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FORUM

Trophic cascades from wolves to grizzly bears or changing abundance of bears and alternate foods?

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Introduction

In ‘Trophic cascades from wolves to grizzly bears in Yellowstone’, Ripple *et al.* (2014) hypothesize that a wolf (*Canis lupus*)-caused trophic cascade has resulted in increased consumption of fruit by grizzly bears (*Ursus arctos*) in Yellowstone National Park (YNP). The authors proposed that in the absence of wolves, competition between grizzly bears and elk (*Cervus elaphus*) for berry-producing shrubs, along with high elk numbers, resulted in decreased fruit availability to grizzly bears. They further hypothesized that post-wolf reintroduction (with a subsequently reduced elk population), there would be an increase in the establishment of berry-producing shrubs and fruit availability to grizzly bears and an increase in the percentage of fruit in grizzly bear diets (Ripple *et al.* 2014). However, for a variety of reasons, the comparisons Ripple *et al.* (2014) used to demonstrate increased fruit availability and consumption by grizzly bears post-wolf reintroduction are flawed and tenuous at best. Importantly, a more parsimonious hypothesis, not sufficiently considered by Ripple *et al.* (2014), exists and is better supported by currently available data I review here.

The case of the missing serviceberry and minimal berry crops

There are two problematic issues with the data Ripple *et al.* (2014) used to demonstrate increased fruit availability to grizzly bears relating to (i) where they researched berry-producing shrubs and (ii) the species of shrub studied.

First, Ripple *et al.* (2014) studied the establishment, age, height and growth of serviceberry (*Amelanchier alnifolia*) inside and outside of ungulate exclosures to infer increased fruit availability to Yellowstone grizzly bears following wolf reintroduction. The area where Ripple

et al. (2014) studied serviceberry is substantially different from where the post-wolf-reintroduction, grizzly bear scats were collected in habitat type, vegetative cover and precipitation (Mattson *et al.* 2004). The researchers studied serviceberry in the higher portion of the northern range of YNP (White, Proffitt & Lemke 2012), whereas post-wolf-reintroduction, grizzly bear scats were collected around Yellowstone Lake (Fortin *et al.* 2013) (Fig. 1). The Yellowstone Lake area is characterized by elevations over 2400 m with large tracts of lodgepole pine (*Pinus contorta*) as well as Engelmann spruce (*Picea engelmannii*) and subalpine fir forest types (Reinhart 1990), whereas the northern range (the serviceberry study area) is much lower, 1500–2400 m, consisting of large areas of steppe, shrub steppe and Douglas fir (*Pseudotsuga menziesii*) (Houston 1982). Given these important differences between the two areas, and because changes in woody browse post-wolf reintroduction are non-uniform across YNP (Ripple & Beschta 2012; see also Mech 2012 for a review), serviceberry data from the northern range cannot be used to infer increased fruit availability in the Yellowstone Lake area (the post-wolf-reintroduction, grizzly bear scat study area). Yellowstone National Park is vast, so documenting an increase in the establishment and height of a shrub in one area by no means implies similar changes in another, especially when the habitats are so different.

Secondly, it is curious that Ripple *et al.* (2014) selected serviceberry as the shrub they studied. Although serviceberry comprised three of the four scats (‘likely grizzly bear’, Ripple *et al.* 2014; Supporting Information) examined in the northern range serviceberry study area, serviceberry was never found in the 778 post-wolf-reintroduction scats (Fortin *et al.* 2013, p. 275) they used to demonstrate increased fruit consumption. Because serviceberry is more common at lower elevations (but can occur at 3000 m) (Fryer 1997), one would not expect grizzly bear scats in the Yellowstone Lake area (above 2400 m) to frequently contain serviceberry. Furthermore, serviceberries in general are infrequent in grizzly bear diets in

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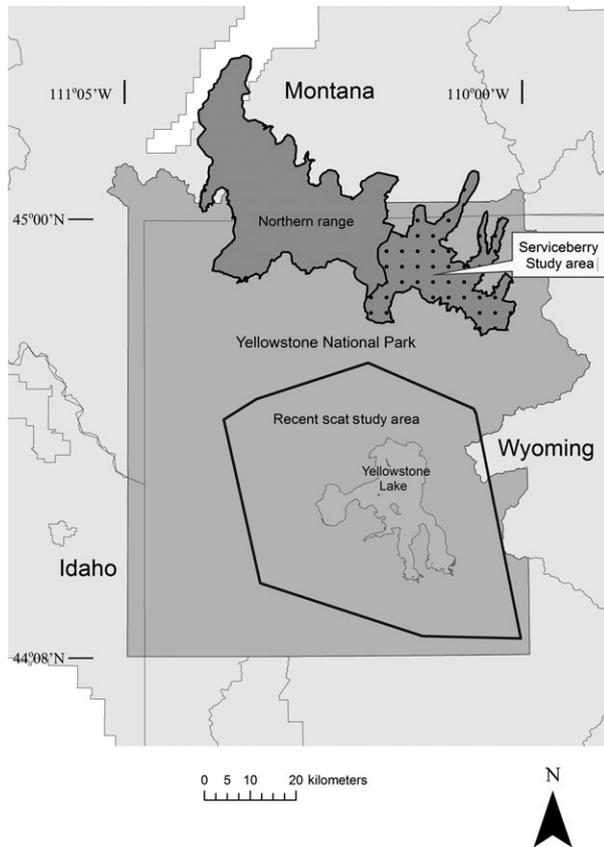


Fig. 1. Approximate locations of the serviceberry study area and the post-wolf-reintroduction, grizzly bear scat study area. The serviceberry study area (dotted dark-grey shaded) was located in the upper-elevation sector of the northern range of Yellowstone National Park [YNP] (plain and dotted dark-grey shaded, White, Proffitt & Lemke 2012; Ripple *et al.* 2014). The post-wolf-reintroduction, grizzly bear scat study area comprised the area surrounding Yellowstone Lake (approximate polygon outlined in black and labelled 'Recent Scat Study Area', see Figure 1 in Fortin *et al.* 2013). Due to differences in scale, the pre-wolf-reintroduction, grizzly bear scat study area (Mattson, Blanchard & Knight 1991) that covered approximately 20 000 km² and extended beyond YNP and included surrounding national forests, could not be pictured here. The actual extent of the pre-wolf-reintroduction, grizzly bear scat study area, that is the Greater Yellowstone Ecosystem, is depicted in the 2012 Interagency Grizzly Bear Study Team Annual Report (p. 43, <http://nrmcs.usgs.gov/products/IGBST>, accessed May 22, 2014).

the Greater Yellowstone Ecosystem (GYE) (i.e. <0.5% of 11 478 scats, Gunther *et al.* 2014). Grizzly bears have adaptive and flexible diets, with some bears 'specializing' (Knight, Mattson & Blanchard 1984; Mattson, Blanchard & Knight 1991; Edwards *et al.* 2011; Van Daele, Barnes & Belant 2012; Gunther *et al.* 2014). Further, 'grizzly bears in the GYE use different food resources depending on where their home ranges are located' (Gunther *et al.* 2014, p. 67). Thus, inferring consumption of one diet item via availability of a different item in a different study area is highly suspect. More appropriate species to use when examining increased fruit availability to, and consumption by, Yellowstone grizzly bears would be *Vaccinium* spp.

(huckleberry, blueberry, etc.) or *Shepherdia canadensis* (buffaloberry) which figure prominently in the frugivorous portion of grizzly bear diets in the GYE (Mattson, Blanchard & Knight 1991; Gunther *et al.* 2014). Unfortunately, Ripple *et al.* (2014) only mention them cursorily.

Rather than using data from the northern range to infer increased fruit availability in the Yellowstone Lake area, one can instead examine alternate data that (i) directly address fruit availability and (ii) come from the same area and period as the post-wolf-reintroduction, grizzly bear scats. In contrast to what Ripple *et al.* (2014) infer from the northern range regarding increased fruit availability, data collected during the post-wolf-reintroduction, grizzly bear scat study around Yellowstone Lake are at best equivocal regarding increased fruit availability. Fortin *et al.* (2013) report that in two of the three years of their study (2007 and 2009), berry crops were 'minimal' (p. 277). Thus, what Ripple *et al.* (2014) extrapolate from the northern range does not reflect actual fruit availability documented around Yellowstone Lake and certainly does not supersede berry crop data from the area and period of actual interest where the post-wolf-reintroduction, grizzly bear scat data were collected (Yellowstone Lake area, 2007–2009; Fortin *et al.* 2013). Therefore, Ripple *et al.*'s (2014) hypothesized increased fruit availability to grizzly bears around Yellowstone Lake is not supported when alternate data from the Yellowstone Lake area are considered.

Invalid comparison between grizzly bear scat study areas

In addition to the concerns regarding the serviceberry data that Ripple *et al.* (2014) used, there are also problems with the grizzly bear scat data they used to document increased fruit consumption post-wolf reintroduction. The authors compare pre-wolf-reintroduction, grizzly bear scat data (1977–1987; Mattson, Blanchard & Knight 1991) and post-wolf-reintroduction, grizzly bear scat data (2007–2009; Fortin *et al.* 2013) as a means of evaluating whether grizzly bears have increased their berry consumption following wolf reintroduction. [Note, here I evaluate Ripple *et al.*'s (2014) analysis comparing pre- and post-wolf-reintroduction grizzly bear scat data, not their separate analysis relating grizzly bear scat data from 1986 to 1987 to elk densities]. This comparison unfortunately is not valid because the pre- and post-wolf-reintroduction, grizzly bear scats were collected in different study areas, with the latter representing a small subset of the former (Fig. 1). The pre-wolf-reintroduction data were collected across approximately 20 000 km² in an area that extended beyond YNP and included surrounding national forests when a 'major portion' of the grizzly bear population ranged outside of YNP (Mattson, Blanchard & Knight 1991, p. 1619), whereas the post-wolf-reintroduction data were collected in a much-reduced area

surrounding Yellowstone Lake within YNP (Fig. 1; Fortin *et al.* 2013). This comparison is not valid due to differences in habitat type, vegetation cover type, precipitation, elk (*Cervus elaphus*) and bison (*Bison bison*) densities and year round use (Green, Mattson & Peek 1997; Mattson 1997; Gunther *et al.* 2014), occurrence of cutthroat trout (*Oncorhynchus clarki*) spawning streams and army cutworm moth (*Euxoa auxiliaris*) aggregation sites (Mattson *et al.* 2004; Gunther *et al.* 2014). These differences in habitats and study area range are especially critical when evaluating grizzly bear diets because of the nature of some bears to specialize on locally available food resources (Mattson, Blanchard & Knight 1991). In the absence of information about changing availability of and preference among differing foods, comparisons of utilization of different food resources are not valid across these different study areas. Because the study areas are so radically different, they do not allow for an appropriate test of a temporal change in diet.

An alternative hypothesis: changing abundance of bears and alternate foods

Data from the post-wolf-reintroduction, grizzly bear scat study reveal berry consumption was lowest during 2009 when, notably, whitebark pine (*Pinus albicaulis*) nuts were abundant (Fortin 2011; Ripple *et al.* 2014). Fortin (2011, p. 17) further reported ‘...berries were mostly used by smaller bears, particularly black bears [*Ursus americanus*] and female grizzly bears’, supporting previous research that indicated larger bears with higher energetic requirements select more energy-dense (in this case, not berries) food items (see Fortin 2011 and Fortin *et al.* 2013 for reviews, p. 20 and 278, respectively). In particular, the gross caloric value of whitebark pine nuts (3.99 kcal g^{-1}) is greater than that of the average for berries (3.24 kcal g^{-1}), and the highest fat content of plant foods consumed by GYE grizzly bears is found in the seeds of whitebark pine (30.5%) (Gunther *et al.* 2014). Knight, Mattson & Blanchard (1984) reported that grizzly bears ‘directed’ their feeding to focus on higher gross energy content foods that could be efficiently foraged (such as whitebark pine seeds) and when these foods were not readily available bears consumed a wide variety of berries and other foods. These data suggest that whitebark pine nuts are a higher quality food or, when available, are more economical than the available berries. If berries are not selected over whitebark pine nuts in Yellowstone, then changes in the frequency of fruit in scat must be evaluated in the context of changing availability of other high-quality foods.

Additional data reveal notable declines in two important YNP grizzly bear foods; whitebark pine and cutthroat trout (see Fortin 2011 for review; Haroldson & Podruzny 2013; Koel *et al.* 2005; Macfarlane, Logan & Kern 2013; Yellowstone Center for Resources 2013). From 2002 to 2012, 73% of mature, cone-bearing

whitebark pine trees monitored for research in the GYE died (Haroldson & Podruzny 2013), and Yellowstone cutthroat trout abundance has been estimated at <10% of historic levels (Koel *et al.* 2005). Because the abundances of high-quality foods such as whitebark pine nuts and cutthroat trout have declined, it would not be surprising to document a corresponding increase in the consumption of other foods (such as berries) even apart from any true change in the availability of these other foods (e.g. berries). [Note: although cutthroat trout in YNP is generally a late spring/early summer grizzly bear food, due to local snowmelt differences around Yellowstone Lake, spawning trout coincide with berry availability in some areas; Kerry Gunther, Bear Management, YNP, National Park Service, personal communication]. Thus, hypothesized, post-wolf-reintroduction, increased-fruit consumption by grizzly bears around the Yellowstone Lake area could be explained by the well-documented declines in other food resources (see Fortin 2011 for review; Haroldson & Podruzny 2013; Koel *et al.* 2005; Macfarlane, Logan & Kern 2013; Yellowstone Center for Resources 2013) regardless of whether fruit availability has increased or not. [Note also that during 1968–1971, prior to wolf reintroduction, grizzly bear scats reflected relatively higher percent frequency of berries that was less than, but similar to that observed during the 2000s after wolf reintroduction (see Fig. 1 in Gunther *et al.* 2014). Thus, the underlying cause for and the biological relevance of the hypothesized, increase in percentage fruit in grizzly bear diets post-wolf reintroduction is further questionable].

Ripple *et al.* (2014) refer to the declines in whitebark pine nuts and cutthroat trout (e.g. p. 226). However, they do not adequately consider the importance of these foods in terms of expected changes in the frequency of occurrence of other foods in grizzly bear scats. Rather they cite McLellan & Hovey (1995) as evidence that berries are selected over whitebark pine nuts. Although McLellan & Hovey (1995) report (as pointed out by Ripple *et al.* 2014, p. 231) that whitebark pine nuts were common (in the Flathead River drainage of south-eastern British Columbia where they studied grizzly bear diets) but did not occur in their scat sample (p. 706, 710), they also report that ‘It is important for managers to realize the possible uniqueness of the Flathead area and not extrapolate information without due caution’ (p. 704). Thus, this reference is not sufficient to counter direct evidence from the post-wolf-reintroduction, grizzly bear scat study (i.e. Yellowstone Lake, 2007–2009) that (i) grizzly bears consumed fewer berries when whitebark pine nuts were abundant (Fortin 2011; Ripple *et al.* 2014), (ii) ‘use of whitebark pine nuts mirrored availability’ (Fortin 2011, p. 17) and (iii) larger grizzly bears were not selecting berries (Fortin 2011, p. 17).

Furthermore, additional data indicate YNP’s grizzly bear population has increased across the two study periods (e.g. in the GYE, there were approx. 250–300 bears in the mid-1980s to at least 600 in 2012, Eberhardt & Knight

1996; Haroldson, van Manen & Bjornlie 2013) with the growth rate slowing during the last decade (Interagency Grizzly Bear Study Team 2012), and density-dependent effects have been observed (Boyce *et al.* 2001; Schwartz *et al.* 2006; Bjornlie *et al.* 2014). Any resulting heightened competition among grizzly bears for limited preferred foods would naturally lead to an increased occurrence of other less preferred foods in scats. Thus, any potential increase of berries in scats (which as discussed above has not been substantiated by Ripple *et al.*'s (2014) invalid comparison across the two scat study areas) may be attributed to (i) the well-documented declines in other high-quality food (whitebark pine nuts and cutthroat trout) (see Fortin 2011 for review; Yellowstone Center for Resources 2013) and (ii) a larger bear population, rather than the result of a trophic cascade.

Although the comparisons of Ripple *et al.* (2014) were insufficient to document increased fruit availability to and fruit consumption by grizzly bears, I do not reject that a trophic cascade could be occurring (perhaps in tandem with changing abundance of grizzly bears and alternate foods), but emphasize that (i) the evidence Ripple *et al.* (2014) present in support of their trophic cascades hypothesis is weakened considerably by problems I have discussed and (ii) that the alternate hypothesis proposed herein is a more parsimonious explanation and is better supported by currently available data.

Insufficient consideration of the data-supported, alternate hypothesis

Ripple *et al.* (2014) address an 'alternate foods hypothesis' in one sentence stating, 'We suggest that the availability of alternative foods may have been an influence, but was likely not the main factor here because grizzly bears in many other interior regions of the world have high-quality alternative foods, but fruit is typically still the dominate [*sic*] grizzly bear food in late summer (McLellan & Hovey 1995; Mattson 1998)' (p. 8–9). Ripple *et al.* (2014) could have formally tested at least a portion of the alternate foods hypothesis by using available data on whitebark pine seed crop size as a covariate in a multivariate model examining frequency of fruit in grizzly bear diets. Ripple *et al.*'s (2014) one sentence addressing the alternate foods hypothesis does not adequately counter this (and the increased grizzly bear population) hypothesis because (i) they do not sufficiently consider the importance of changing abundance of these alternate foods and grizzly bears (as detailed above) with respect to expected changes in the frequency of occurrence of other food items in grizzly bear scats and (ii) because they did not cite contradictory research.

Alternate evidence reveals: (i) grizzly bear diets in drier parts of Montana were similar to that of 'the average Yellowstone grizzly bear' (Mattson, Blanchard & Knight 1991, p. 1626), (ii) three other brown bear populations in North America (at either high latitudes or altitudes) similarly ate as few fleshy fruits and (iii) brown bears in

central Siberia likewise consumed mainly ungulates and seeds with little fleshy fruit in the diet (see Mattson, Blanchard & Knight 1991 for review). Furthermore, whereas YNP's habitat is generally recognized as having a relative paucity of fleshy fruits (Mattson, Blanchard & Knight 1991), in nearby Glacier National Park, where berries are important in grizzly bear diets, both the abundance and the availability of whitebark pine nuts and ungulates are lower than in YNP (Katherine Kendall, US Geological Survey, Northern Rocky Mountain Science Center, personal communication). This highlights, once again, the importance of considering relative abundance and availability of alternate foods (and changes in them) when assessing fruit consumption in grizzly bear diets.

Proceed with caution

A critical point, in evaluating potential trophic cascades in YNP, is that many other factors have also changed during wolf restoration. As Kauffman, Brodie & Jules (2013) detail, important changes in moose (*Alces alces*) abundance, grizzly bear abundance, grizzly bear predation on elk calves, drought conditions and winter snow packs were all occurring while wolves were being restored to YNP. Mech (2012) also notes changing elk harvests and the increased growing season in YNP. Kauffman, Brodie & Jules (2013) make the salient argument that "natural experiments" such as this one [wolf reintroduction to YNP] are fraught with confounding factors that need to be openly discussed and rejected before assigning all causation to wolves' (p. 1428). Unfortunately, Ripple *et al.* (2014) have not convincingly done so before drawing their conclusions.

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