in aspen

465   communities, which cascade down through multiple trophic levels (Ripple and Beschta 2007).

466   However, we know little about how context can influence these effects.

467   Looking beyond aspen communities, Estes et al. (2011) documented top-down food web

468   effects driven by apex predators in a variety of ecosystems worldwide. These relationships are

469   ecologically ubiquitous (Schmitz 2000). Experiments have found strong causational links

470   between predators and trophic cascades, primarily in aquatic systems (Borer et al., 2005). We

471   suggest that the context and strengths of these effects remain to be fully explored in terrestrial

472   large mammal communities. Further, these relationships can be influenced by a variety of

473   factors. For example, recent studies of wolves, elk, and willows have documented bottom-up

474   effects and trophic trickles (Creel et al., 2008; Creel and Christianson 2009; Martin 2012), while

475   others have found strong top-down effects in the same landscape (Beyer 2006). Studies

476   conducted in the same location get different results due to differences in scale, methodology, and

477 response variables (Schmitz et al., 2000). Further, communities can display both top-down and

478 bottom-up control, with both dominating at different times, depending on ecological

479 circumstances (Schmitz et al., 2006).

480   During the 1980s-1990s, dozens of experimental studies investigated trophic cascades in

481 aquatic systems and terrestrial invertebrate systems (Schmitz et al., 2000; Borer et al., 2005).

482 Beyond these experiments, reviews and meta-analyses explored the theory behind trophic

483 cascades, including establishment of alternative stable states and tipping points (Hunter and Price

484 1991; Power 1992). Most of these studies found complex, multi-causal food web relationships.

485 We suggest that perhaps it is time for the scientific community to revisit such topics and their

486 application to aspen communities and other terrestrial systems that contain large mammals.

487 Advances in analysis methods, such as the development of structural equation modeling (Grace

488 2006), invite such scientific exploration. Such methods have been applied to experimental work

489 on the effects of ungulate herbivory in willows (Baker et al., 2005; Johnston et al., 2007). Other

490 possible analysis methods to deepen our understanding of aspen food webs could include

491 hierarchical and landscape modeling.

492   Lack of direct information about predation risk is a basic weakness of many of the studies

493 discussed in this paper. Researchers used subjective criteria to make assumptions about which

494 habitats were risky and which were safe. Later studies have shown that some of these earlier

495 assumptions about risky habitats were wrong. For example, early studies and some subsequent

496 work assumed that wide open habitats were safe for elk (Ripple and Beschta 2004; Halofsky and

497 Ripple 2008; Eisenberg 2012). Other studies using telemetry data have commonly found that

498 these are the places where elk are more vigilant and more likely to be killed by wolves

499 (Hebblewhite et al., 2005b; Kauffman et al., 2007). Predator-prey dynamics are complex and

500   subject to change via stochastic effects and environmental context (Brown 1999). Further, little

501   is known about the effects on a food web of the interaction between density-mediated and

502   behaviorally mediated effects (Lima 1998). Current research is underway in YNP to further

503   clarify these relationships (Doug Smith personal communication).

504   Several topics have yet to be addressed in wolf→elk→aspen food web studies. Research

505   horizons include plant defense compound effects and genetics, factors that can influence aspen

506   growth and dynamics (Mock et el., 2008; Lindroth and St. Clair, this issue). Aspen response to

507   climate variability on a landscape-scale and how this influences food web relationships

508   represents another information gap (Schmitz et al., 2003).

509

510   **7.   Conclusion**

511   Trophic cascades driven by apex predators via top-down effects have been identified in

512   ecosystems worldwide (Estes et al., 2011). Accordingly, ecologists recommend conserving apex

513   predators and including top-down effects in management strategies (Estes et al., 2011).

514   Generalizations about the ecological importance of apex predators to aspen communities

515   are tempting due to the pressing conservation issues at stake (e.g., wolf removal from the

516   Endangered Species List and subsequent control of this species; addressing Sudden Aspen

517   Decline). However, we suggest caution in broadly ascribing strong top-down trophic effects to

518   wolves, given recent research findings about the context dependence and complexity of these

519   relationships (Binkley et al., 2006). Further, it is likely that cascading effects of wolves in aspen

520   communities may be even more variable outside of places such as YNP or GNP and other

521   national parks, due to the anthropogenic influences on wolves, elk, and forest communities in

522   those multi-use systems (Mech 2012).

523   Important goals for future research include understanding how context influences food

524   web relationships in aspen communities. Further research is needed on a landscape scale, as most

525   aspen trophic studies have been done on a localized scale (Table 1). Fertile areas for research

526   include experimental studies on the mechanisms underlying aspen response to disturbance, such

527   as fire, within a wolf-driven trophic cascades model. In moving forward, the effects of climate

528   may become more apparent as the functional and numerical responses of wolves change in

529   response to elk density (White and Garrott 2005). Such approaches would explore food web

530   relationships as a complex of inter-level interactions in a more integrated, quantitative manner.

531   We recommend that aspen management strategies incorporate what we are learning about

532   wolf→elk→aspen food webs. Wolves can have powerful effects in food webs. These effects

533   have been linked to aspen recruitment (Table 1). Therefore, applying the precautionary principle

534   to create healthier, more resilient aspen forests would suggest conserving apex predators, as

535   feasible, where their ranges coincide with aspen (Kreibel et al., 2001). However, use of trophic

536   cascades concepts for aspen management will not be a "one-size-fits-all" prescription, due to the

537   effect of context on food web relationships and the broad spectrum of bottom-up effects, such as

538   fire. Lacking apex predators, it is possible to use management tools that create barriers to

539   ungulates (e.g., coppicing, fencing) to mimic apex predator effects, combined with fire

540   treatments. More science needs to be done in order to make such applications effective.

541   Finally, we suggest shifting the emphasis and lexicon in future aspen/wolf ecology

542   literature from trophic cascades to food web relationships. This shift would more accurately

543   reflect our emerging scientific awareness that, while they may be important, wolf effects are but

544   one of the suite of physical factors and ecological interactions that can influence aspen growth

545   and dynamics.

546

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